THE STRUCTURAL AND FUNCTIONAL DYNAMICS OF SELECTED SPECIES-POPULATIONS OF FRESHWATER SNAILS: TOWARDS A SYSTEMS APPROACH

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October, 1972.

Department of Zoology.

VOLUME

II

(Figures & Appendices)

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FIGURES

FIG. 1 : A map of the Pennine region in Yorkshire to show the general location of Malham Tarn. (after Broadhead, 1958).

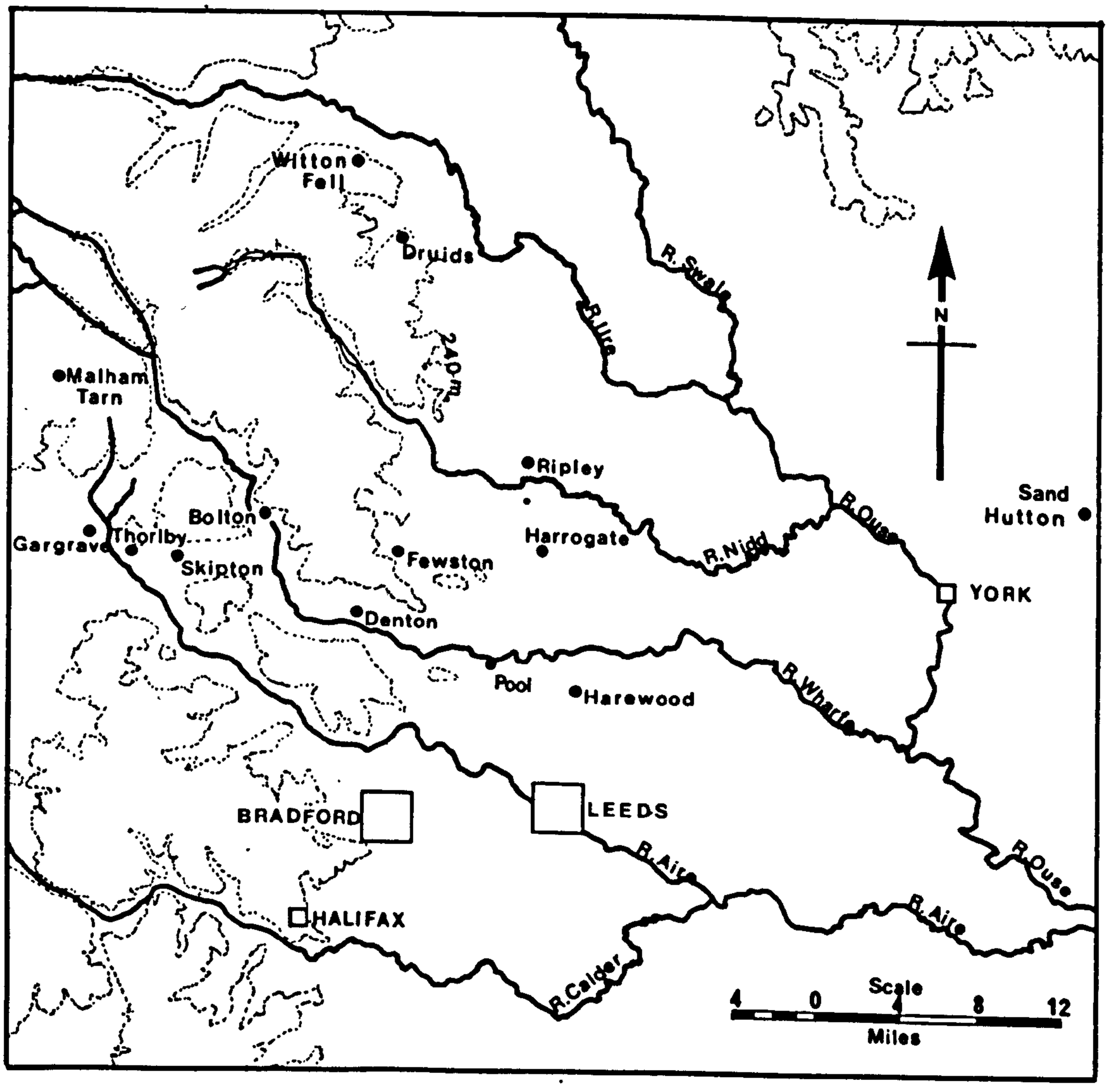

Witton Fell
Druids
R. Swale
R. Ure
240 m.
Malham Tarn
Ripley
Sand Hutton
Bolton
Thorlby
Gargrave
Skipton
Harrogate
R. Nidd
R. Ouse
Fewston
YORK
Denton
Pool
Harewood
R. Wharfe
BRADFORD
LEEDS
R. Aire
HALIFAX
R. Calder
N
Scale
4 0 4 8 12
Miles

FIG. 2 : A map showing the detailed geography of the Malham area. Numerals to the right and along the bottom margin of the figure indicate grid references, (after Stratton, 1956).

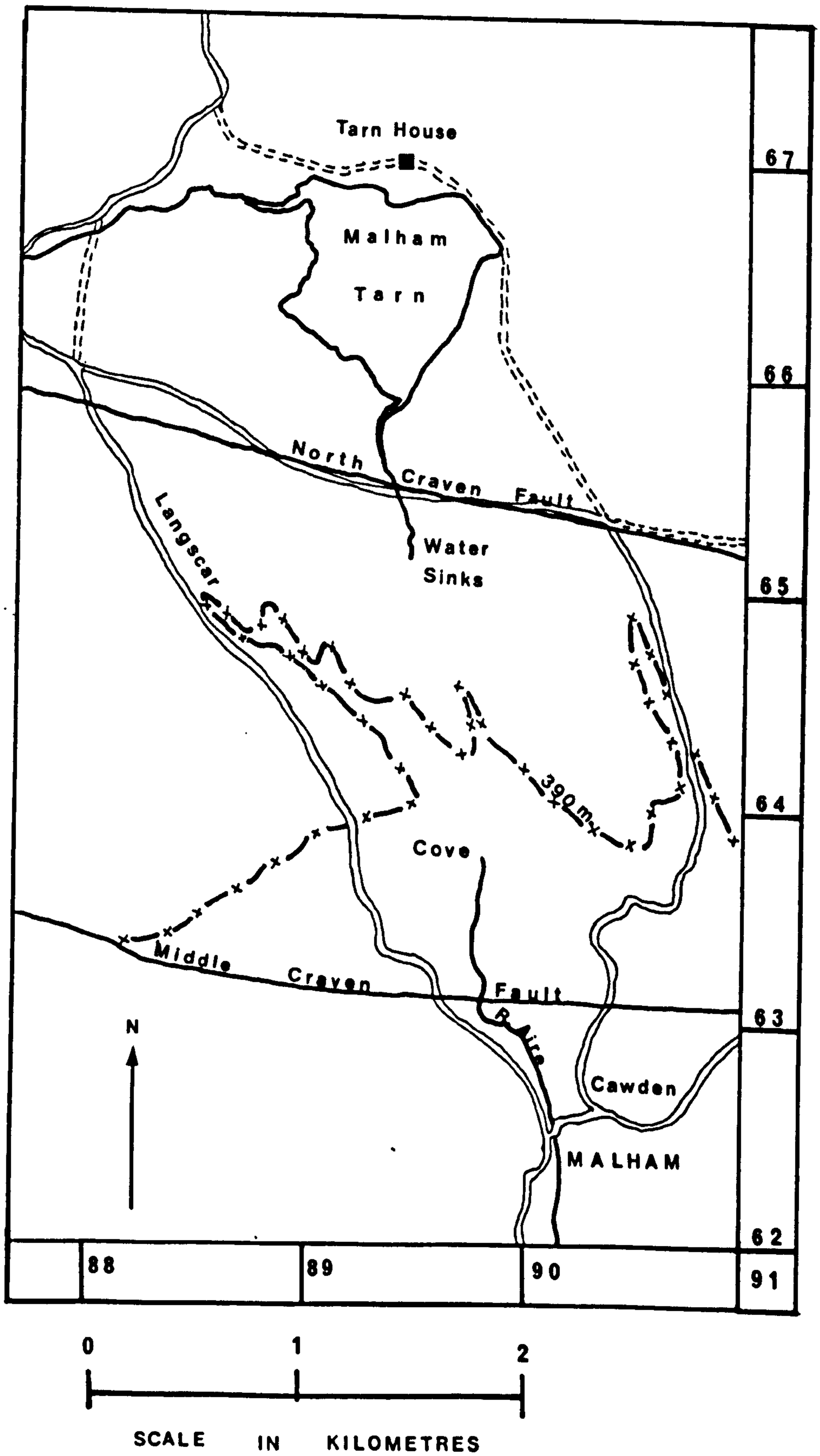

Tarn House
Malham
Tarn
North Craven Fault
Water Sinks
Langscar
390m
Cove
Middle Craven Fault
Barrie
Cawden
MALHAM
N
67
66
65
64
63
62
88
89
90
91
0
1
2
SCALE IN KILOMETRES

FIG. 3 : A sketch map of Malham Tarn to show its depth contours. (After Phillipson, 1968).

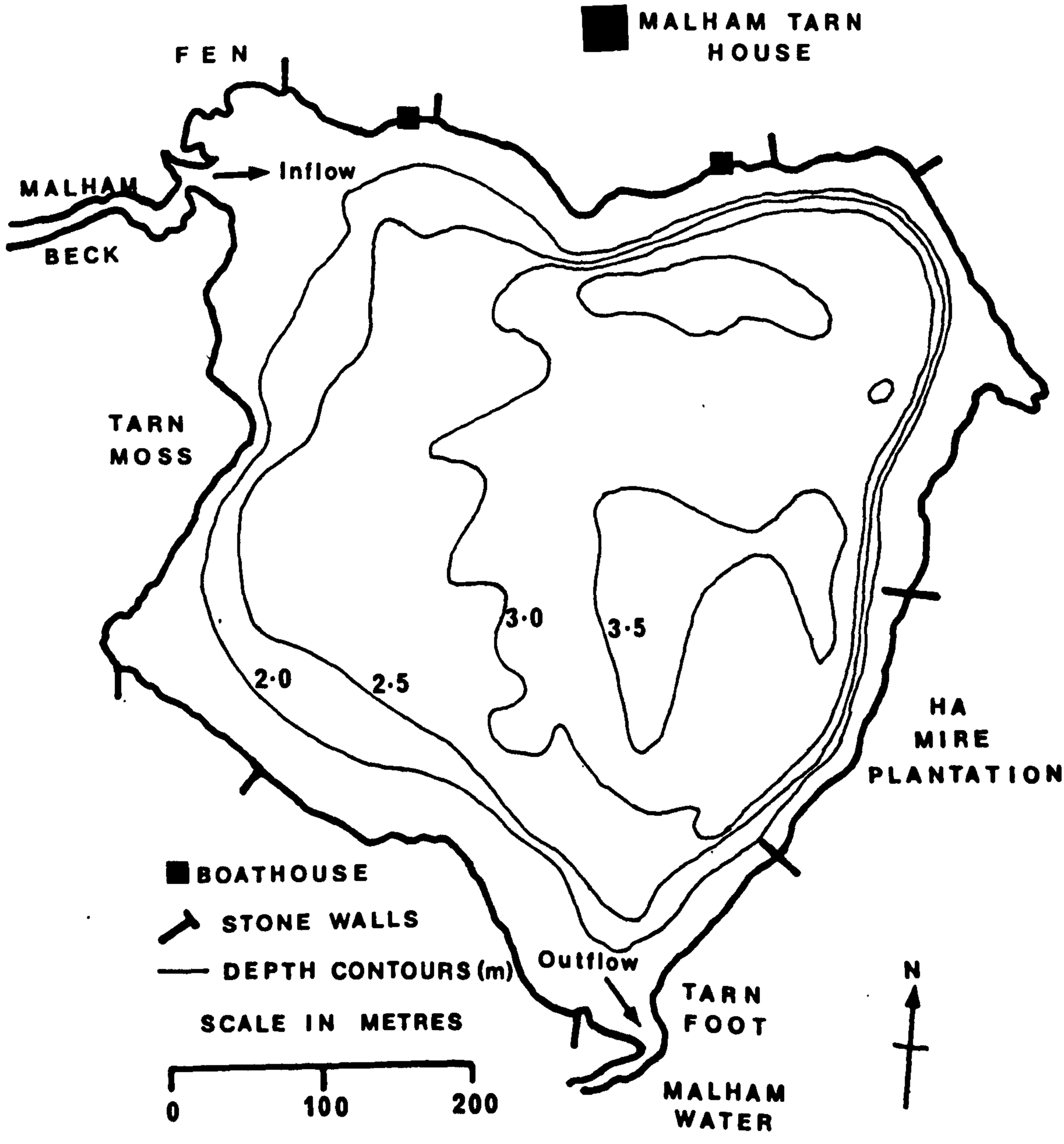

MALHAM TARN HOUSE
FEN
Inflow
MALHAM BECK
TARN MOSS
3·0
3·5
2·0
2·5
HA MIRE PLANTATION
BOATHOUSE
STONE WALLS
DEPTH CONTOURS (m)
SCALE IN METRES
0
100
200
Outflow
TARN FOOT
MALHAM WATER
N

FIG. 4 : Mean monthly temperature records for the littoral region of Ha Mire shore. For key to the sampling code see DATA APPENDIX 1.

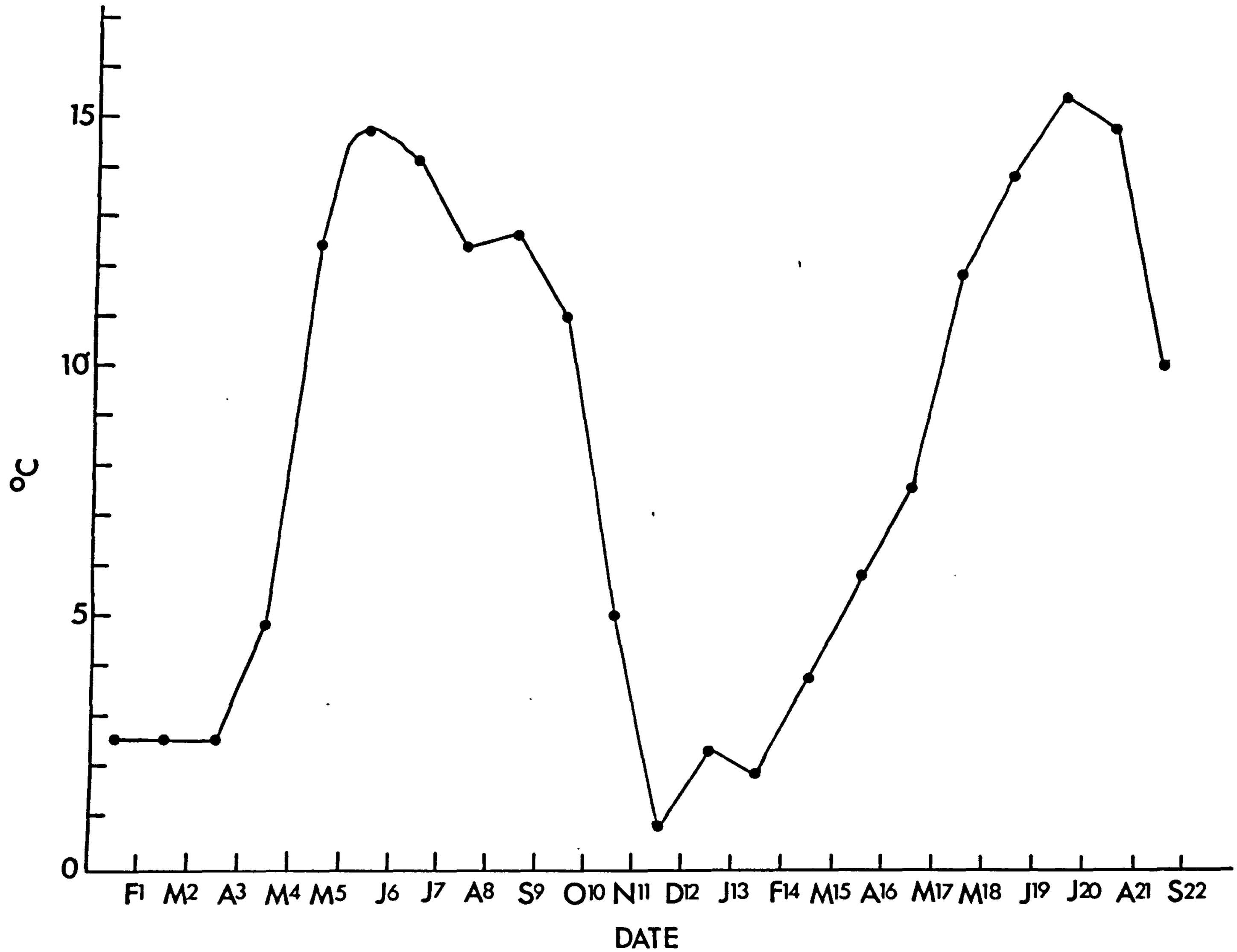

15
10
5
0
°C
F1 M2 A3 M4 M5 J6 J7 A8 S9 O10 N11 D12 J13 F14 M15 A16 M17 M18 J19 J20 A21 S22
DATE

FIG. 5 : Histograms showing the average monthly wind speeds (A) and the total number of days per month over which winds were observed at Malham Tarn (B). Open blocks represent winds blowing from east to west, and hatched blocks represent winds blowing in the opposite direction. Horizontal bars within the blocks of B, represent the proportion of time winds were in excess of 5 knots.

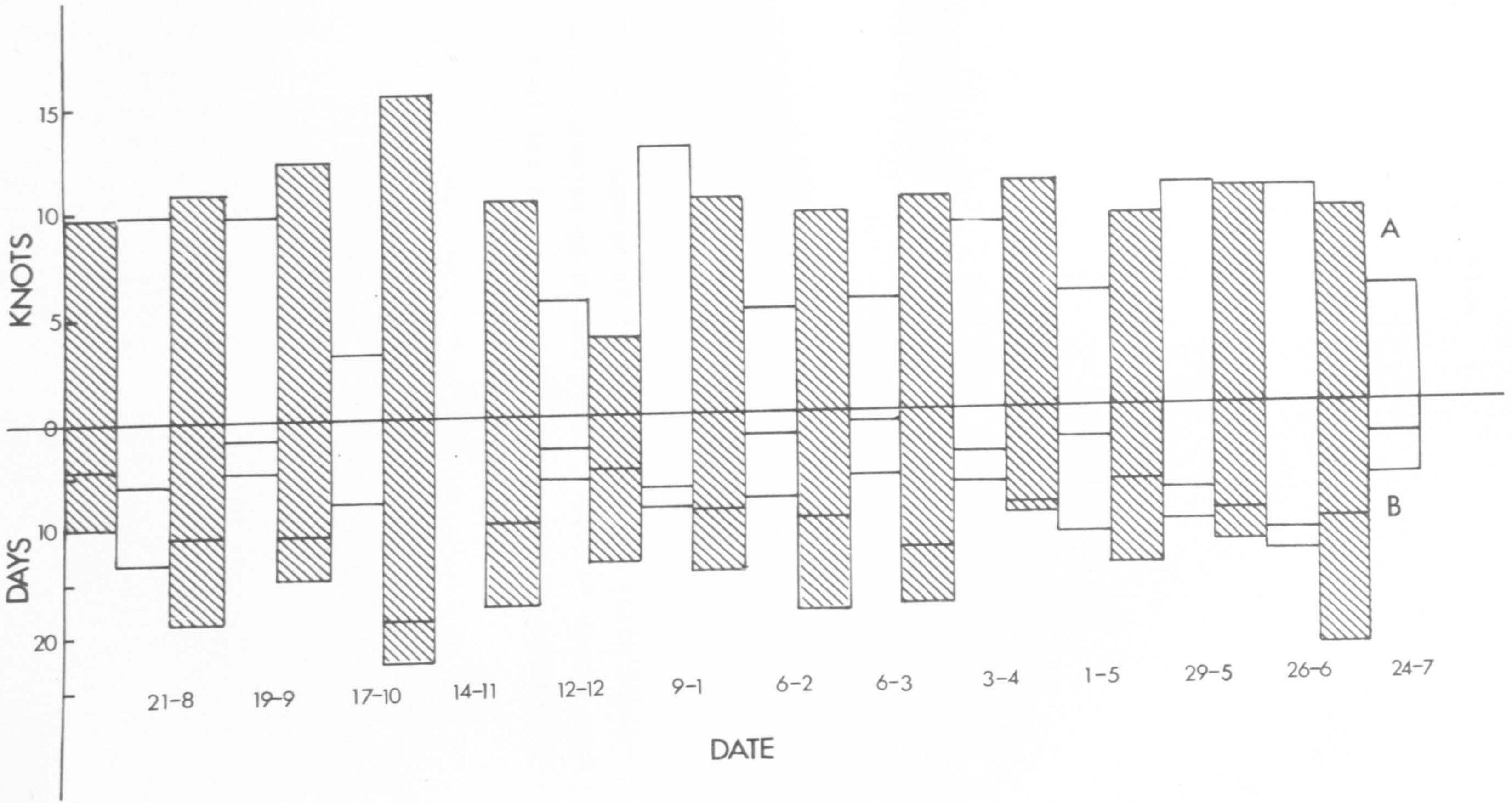

15
10
5
0
10
20
KNOTS
DAYS
A
B
21–8
19–9
17–10
14–11
12–12
9–1
6–2
6–3
3–4
1–5
29–5
26–6
24–7
DATE

FIG. 6 : The total number of days per month on which winds were observed at Malham Tarn. Hatched blocks represent the number on which winds were in excess of 5 knots.

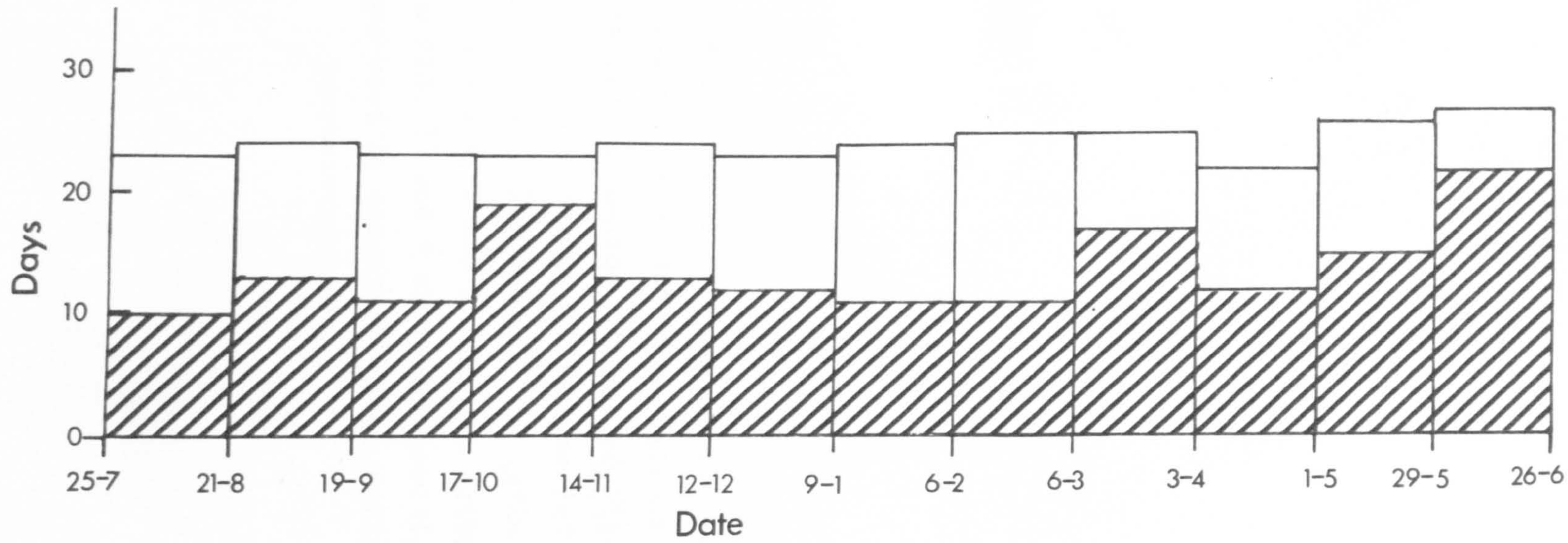

30
20
10
0
Days
25-7
21-8
19-9
17-10
14-11
12-12
9-1
6-2
6-3
3-4
1-5
29-5
26-6
Date

FIG. 7 : The location and outline of Ha Mire shore. The broken line off-shore represents the approximate position of the old shore-line and dotted lines set at right angles to the present shore-line indicate sector delimitations. The sectors are defined as A, B and C. Points X, Y and Z indicate transect positions (see FIG. 8) and T shows the position of sugar solutions used in measuring mean monthly temperatures.

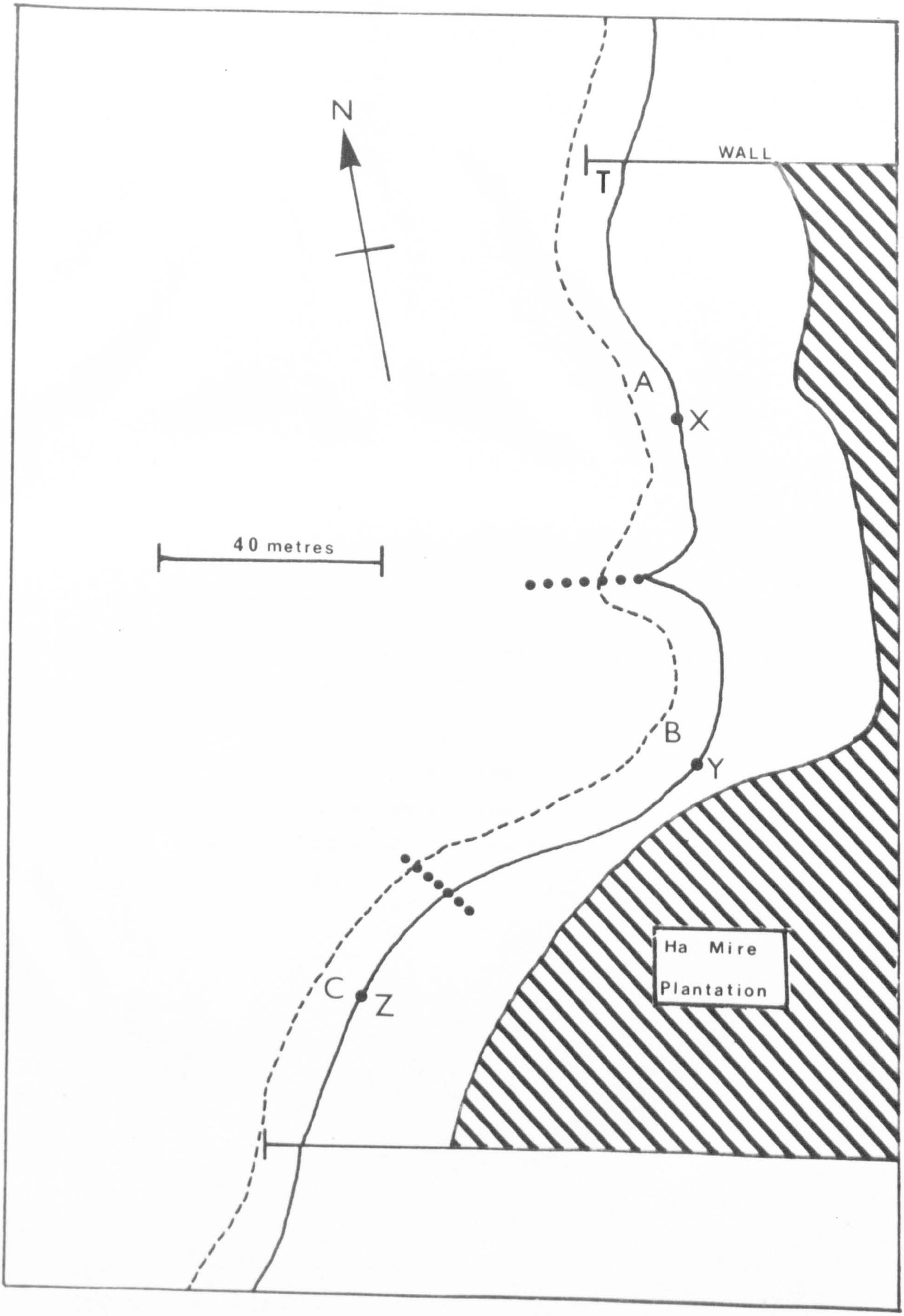

N
WALL
T
A
X
40 metres
B
Y
C
Z
Ha Mire
Plantation

FIG. 8 : Depth profiles along transect X (A), transect Y (B), and transect Z (C).

Key

W = water level

S = splash zone

OS = Old shore-line.

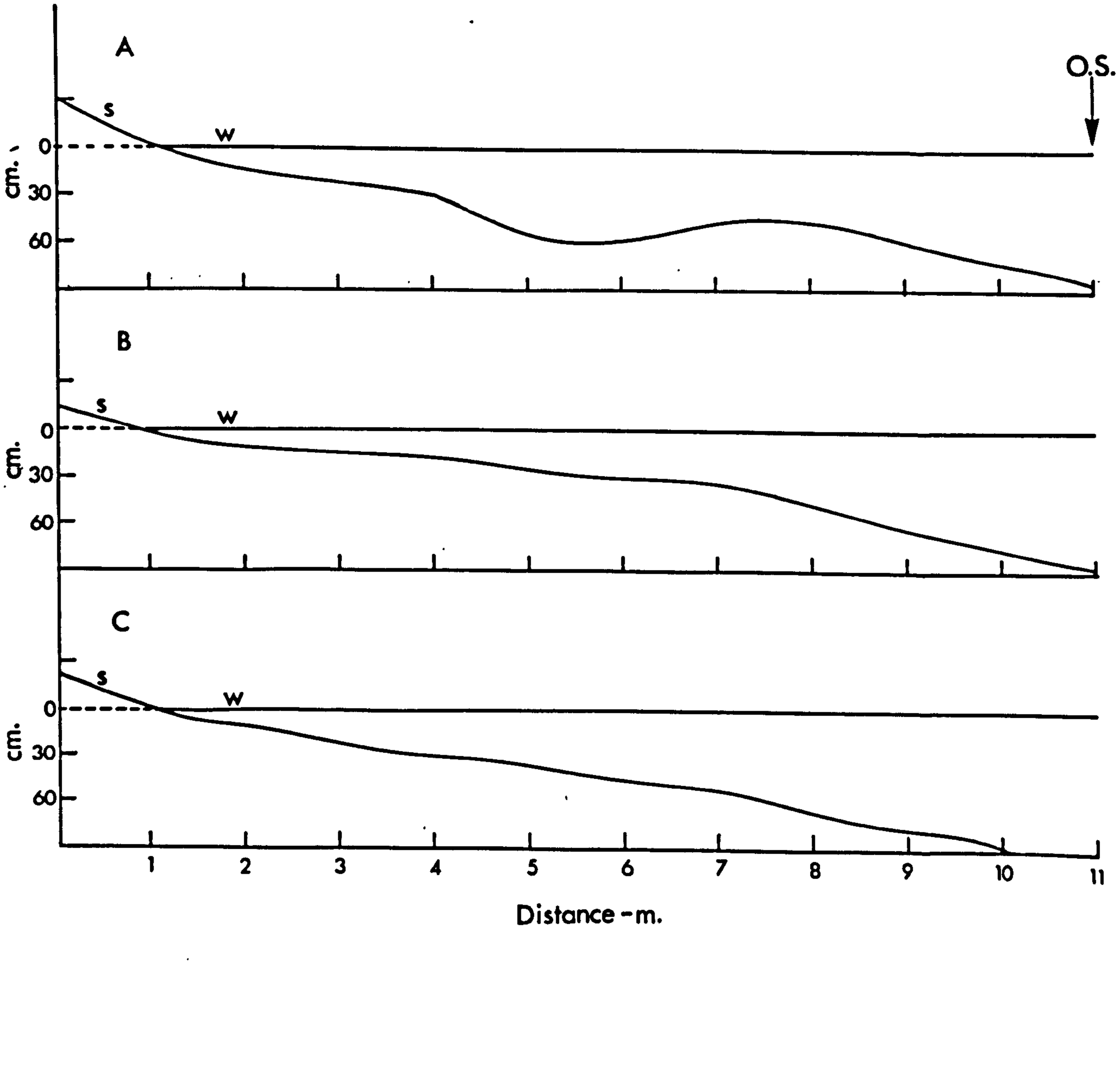

A
O.S.
s
w
0
30
60
cm.
B
s
w
0
30
60
cm.
C
s
w
0
30
60
cm.
1
2
3
4
5
6
7
8
9
10
11
Distance - m.

FIG. 9 : Distribution of the major weed beds in Malham Tarn, (after Philipson, 1968, but checked in August, 1969), together with the position of littoral (nos. in circles) and weed-bed (nos. in squares) sampling stations.

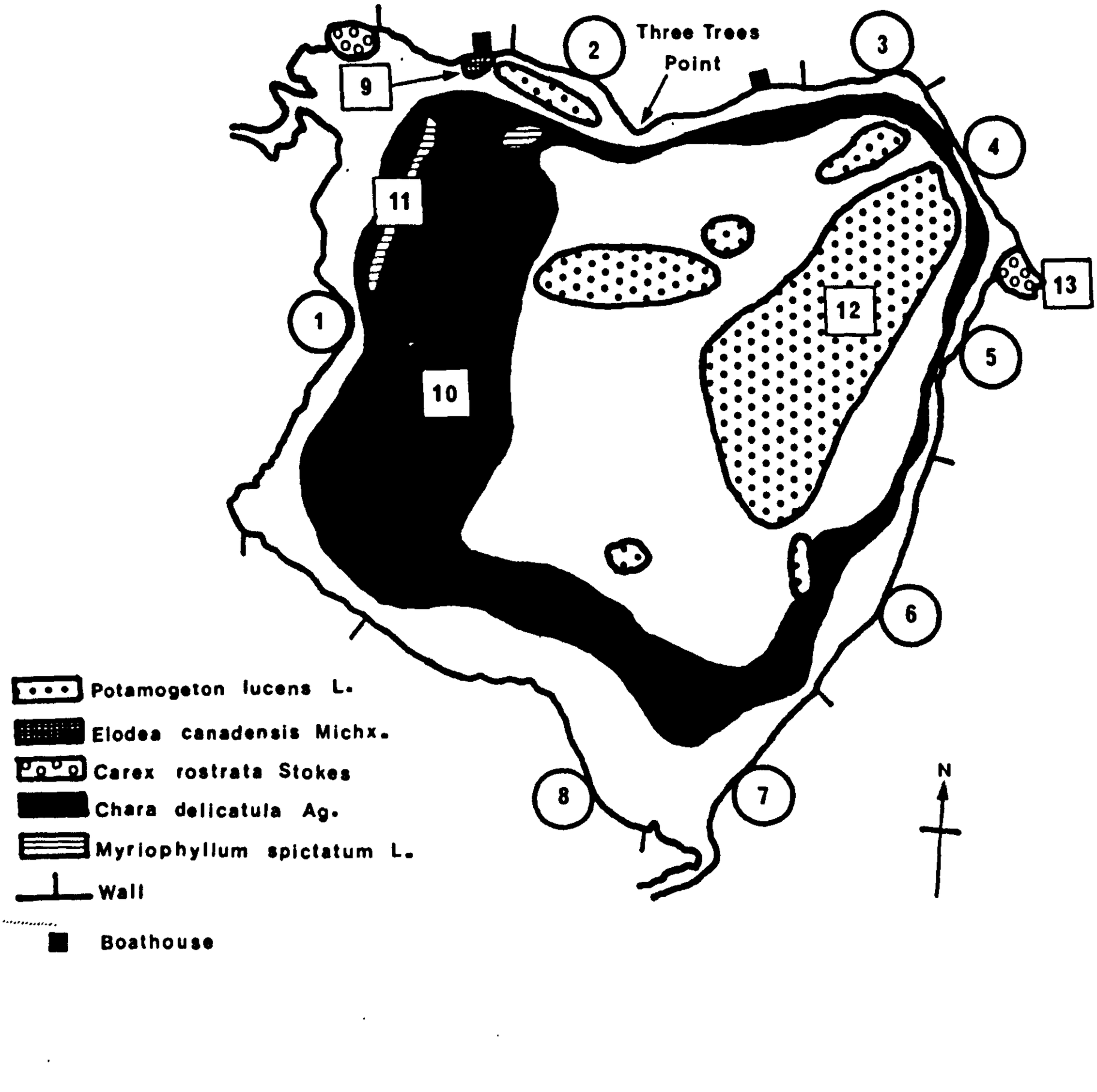

Three Trees
Point
1
2
3
4
5
6
7
8
9
10
11
12
13
N
Potamogeton lucens L.
Elodea canadensis Michx.
Carex rostrata Stokes
Chara delicatula Ag.
Myriophyllum spictatum L.
Wall
Boathouse

FIG 10 : The relationship between the Quotient of Similarity, QS (Sørensen, 1948) and the Index of Similarity, I (Mountford, 1962) for equivalent habitat pairs at Malham.

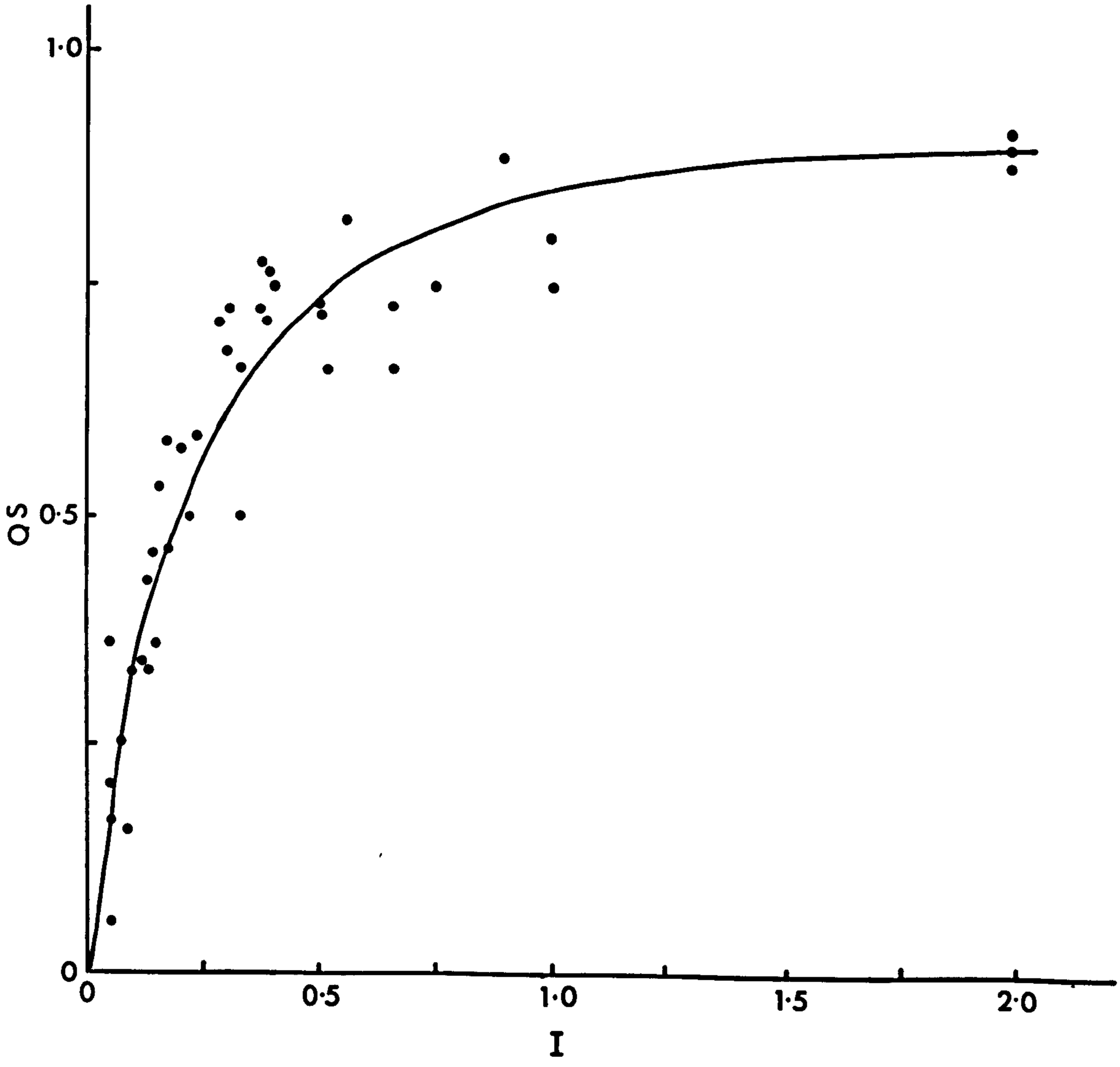

1·0
0·5
QS
0
0
0·5
1·0
1·5
2·0
I

FIG. 11 : A dendrogram showing the degree of association, in terms of snail, "community structures", between selected habitats at Malham Tarn. For key to habitats, see FIG. 9.

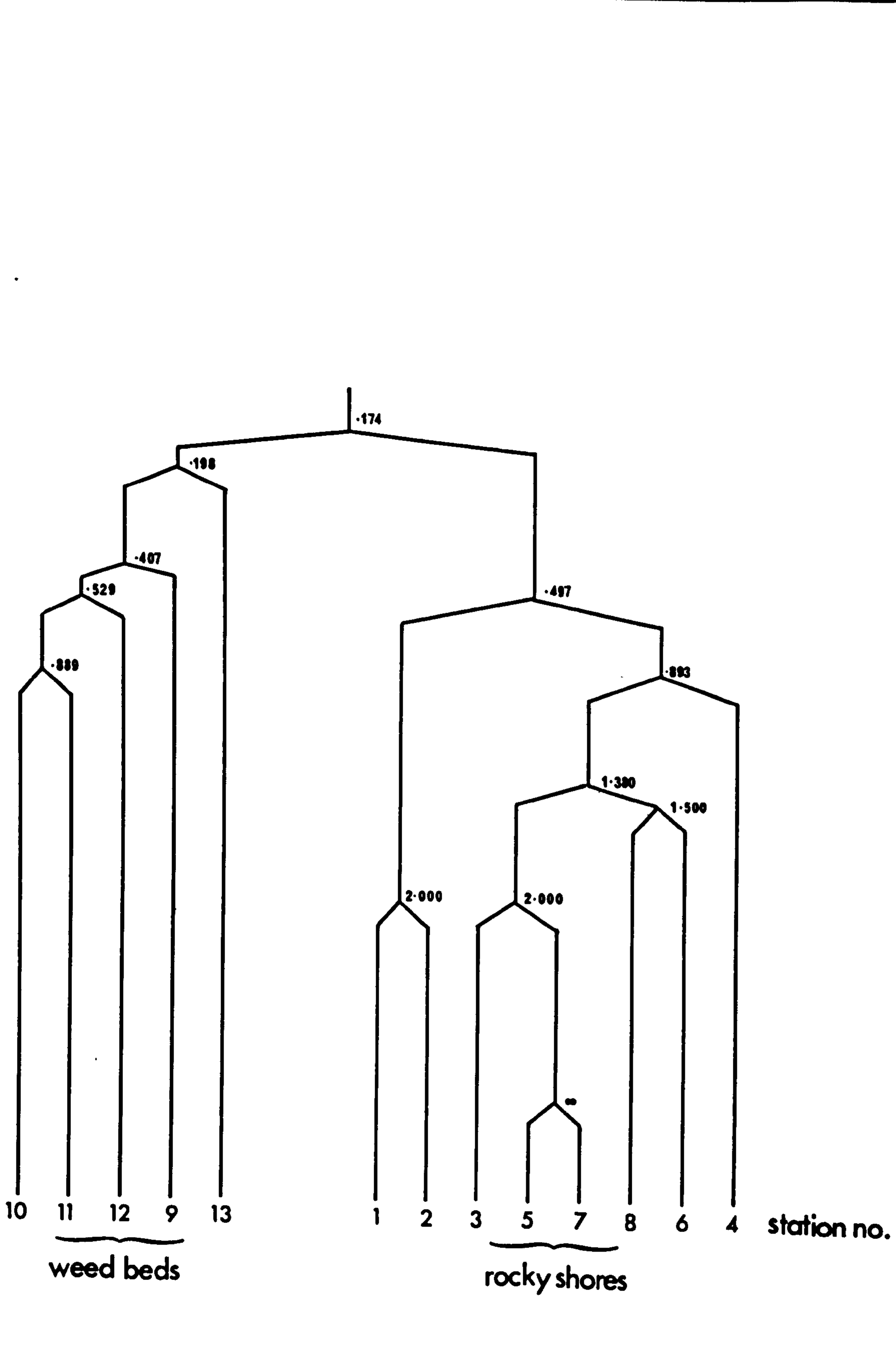

·174
·198
·407
·529
·889
·497
·893
1·380
1·500
2·000
2·000
10
11
12
9
13
1
2
3
5
7
8
6
4
station no.
weed beds
rocky shores

FIG. 12 : The distribution of P.leucostoma, along a transect taken through the N.E. Sedge Bed from open water (edge) to land, with samples taken at 1m. intervals.

S.D.W. = spun-dry-weight.

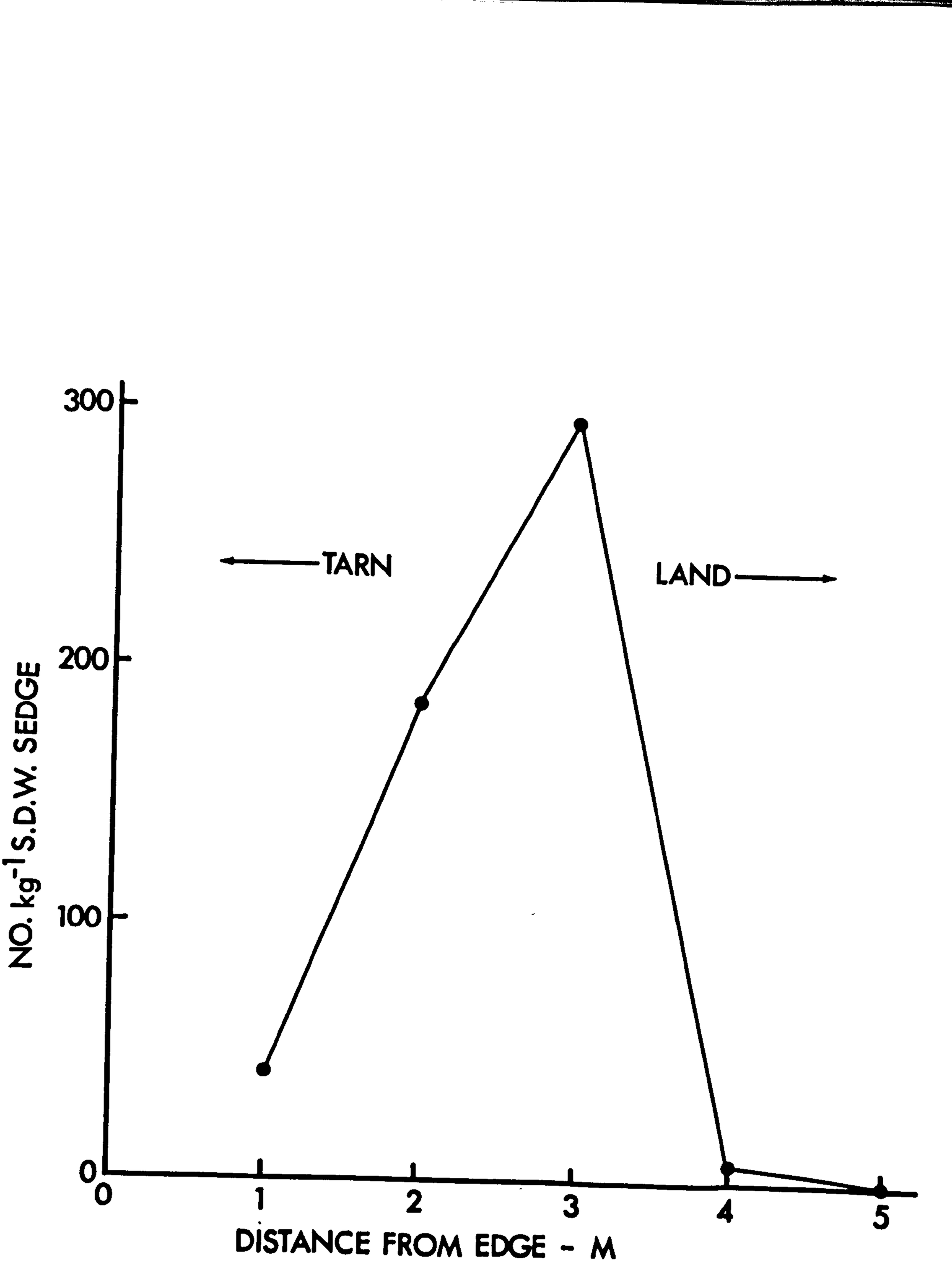
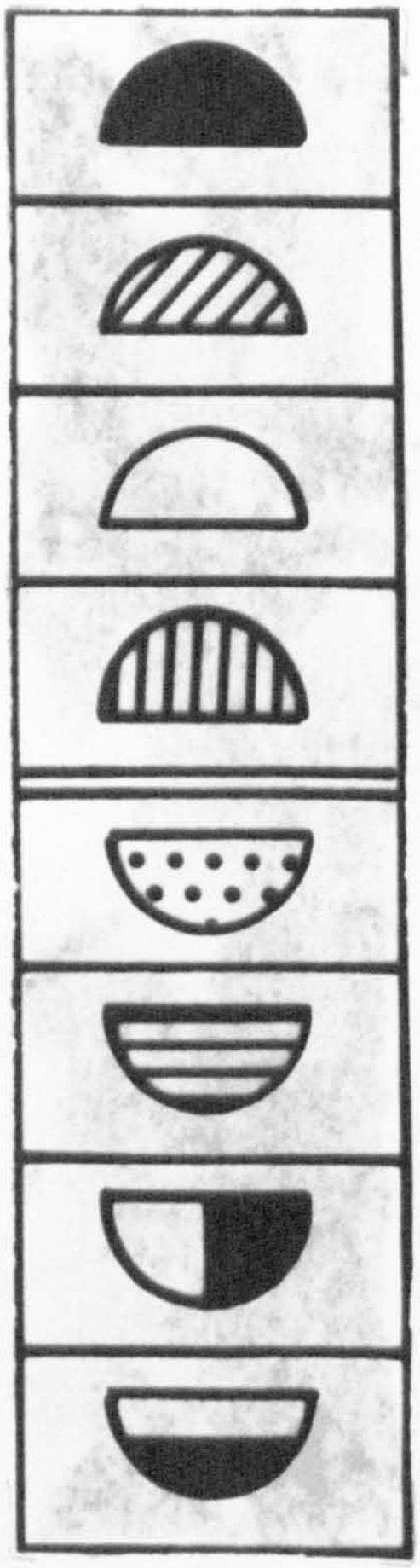

300
200
100
0
NO. kg^{-1}S.D.W. SEDGE
TARN
LAND
0
1
2
3
4
5
DISTANCE FROM EDGE - M

FIG. 13 : The distribution of the two most dominant species of littoral gastropods (i.e. P.contortus and A. fluviatilis) at Malham Tarn.

Key



Species	Relative abundance	
A.fluviatilis	70%	
A.fluviatilis	40%	70%
P.contortus	70%	
P.contortus	40%	70%
A.fluviatilis	15%	40%
P.contortus	20%	40%
A.fluviatilis	5%	
P.contortus	5%	

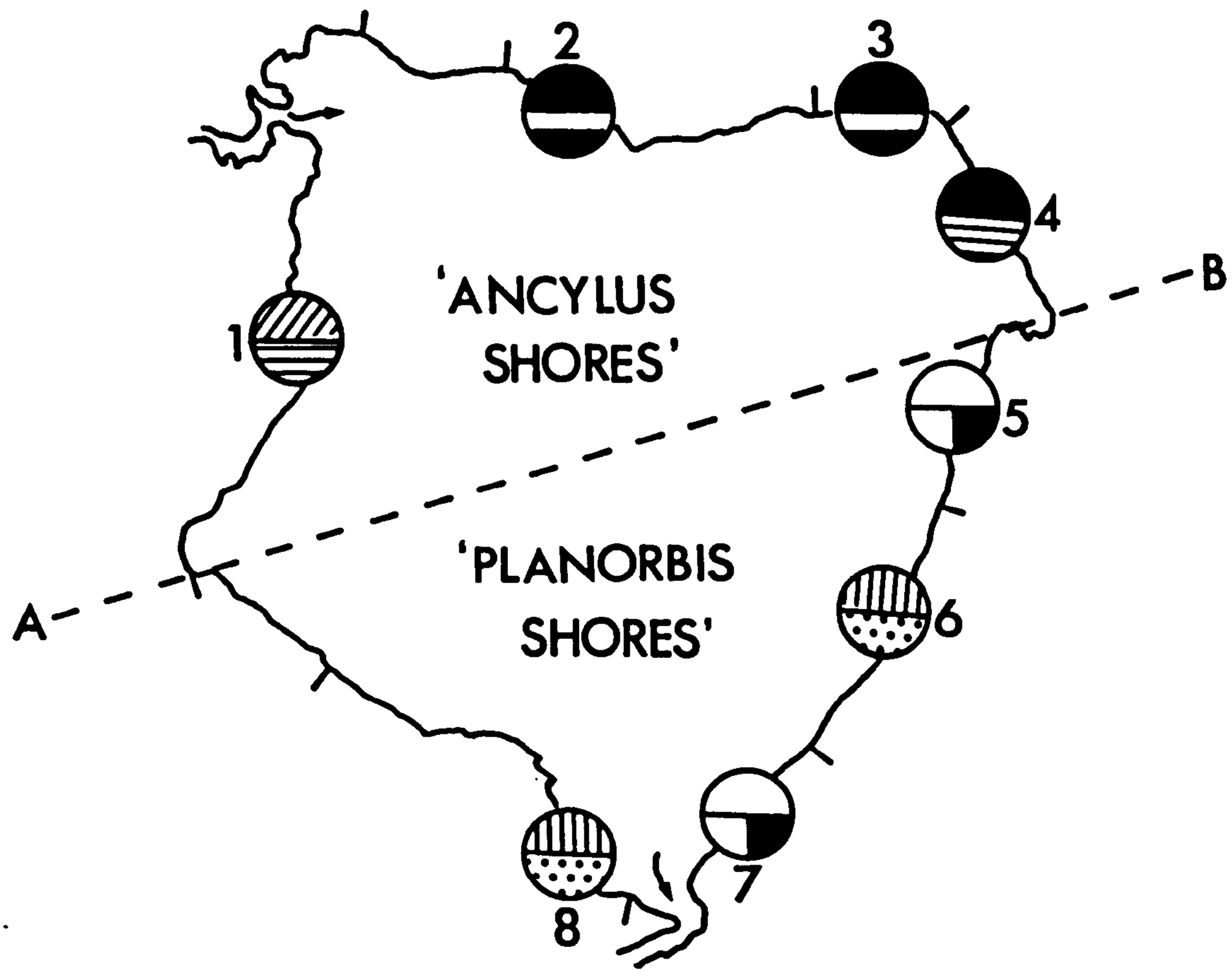

2
3
4
1
'ANCYLUS
SHORES'
B
5
A
'PLANORBIS
SHORES'
6
8
7

FIG. 14 : The position of transects taken at selected stations (denoted by numbers) throughout the Tarn. The in-set xy shows details of STATION 6, and the positioning of transects (1-15) within SECTORS A, B, and C.

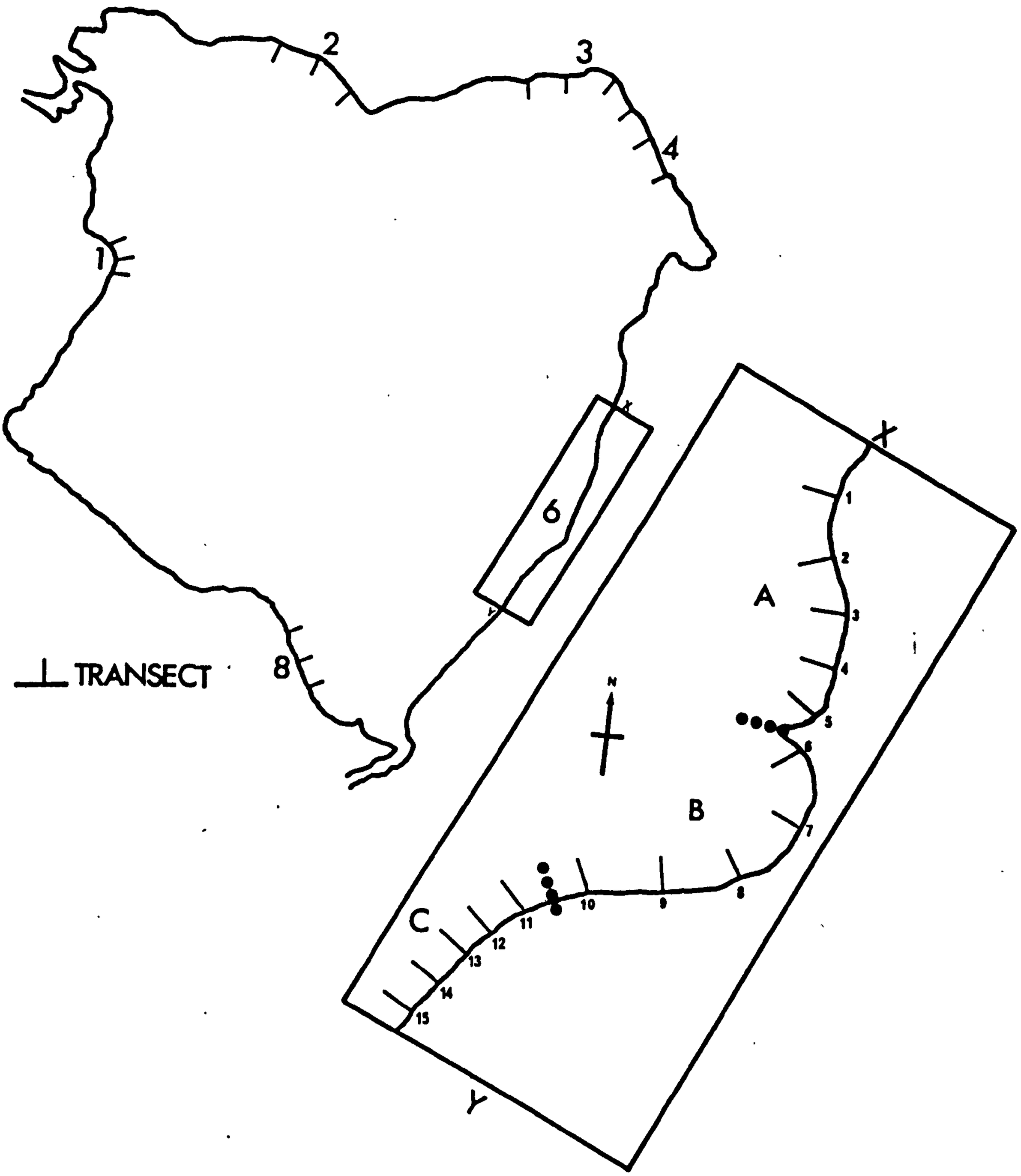

2
3
4
1
6
8
X
1
2
A
3
4
5
6
N
B
7
8
9
10
C
11
12
13
14
15
Y
TRANSECT

FIG. 15 : The depth distribution of P.contortus (A), and A.fluviatilis (B) along Ha Mire shore. Confidence limits represent two standard errors.

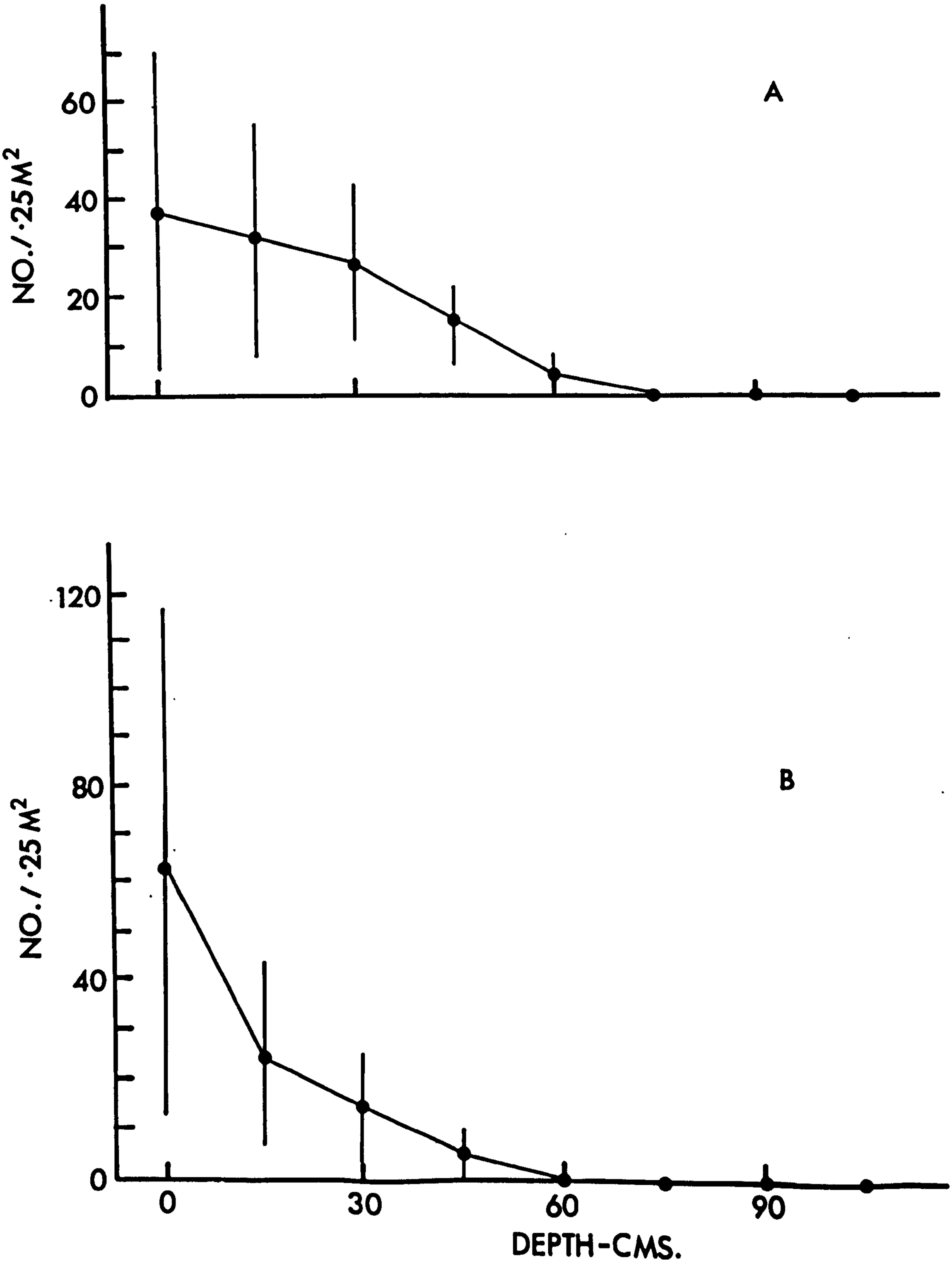

A
NO./·25 M²
60
40
20
0
B
NO./·25 M²
120
80
40
0
0
30
60
90
DEPTH-CMS.

FIG. 16 : The accumulation of sediment (mg./200cm²/day) at various depth locations on Ha Mire shore in August, 1970. The solid, horizontal block represents the depths at which the Tarn bottom was not visible, on a calm day.

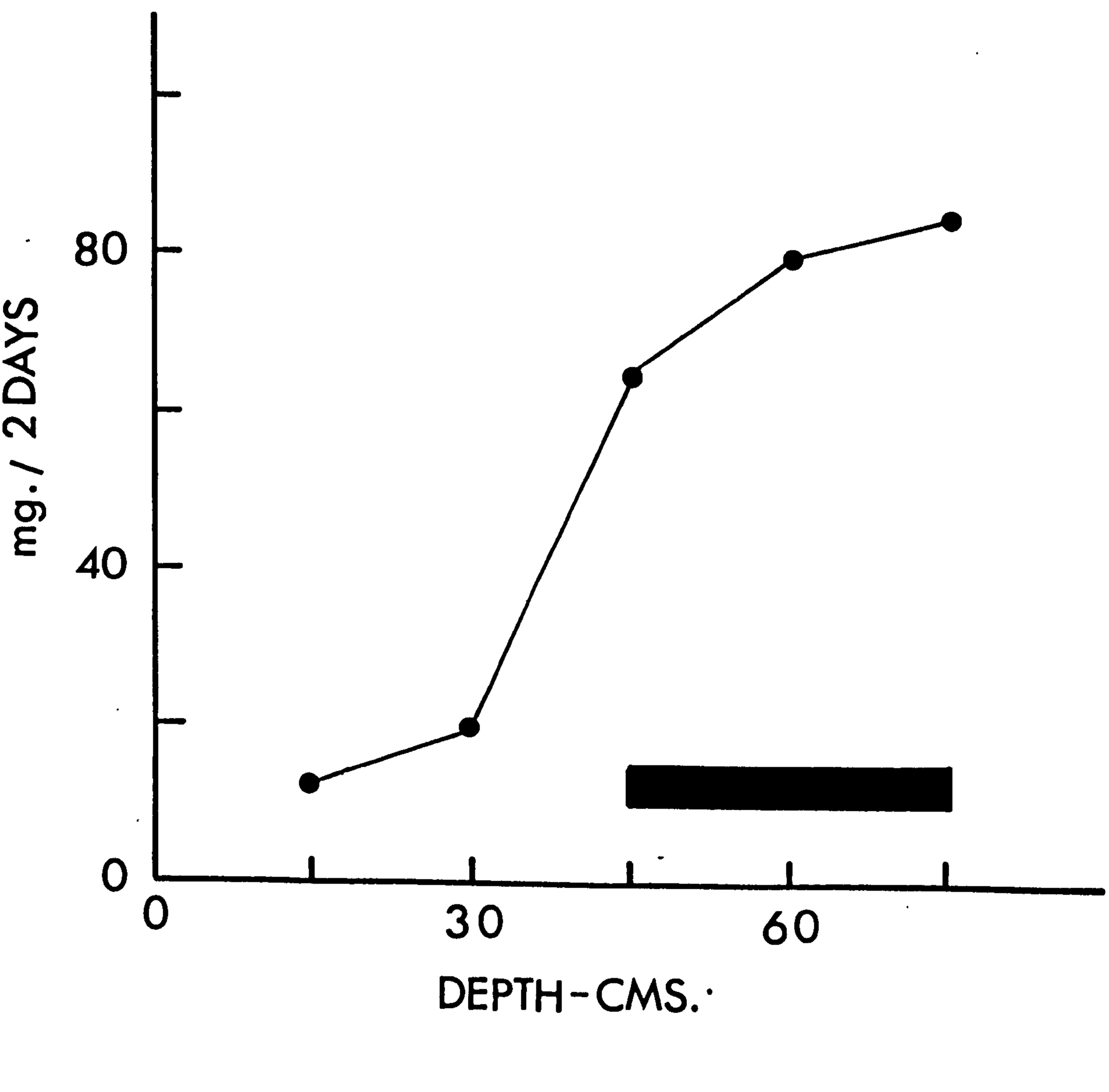

mg./ 2DAYS
80
40
0
0
30
60
DEPTH-CMS.

FIG. 17 : The proportions (%) of the population sample of P.contortus (A) and A.fluviatilis (B) found in each sector, on Ha Mire, in Aug-Sept., 1969.

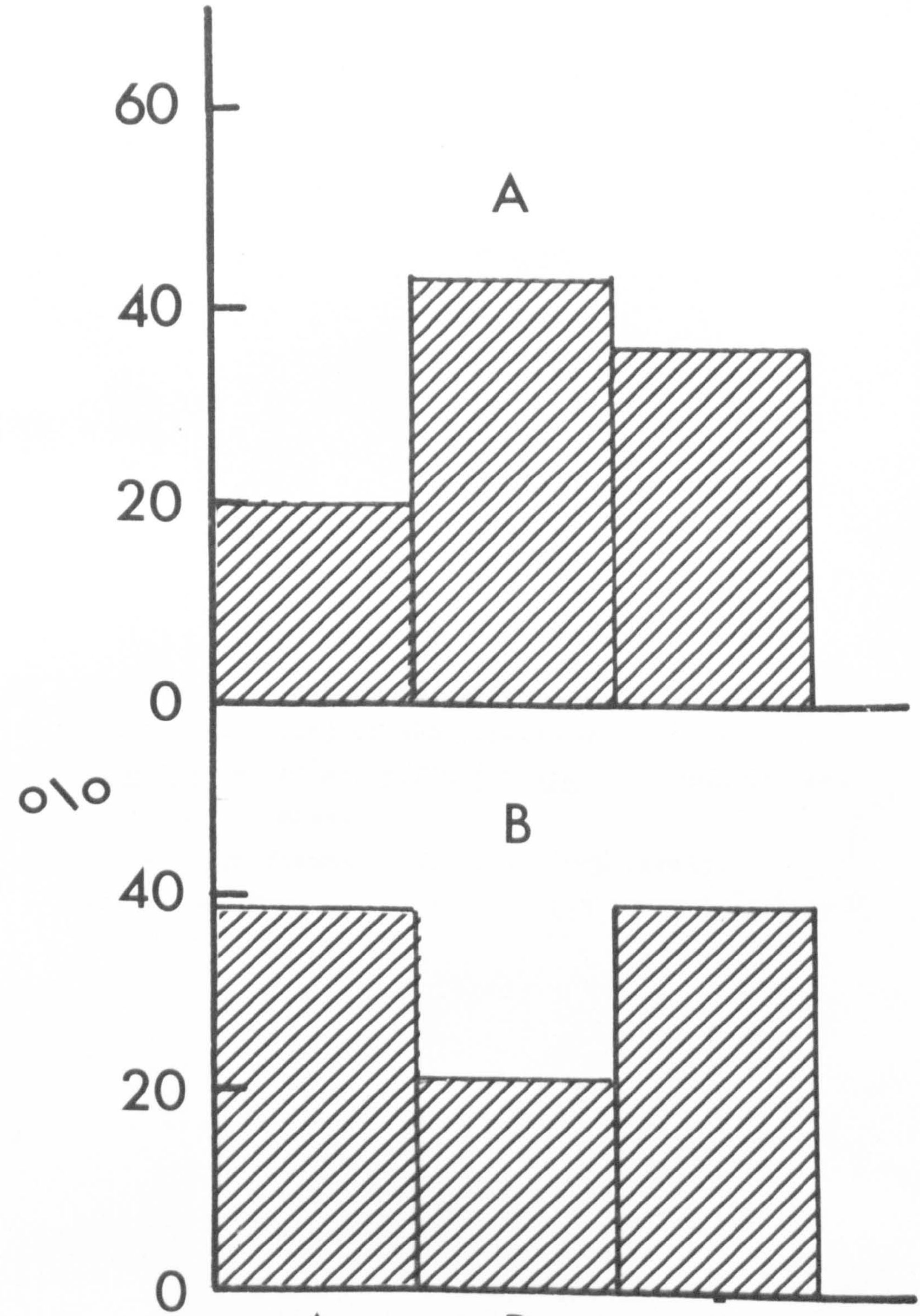
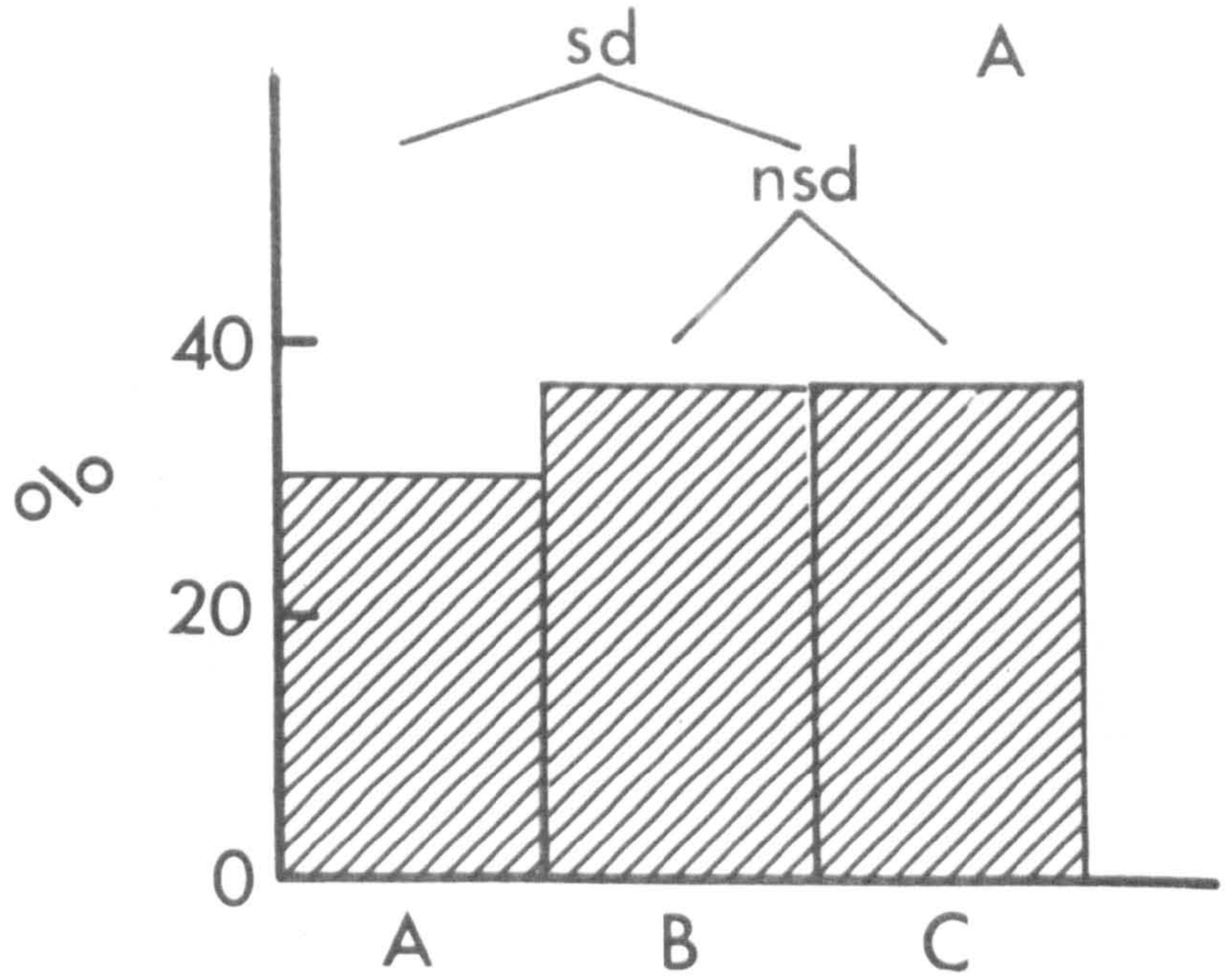

60
40
20
0
%
A
40
20
0
B
A
B
C
SECTOR

FIG. 18 : The mean proportions (%, after arcsine transformation and manipulation) of the population samples of P.contortus (A) and A.fluviatilis (B) found in each sector on Ha Mire.

sd = significant difference (95% level).

nsd = no " " (" ").


sd
nsd
A
40
%
20
0
A
B
C

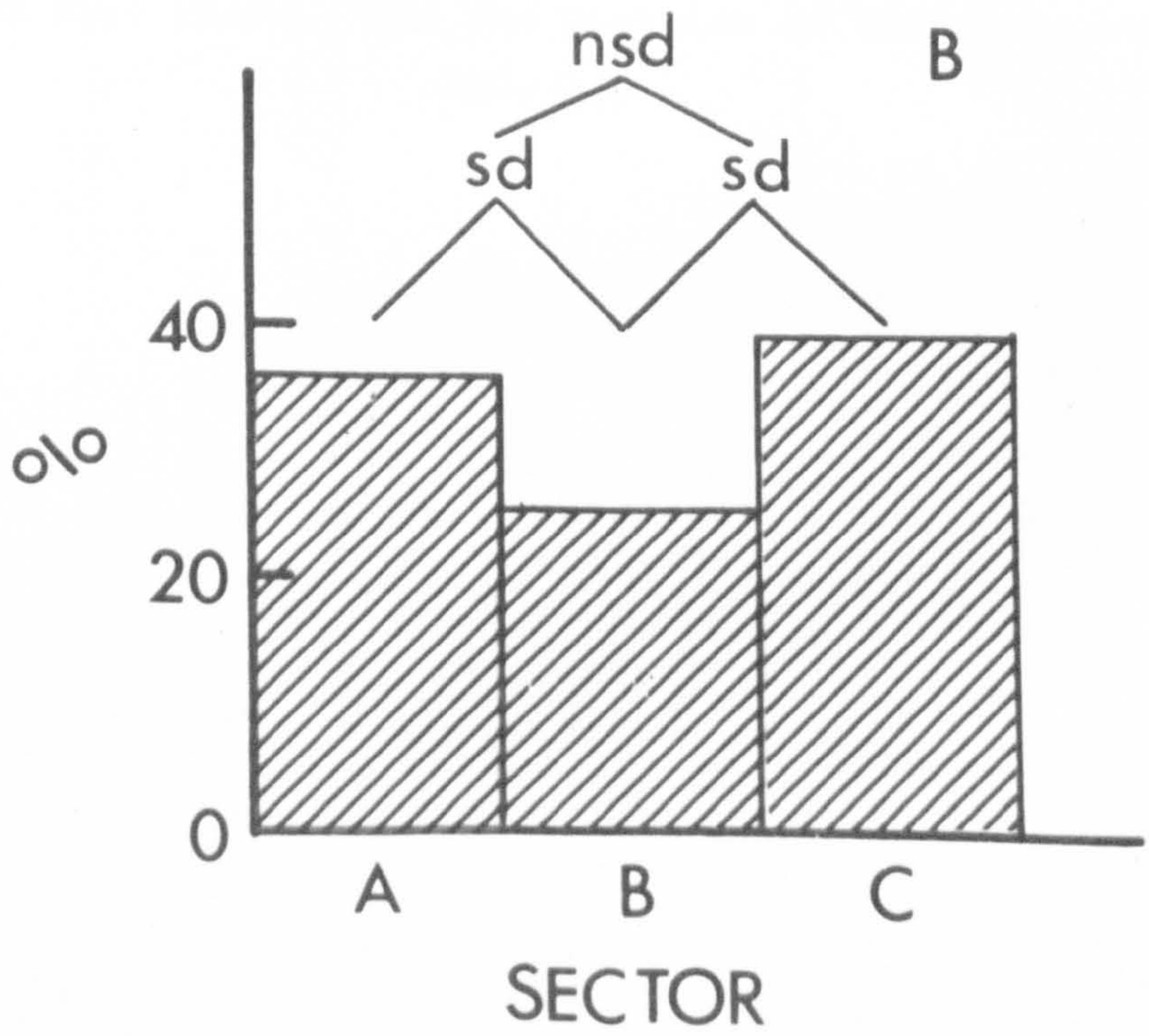

nsd
sd
sd
B
40
%
20
0
A
B
C
SECTOR

FIG. 19 : The textural distribution of stones (blocks) and sediment accumulation (points) in each sector at Ha Mire shore. For the position of transects see FIG. 14.

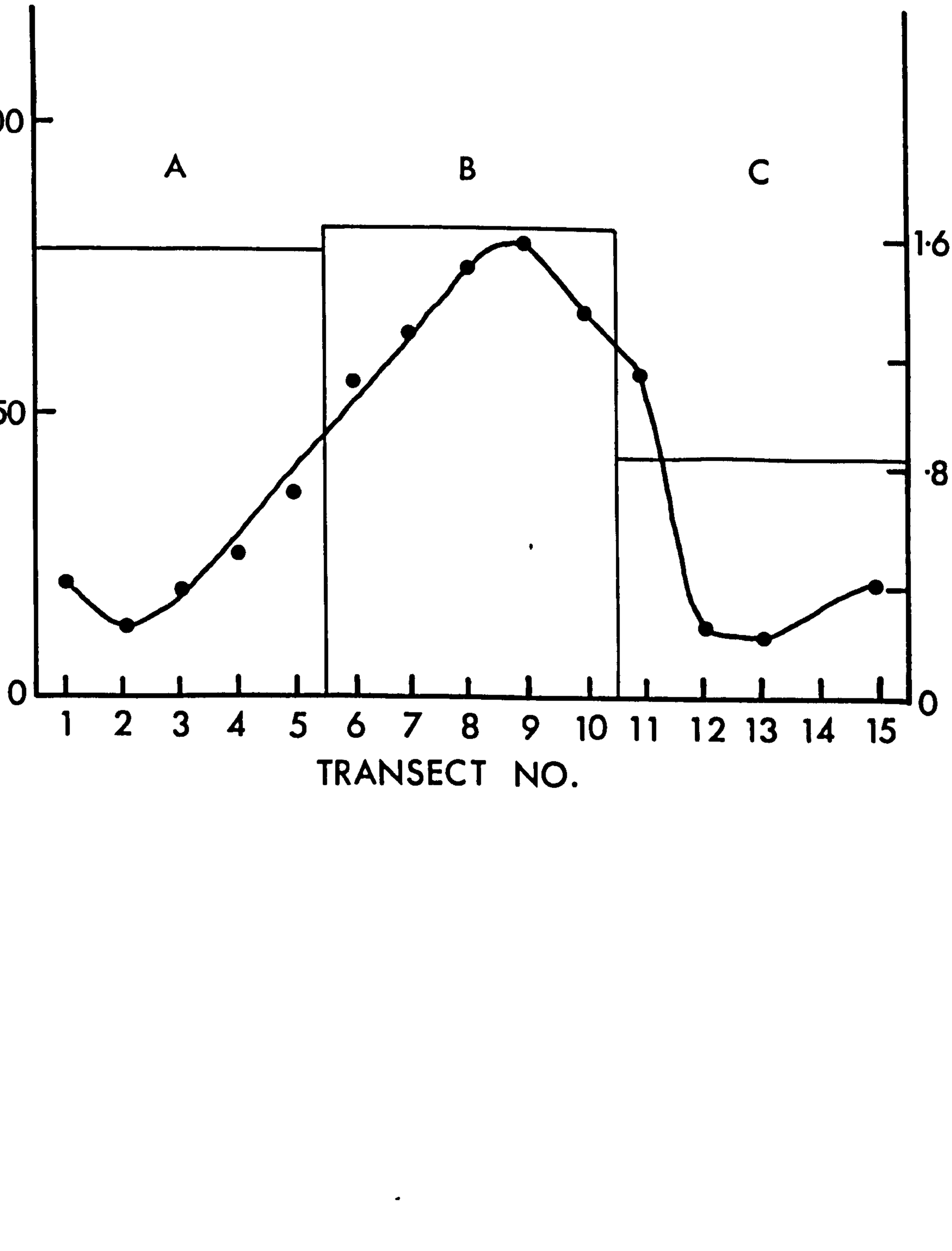

100
A
B
C
% 50
0
1·6
·8
0
g SEDIMENT / 250 ml
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
TRANSECT NO.

FIG. 20 : The mean number of snails per stone, $\bar{X}$, (P.contortus in A, and A.fluviatilis in B) plotted against sample variance, S^2 . Lines P indicate the Poisson expectations.

Key

Stone size category *

VS = very small

S = small

M = medium

L = large

VL = very large

* further explanation in-text.

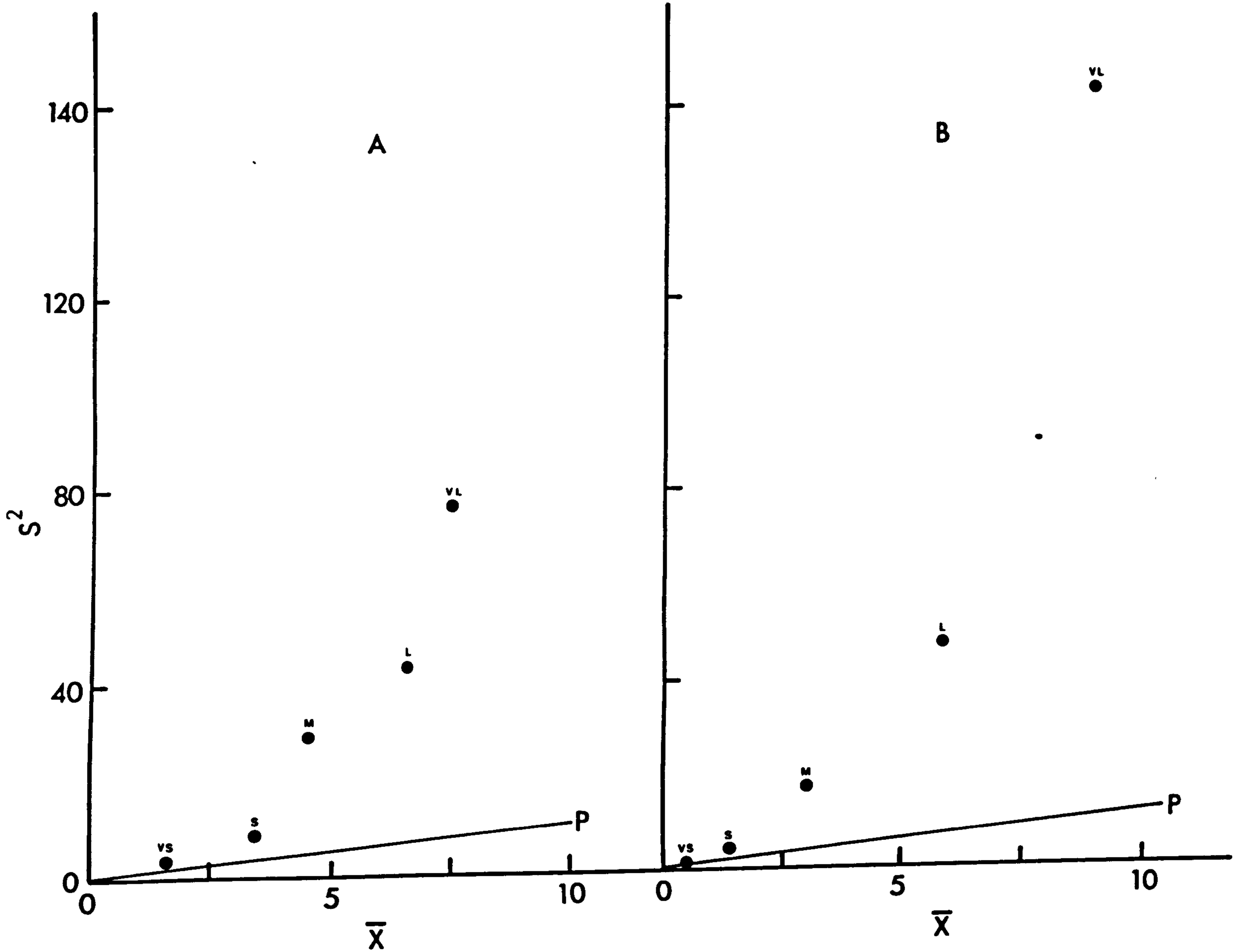

A
B
140
120
80
40
0
S^2
VL
L
M
S
VS
P
0
5
10
$\overline{X}$

FIG. 21 : The mean number of snails per stone, $\bar{X}$, (A for P.contortus; B for A.fluviatilis) plotted against standard deviation, S (i.e. $\sqrt{S^2}$). The regression lines are calculated from the Ha Mire data. Crosses represent data from Ha Mire whereas solid spots represent data from STATION 2 (see FIG. 9).

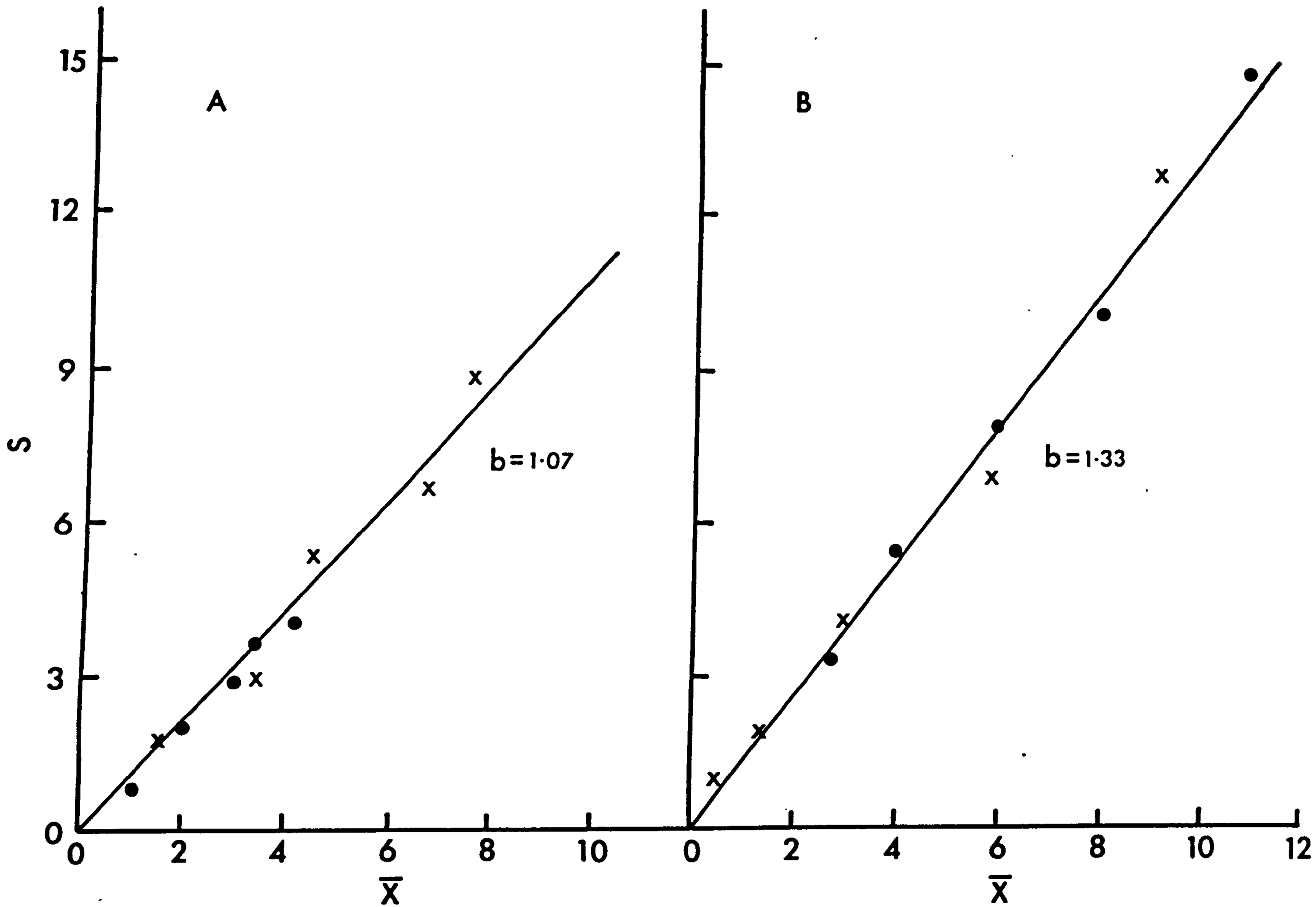

A
B
15
12
9
6
3
0
S
x
b = 1·07
b = 1·33
0
2
4
6
8
10
12
$\overline{X}$

FIG. 22 : The mean number of snails per stone, $\bar{X}$, (A for P.contortus; B for A.fluviatilis) plotted against standard deviation, S, for data at different times of the year.

Key

▲ = over-wintering population

● = fertilisation

○ = oviposition

■ = post-emergence

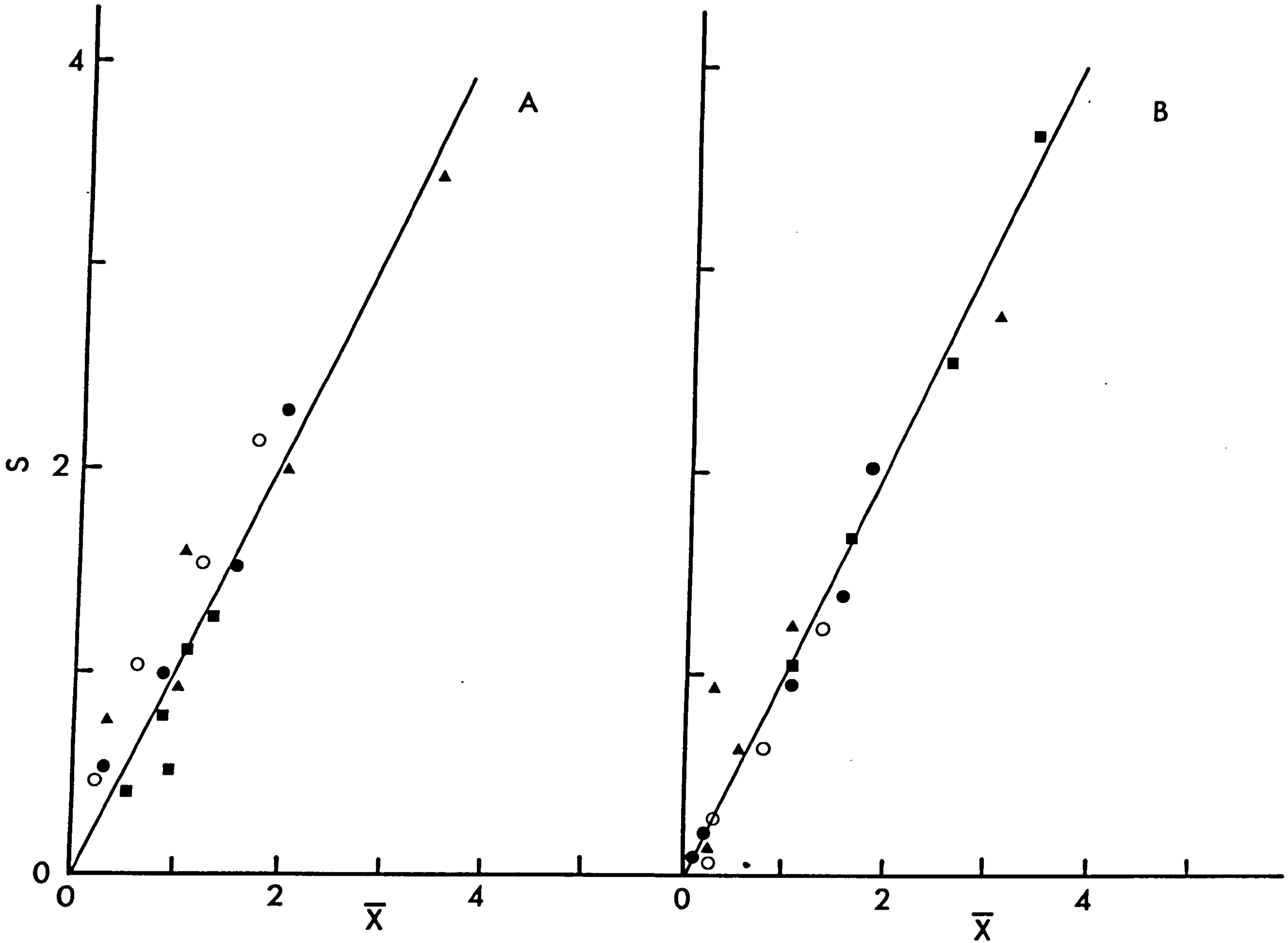

A
B
S
4
2
0
0
2
4
X̄
0
2
4
X̄

FIG. 23 : The proportions (%) of rough and smooth stones in each monthly sample of 100 (A), and the value of ν for P.contortus (solid squares) and A.fluviatilis (solid spots) at different times of the year.

$$\nu = \frac{\text{mean no. of snails/ smooth stone}}{\text{mean no. of snails/ rough stone}}$$

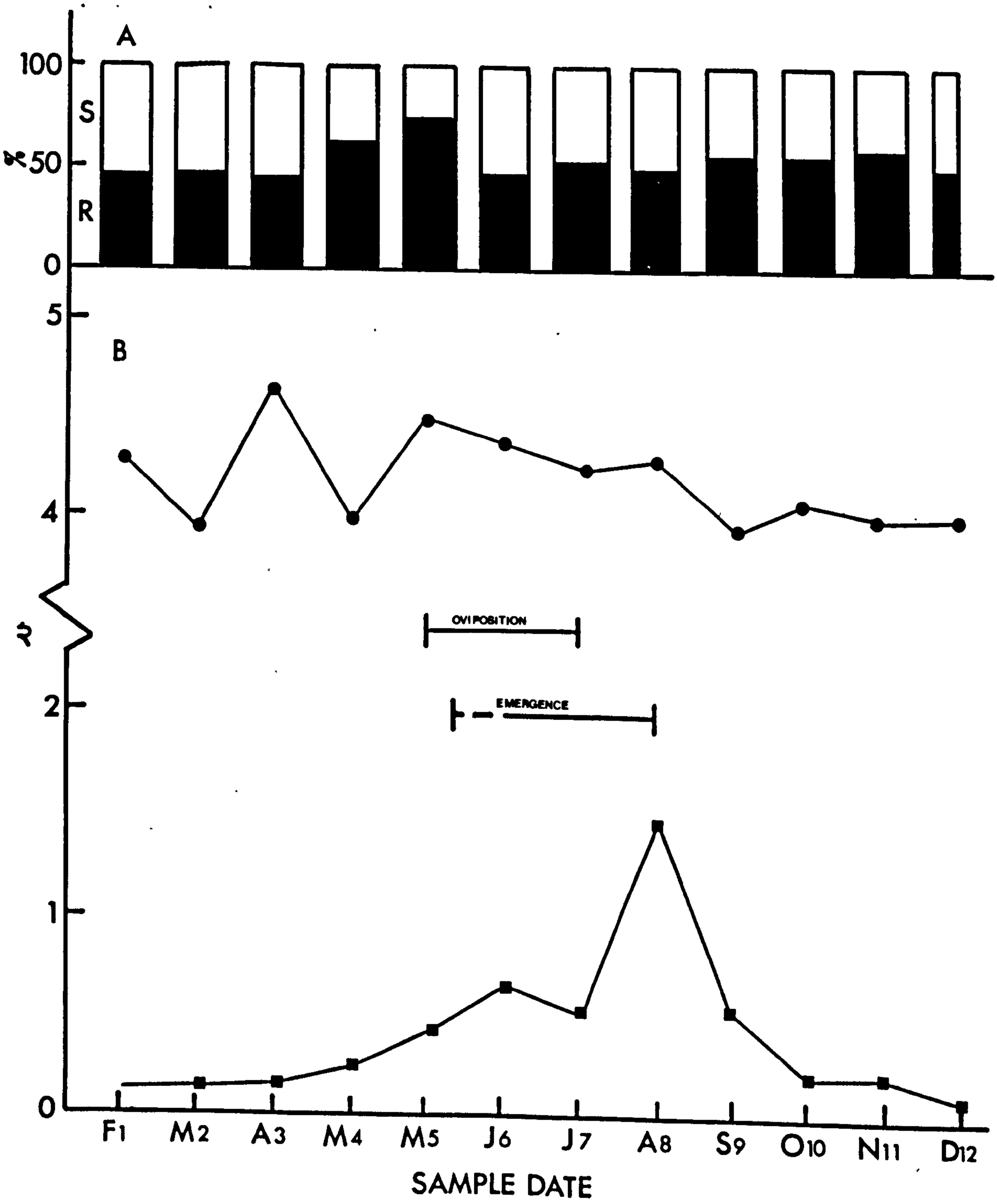

A
100
S
%
50
R
0
5
B
4
2
1
0
OVIPOSITION
EMERGENCE
F1
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
SAMPLE DATE

FIG. 24 : The relationship between the density of P.contortus (no./stone) and stone size.

Key

L = longest length

P = longest perimeter

Vertical bars indicate 95% confidence limits.

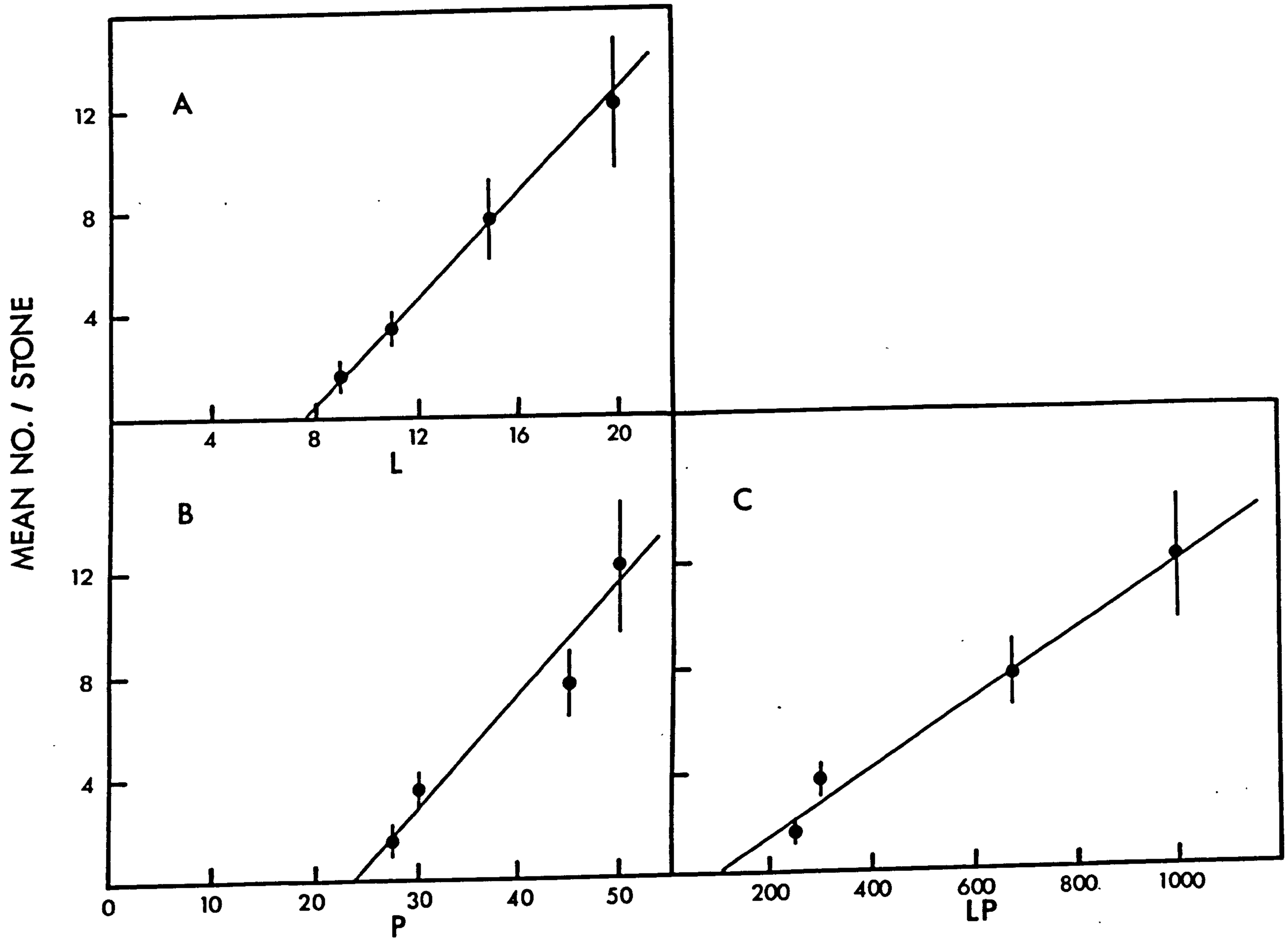

A
MEAN NO. / STONE
12
8
4
4
8
12
16
20
L
B
12
8
4
0
10
20
30
40
50
P
C
200
400
600
800
1000
LP

FIG. 25 : The relationship between the density of A.fluviatilis (no./stone) and stone size. L, P and the confidence limits are defined in FIG. 24.

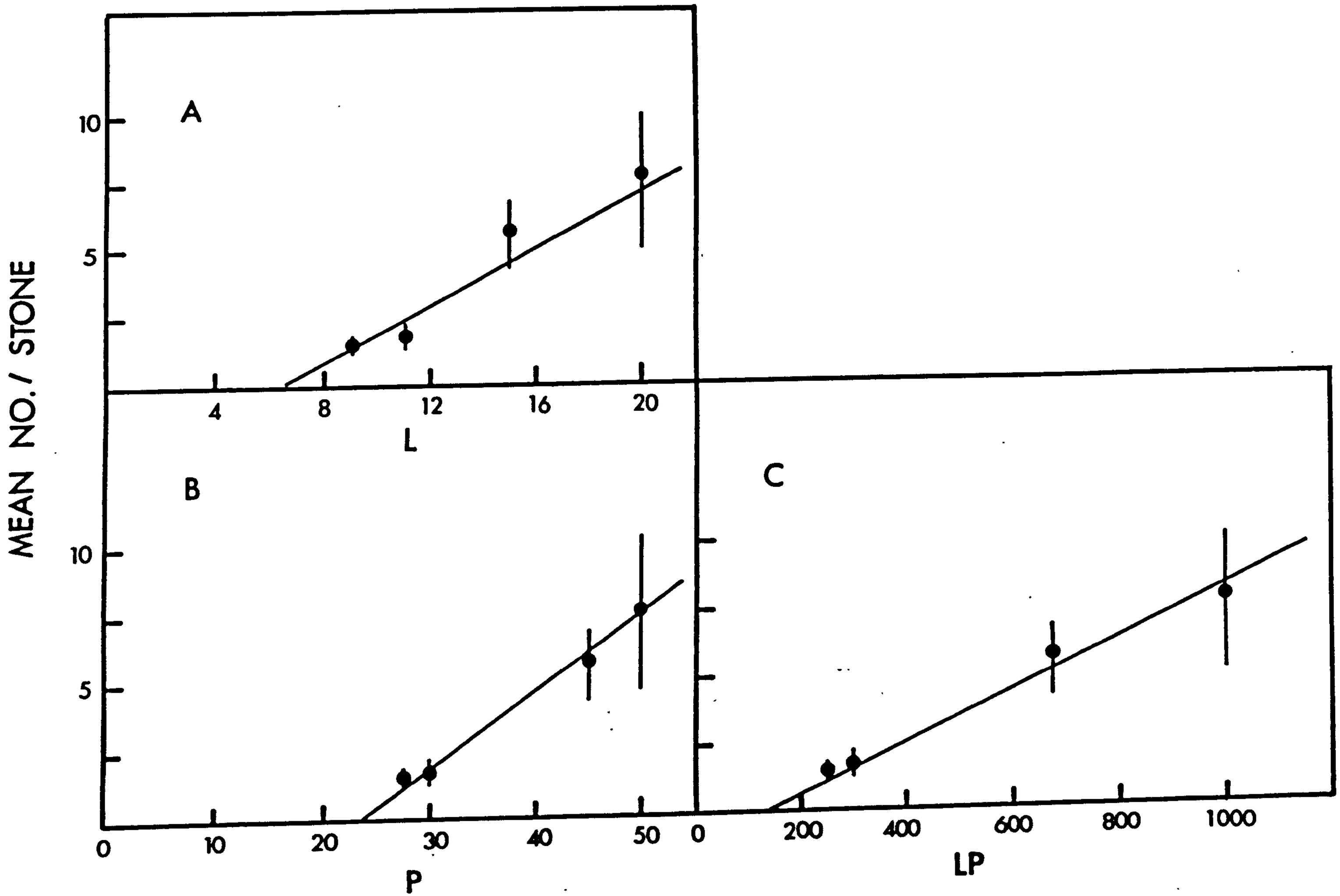

A
B
C
MEAN NO. / STONE
10
5
4
8
12
16
20
L
10
5
0
10
20
30
40
50
P
0
200
400
600
800
1000
LP

FIG. 26 :A diagrammatic representation of a generalised, submerged stone on Ha Mire shore, with information on stone-surface, zonation patterns and the influence of depth.

Key

a, b, c, = various stone shapes

f = the point of contiguity between stones

A = Blue-green algae

B = Diatoms.

C = other algae

D = detritus

T = tufa

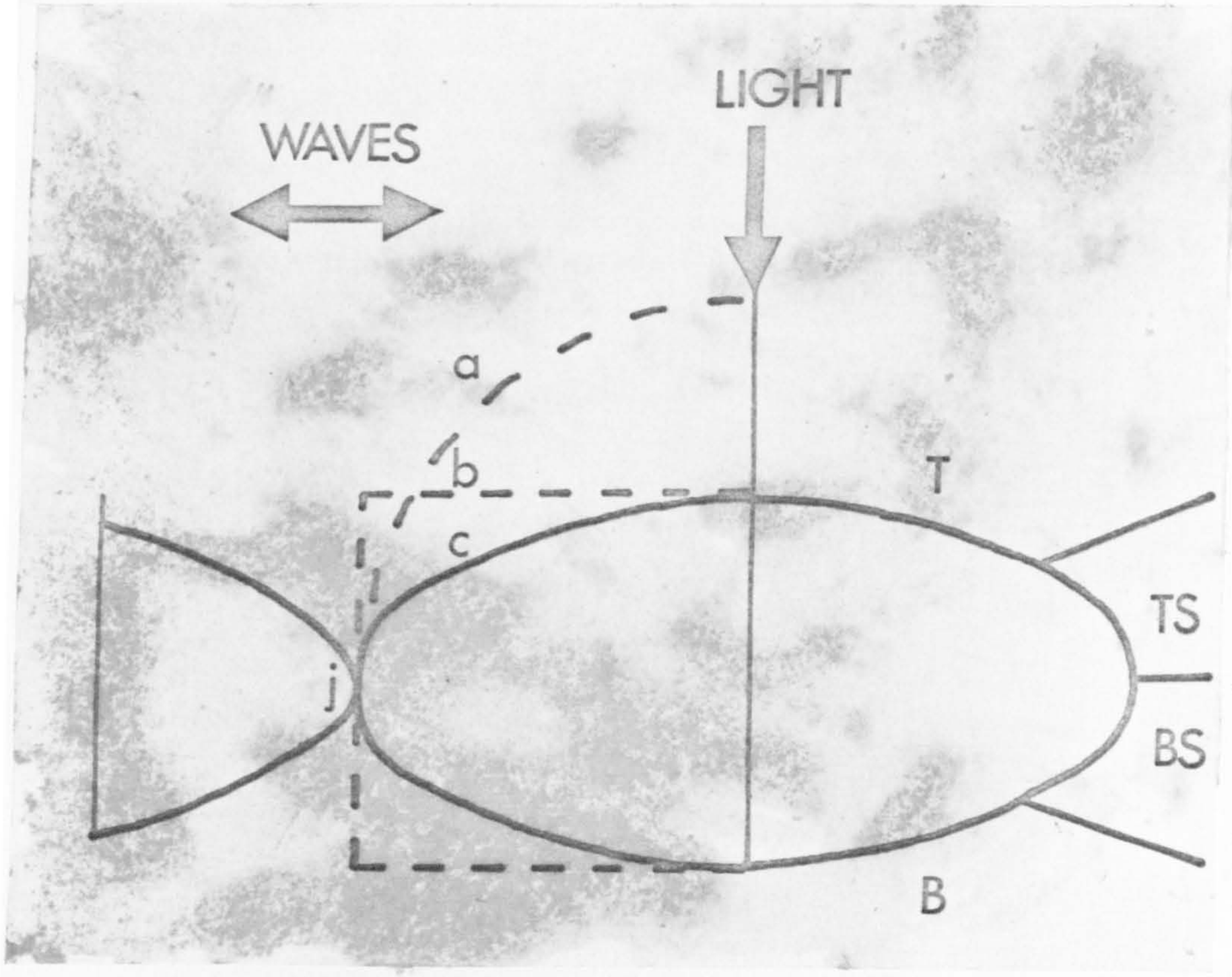
XX = extent of tufal encrustation

W = Kendall's coefficient of Concordance

P = the probability of rejecting Ho (no concordance) when this interpretation is correct

* = concordance not calculated.

The figures in the table represent the "true" ranking order (see text).



ALGAL AND DETRITAL COVER OF

DIFFERENT STONE ASPECTS

Depth Contour	0-15cm.							15-30cm.							45-60cm.						
Cover	A	B	C	D	W	P	T	A	B	C	D	W	P	T	A	B	C	D	W	P	T
Top (T)	2	1	3	4	.8	≤ .05	-	1	1	4	3	.81	≤ .05	-	1	2	4	3	.93	≤ .05	X X X
Top Side (TS)	2	1	3	4	.84	≤ .05	-	1	2	3	4	.90	≤ .05	X X X X X	1	2	3	4	.94	≤ .05	X X X X X
Bottom Side (BS)	-	2	-	1	*	*	-	-	2	-	1	*	*	-	-	2	-	1	*	*	-
Bottom (B)	-	-	-	1	*	*	-	-	-	-	1	*	*	-	-	-	-	1	*	*	-

FIG. 27 : The mean, monthly density fluctuations in the Ha Mire population of P.contortus (confidence limits represent 2 standard errors). Temperature fluctuations are also included.

Key

■ = GENERATION 1

● = " 2

▲ = " 3

ov = Oviposition period

FE = First egg observed

FY = First young

T = Critical oviposition temperature (see text).

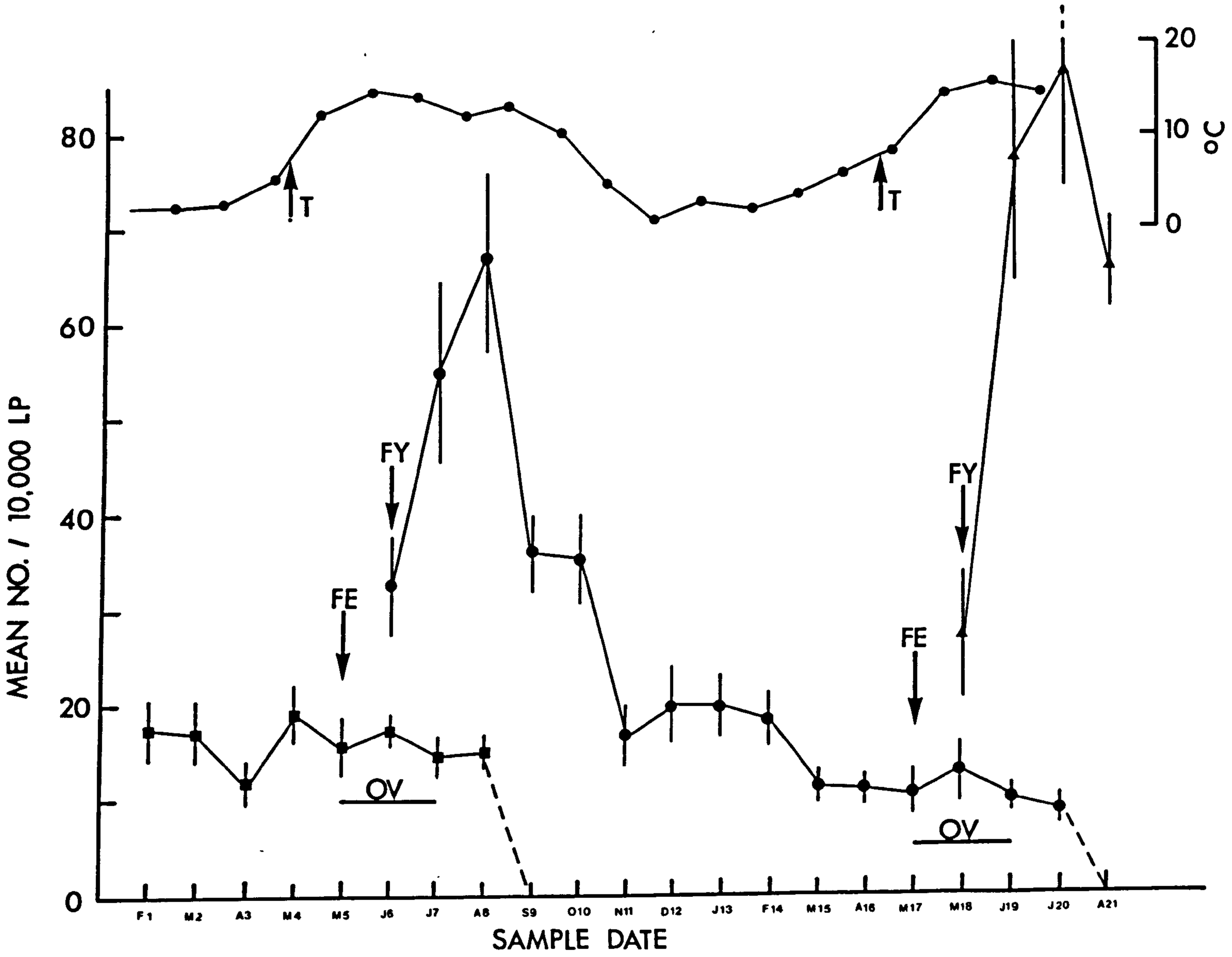

80
60
40
20
0
MEAN NO. / 10,000 LP
20
10
0
°C
T
T
FY
FY
FE
FE
OV
OV
F1
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
F14
M15
A16
M17
M18
J19
J20
A21
SAMPLE DATE

FIG. 28 : The mean, monthly density fluctuations in the Ha Mire population of A.fluviatilis . The terms are as defined in FIG. 27 except :

FF = first fertilisation.

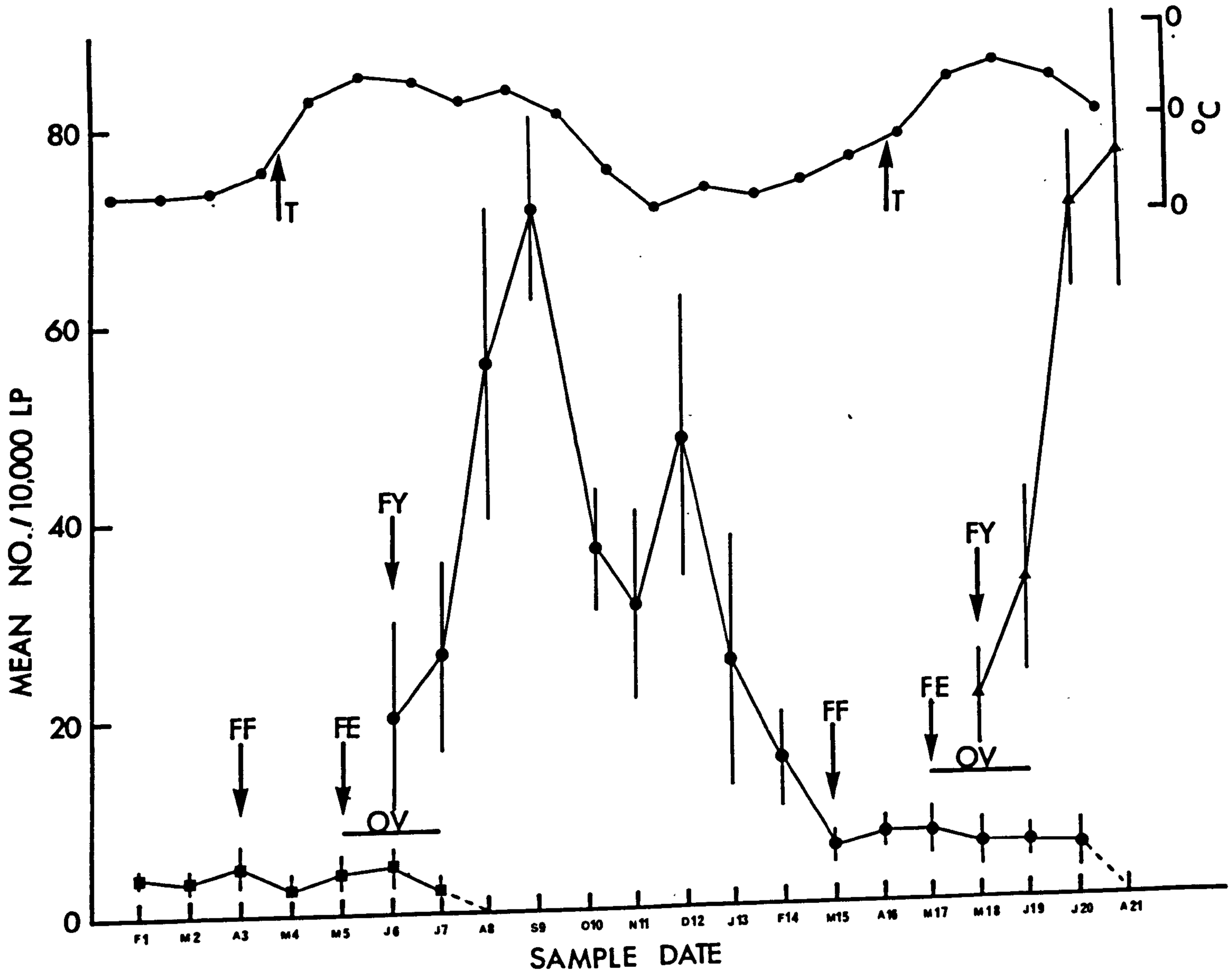

80
60
40
20
0
MEAN NO./10,000 LP
T
T
FY
FY
FF
FE
FF
FE
OV
OV
0
0
0
°C
F1
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
F14
M15
A16
M17
M18
J19
J20
A21
SAMPLE DATE

FIG. 29 : Monthly variations in the size frequency distribution of the Ha Mire population of P.contortus. The numbers of individuals involved in each sample are indicated above the histograms.

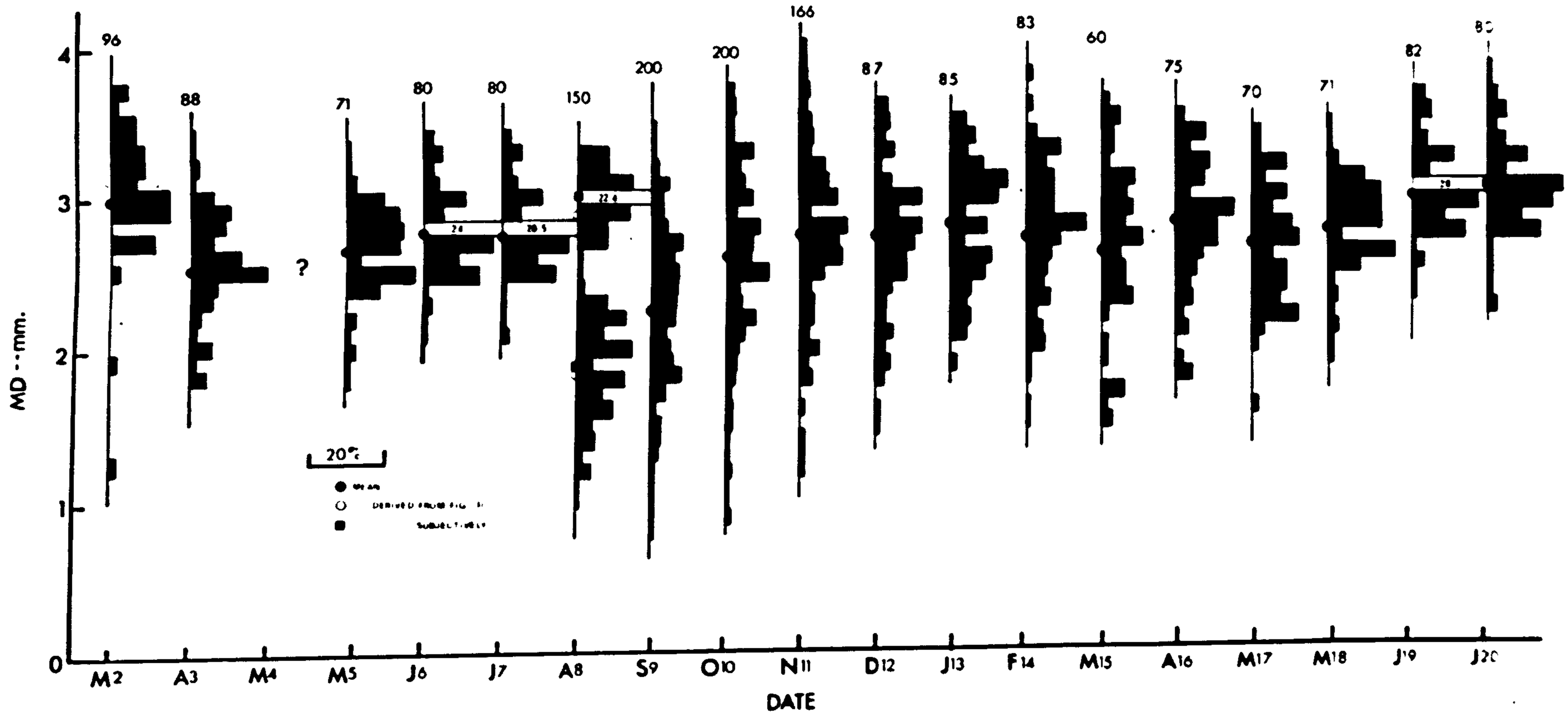

MD - - mm.
4
3
2
1
0
96
88
71
80
80
150
200
200
166
87
85
83
60
75
70
71
82
80
?
20%
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
F14
M15
A16
M17
M18
J19
J20
DATE

FIG. 30 : Monthly variations in the size frequency distribution of the Ha Mire population of A.fluviatilis. The numbers involved in each sample are indicated above the histograms.

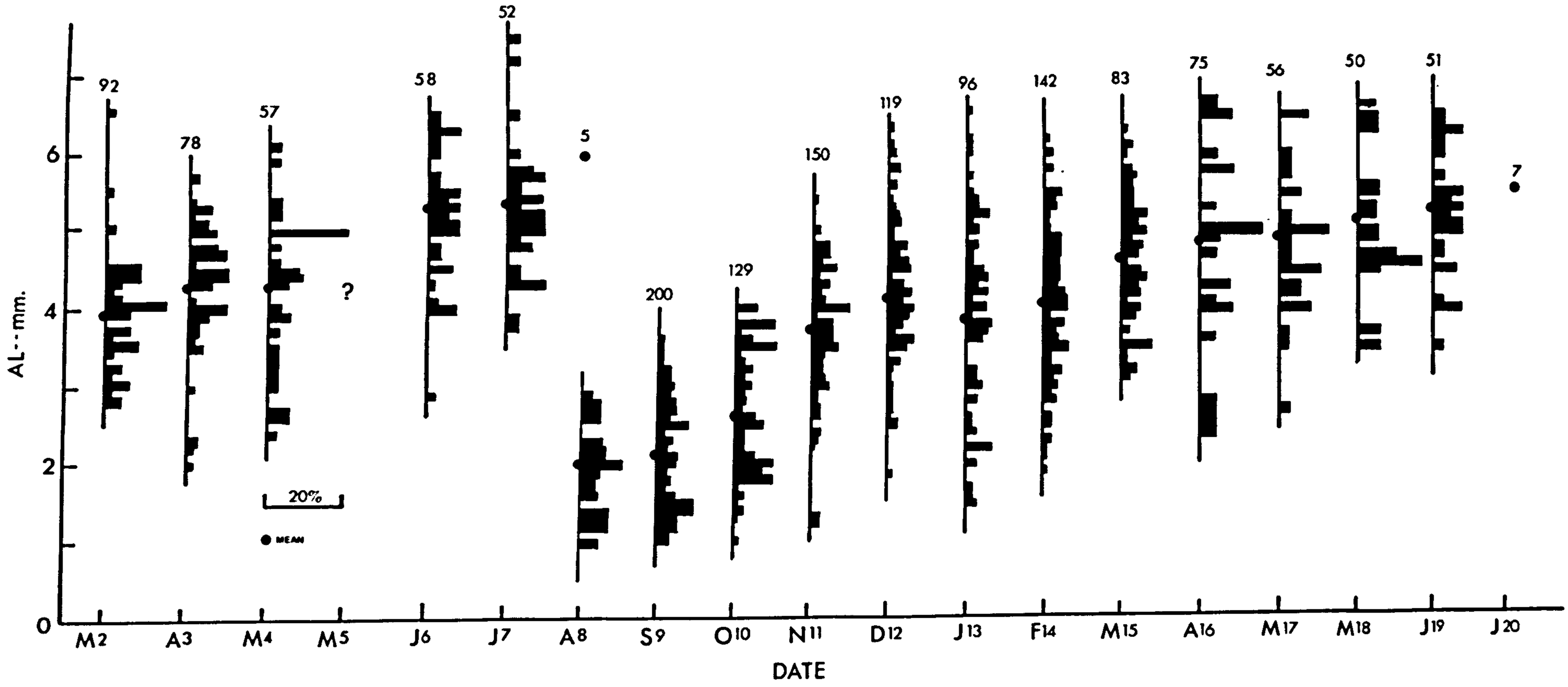

AL--mm.
0
2
4
6
92
78
57
58
52
5
?
150
119
96
142
83
75
56
50
51
7
200
129
20%
MEAN
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
F14
M15
A16
M17
M18
J19
J20
DATE

FIG. 31 : Graphical analysis, by probability paper, of the frequency distribution of P.contortus in sample A8 (see FIGS. 27 and 29).

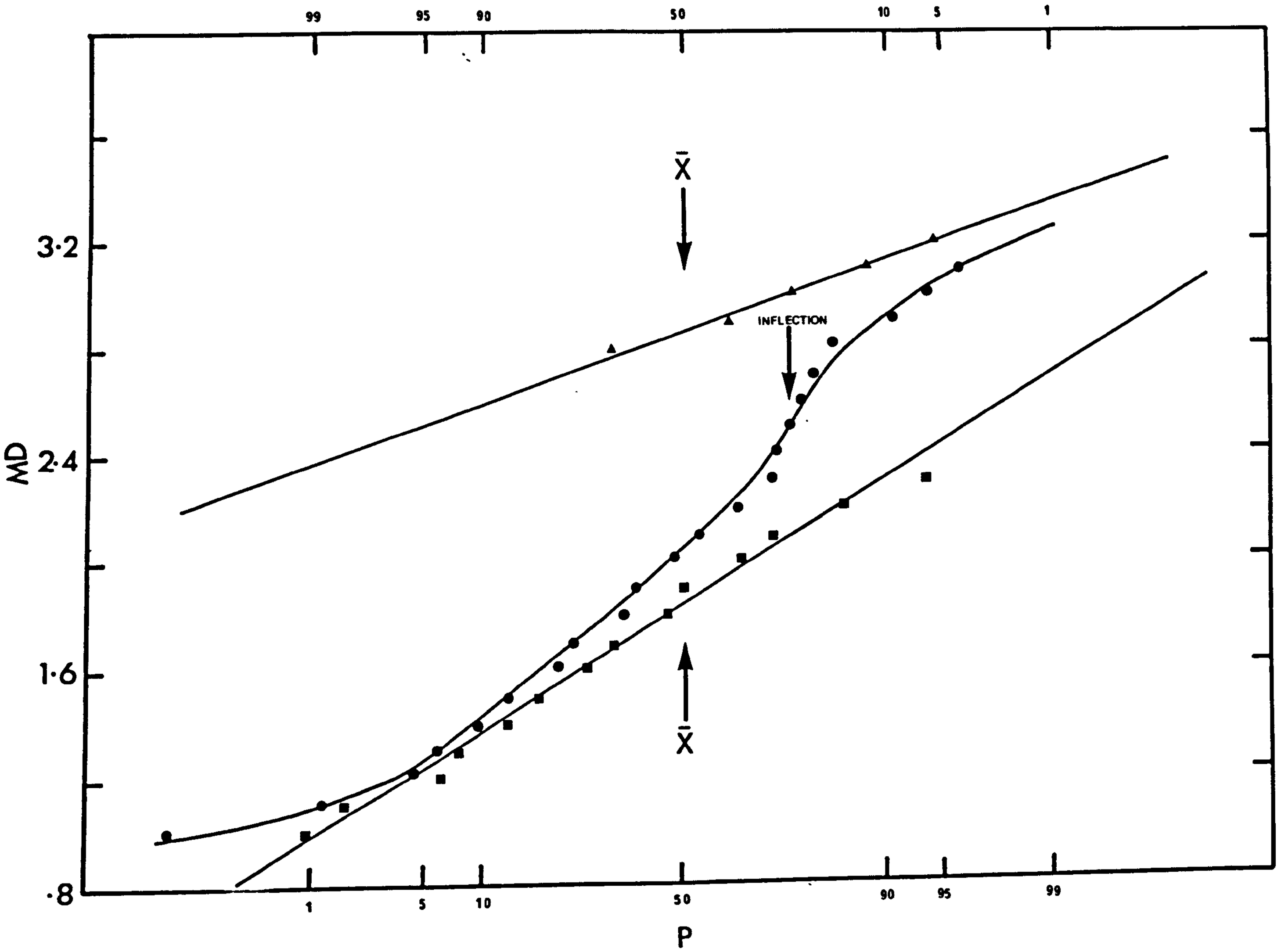

99
95
90
50
10
5
1
$\bar{X}$
3·2
INFLECTION
MD
2·4
1·6
·8
$\bar{X}$
1
5
10
50
90
95
99
P

FIG. 32 : Graphical analysis, by probability paper, of the frequency distribution of P.contortus in sample S9 (see FIGS. 27 and 29).

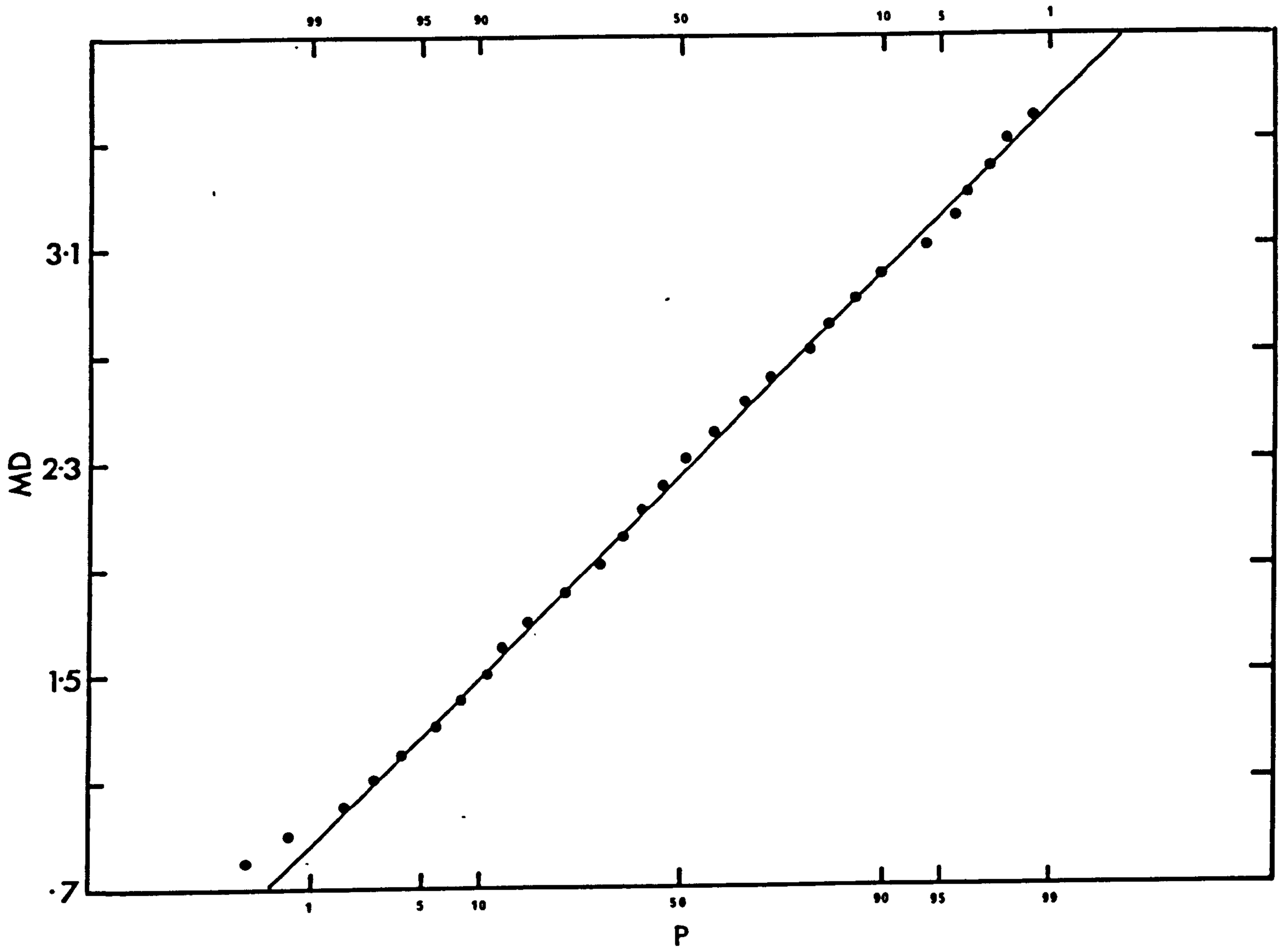

99
95
90
50
10
5
1
3·1
2·3
1·5
·7
MD
1
5
10
50
90
95
99
P

FIG. 33 : Diagrammatic representation of a generalised pulmonate egg-capsule (constructed from Bondesen, 1950).

Key

EC - Egg cell

Egg
- A - Albuminous material
- I - Internal membrane
- E - External membrane (Lacking in Planorbidae, Ancylidae & Acroloxidae)

Formed by proximal portion of genitalia

Egg Capsule

- G - Gelatinous packing — Formed by distal portion of genitalia

Capsule Membranes
- T - Tertiary membrane — Formed by distal portion of genitalia
- Q - Quaternary membrane (Only present in Ancylidae & Acroloxidae) — foot secretion

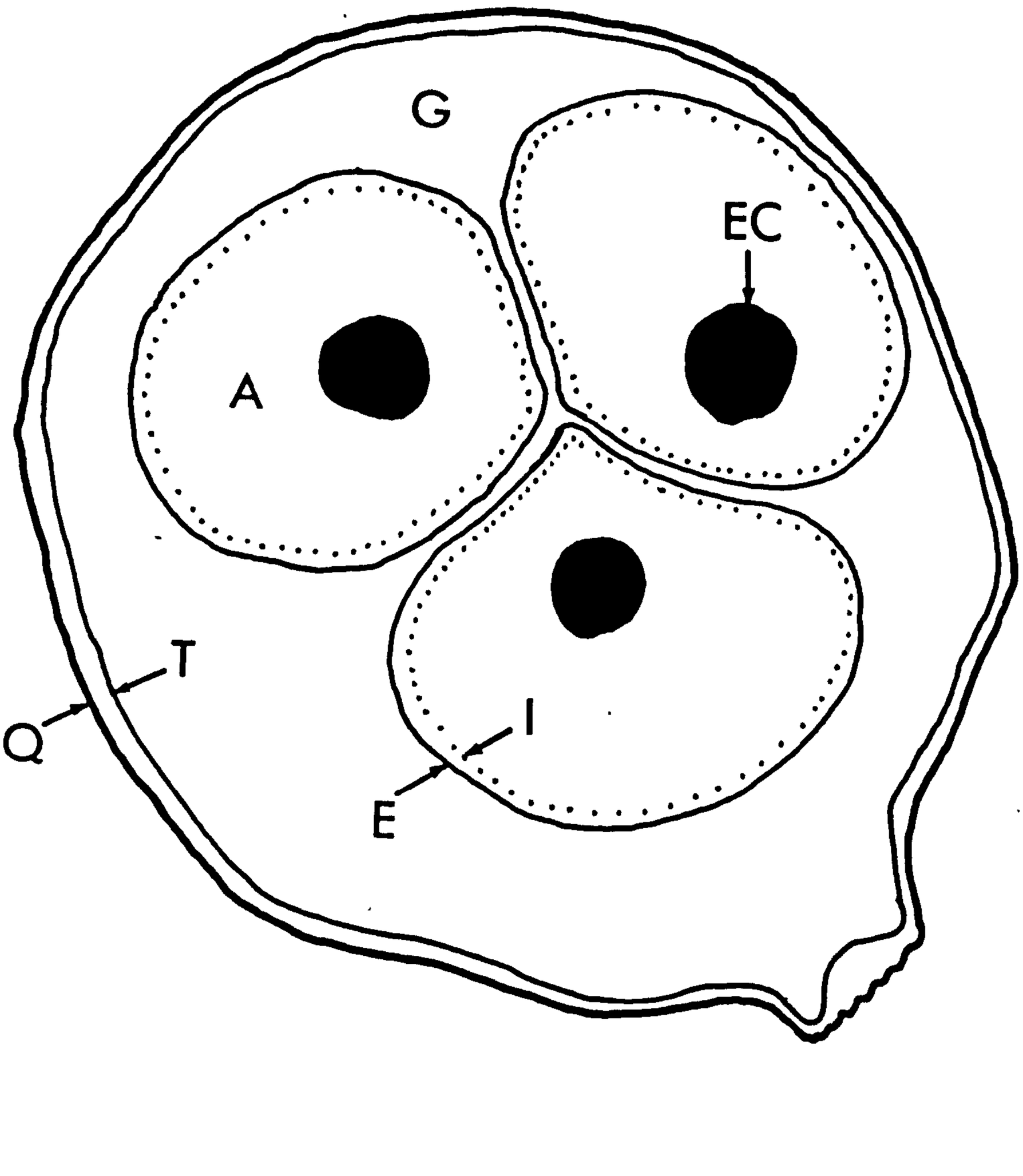

G
EC
A
T
Q
I
E

FIG. 34 : The distribution of egg-capsules (% total produced), on stones in experimental cages, with respect to stone texture (R = rough; S = smooth) and aspect (T = top = T + TS; B = bottom = B + BS) when A. fluviatilis and P.contortus were isolated (A & B respectively) and intermixed (C & D respectively). The numbers in parenthesis indicate the average number of capsules produced/individual/week.

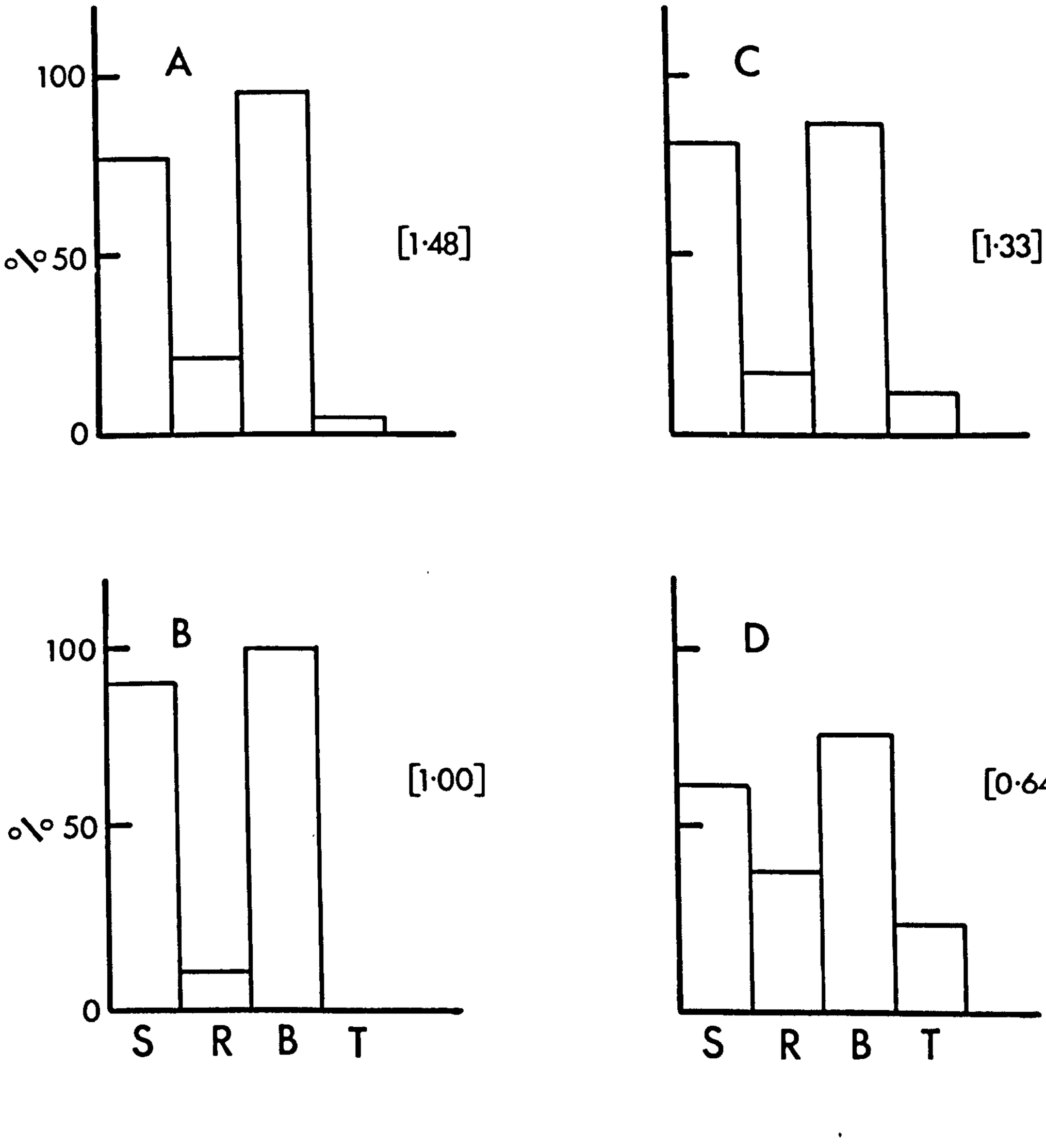

A
100
%
50
0
[1·48]
C
[1·33]
B
100
%
50
0
[1·00]
S
R
B
T
D
[0·64]
S
R
B
T

FIG. 35 : The capsule chronologies of P.contortus and A. fluviatilis in two regions of Malham Tarn. The Σ - values represent the total number of capsules produced by a, "standard" individual over the whole oviposition interval.

Key

A - P.contortus on Ha Mire

B - P.contortus at STATION 2

C - A.fluviatilis at STATION 2

D - A.fluviatilis at Ha Mire

E - Average weekly temperatures.

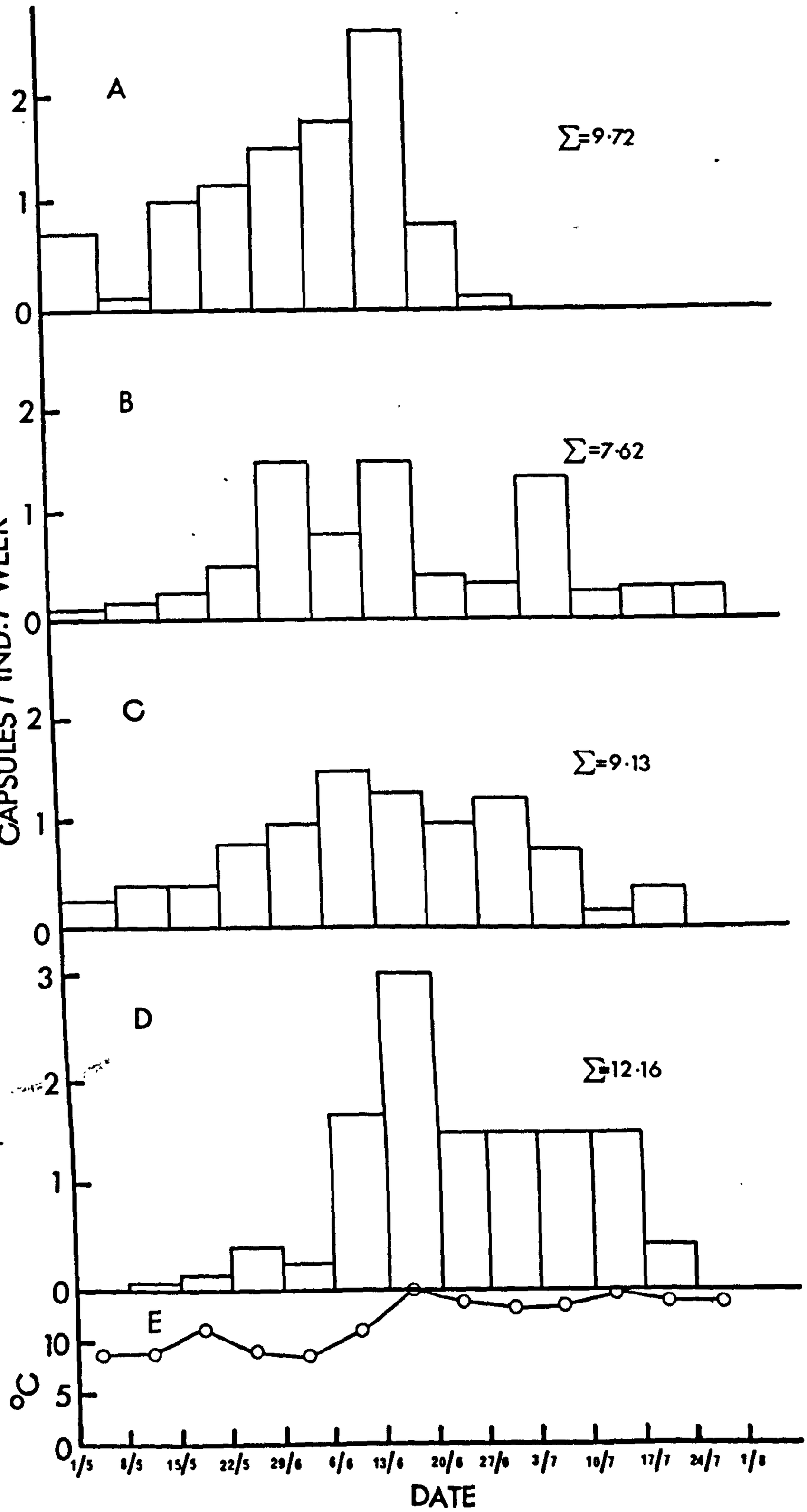

A
2
1
0
Σ=9·72
B
2
1
0
Σ=7·62
C
2
1
0
Σ=9·13
CAPSULES / IND. / WEEK
D
3
2
1
0
Σ=12·16
E
10
5
0
°C
1/5
8/5
15/5
22/5
29/5
6/6
13/6
20/6
27/6
3/7
10/7
17/7
24/7
1/8
DATE

FIG. 36 : The % loss of whole egg capsules from marked stones situated on Ha Mire shore (A represents the results for A.fluviatilis and B for P. contortus.)

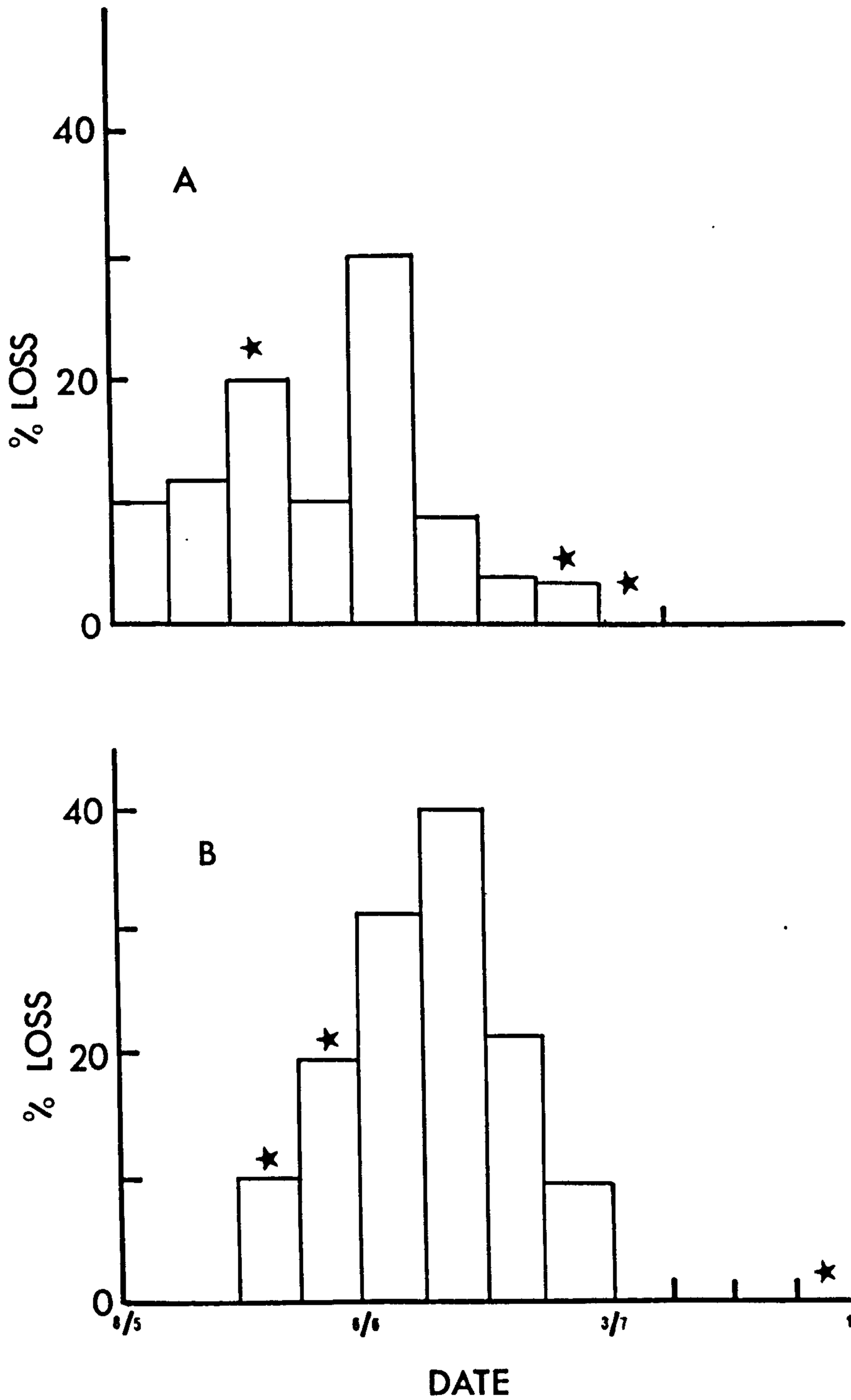

40
A
% LOSS
20
0
★
★
★
40
B
% LOSS
20
0
★
★
★
8/5
6/6
3/7
1/8
DATE

FIG. 37 : The predicted (blocks, see text) and actual (points) egg capsule standing crops on Ha Mire in 1970. (A is for A.fluviatilis and B for P.contortus).

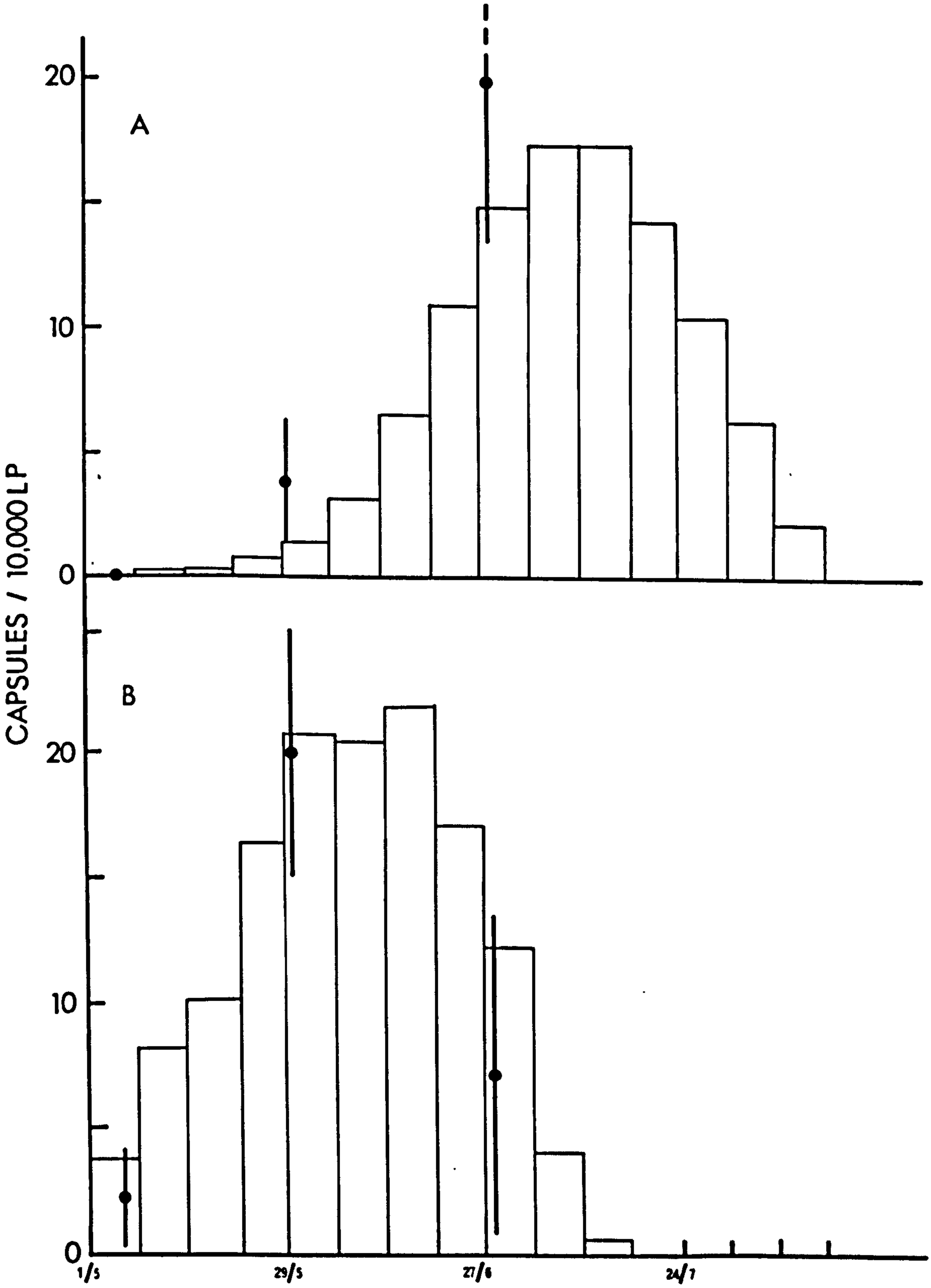
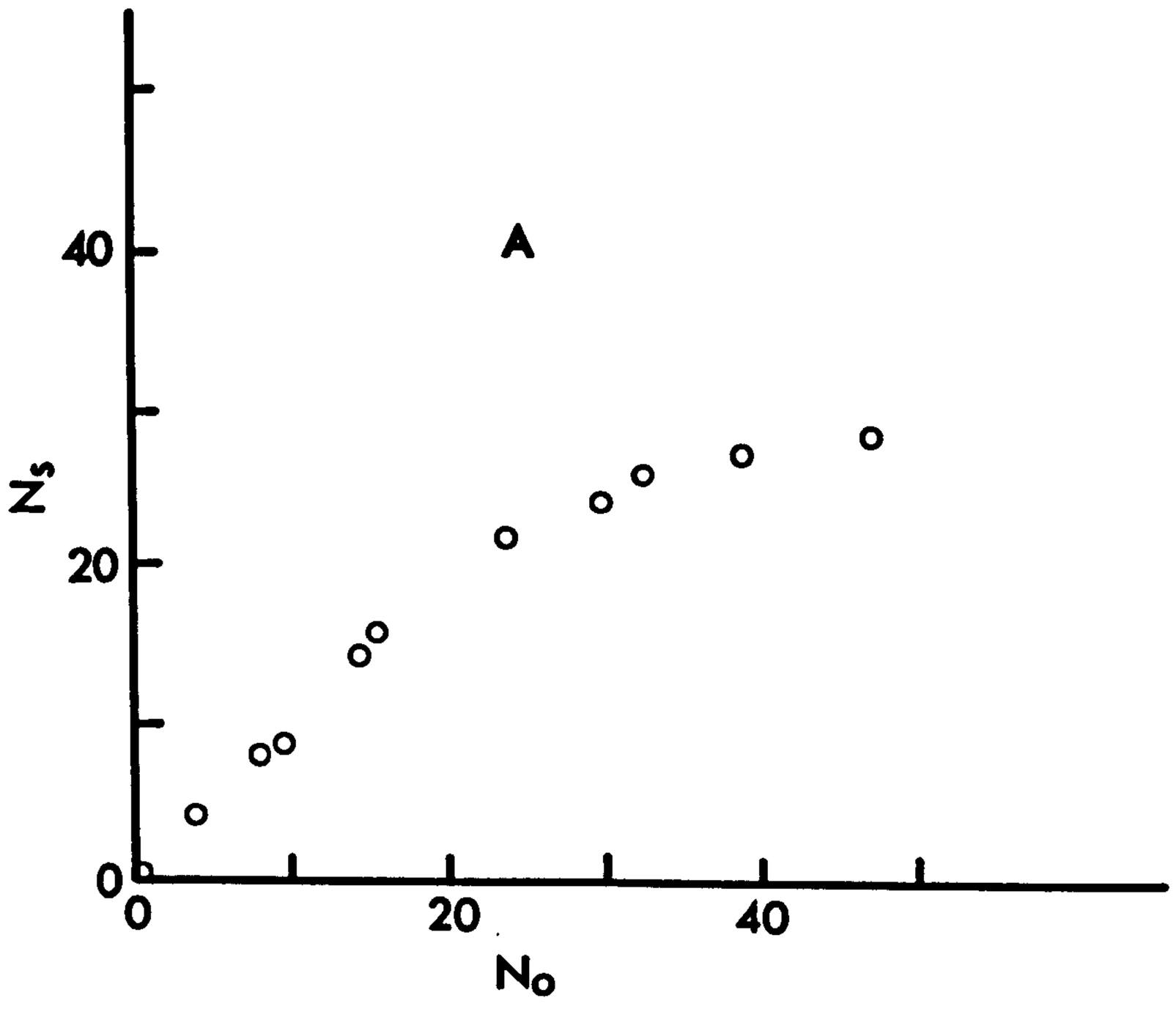

A
B
20
10
0
20
10
0
CAPSULES / 10,000 LP
1/5
29/5
27/6
24/7
DATE

FIG. 38 : Raw data plots of the number of egg capsules entering each weekly interval (No.) against the number of egg capsules surviving to the end of the interval (Ns). A, represents P.contortus and, B, A.fluviatilis.


A
40
20
0
N_s
0
20
40
N_o

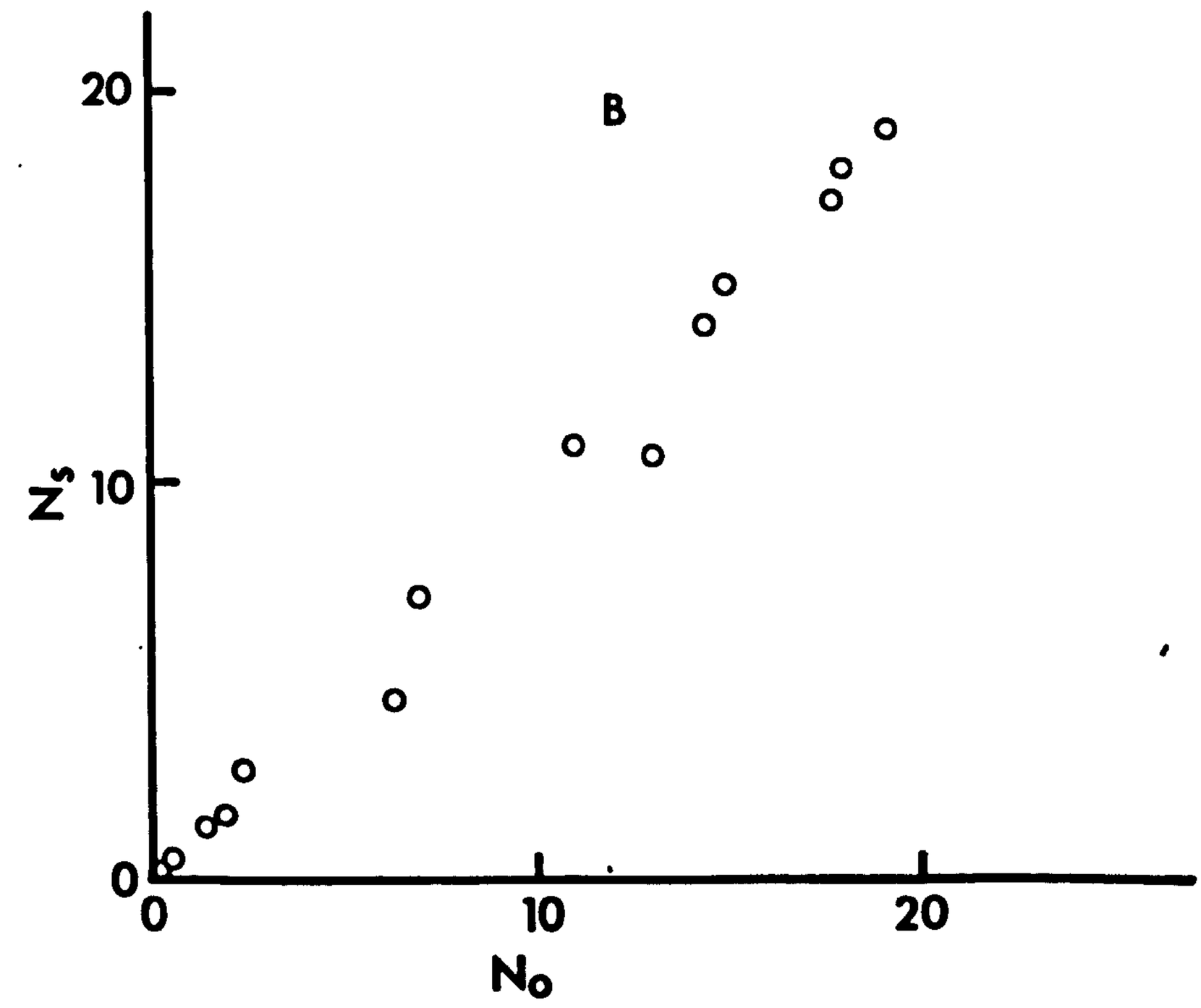

B
20
10
0
N_s
0
10
20
N_o

FIG. 39 : Logarithmic plots of Ns against No for P.contortus. The raw data was multiplied by 10 prior to transformation.

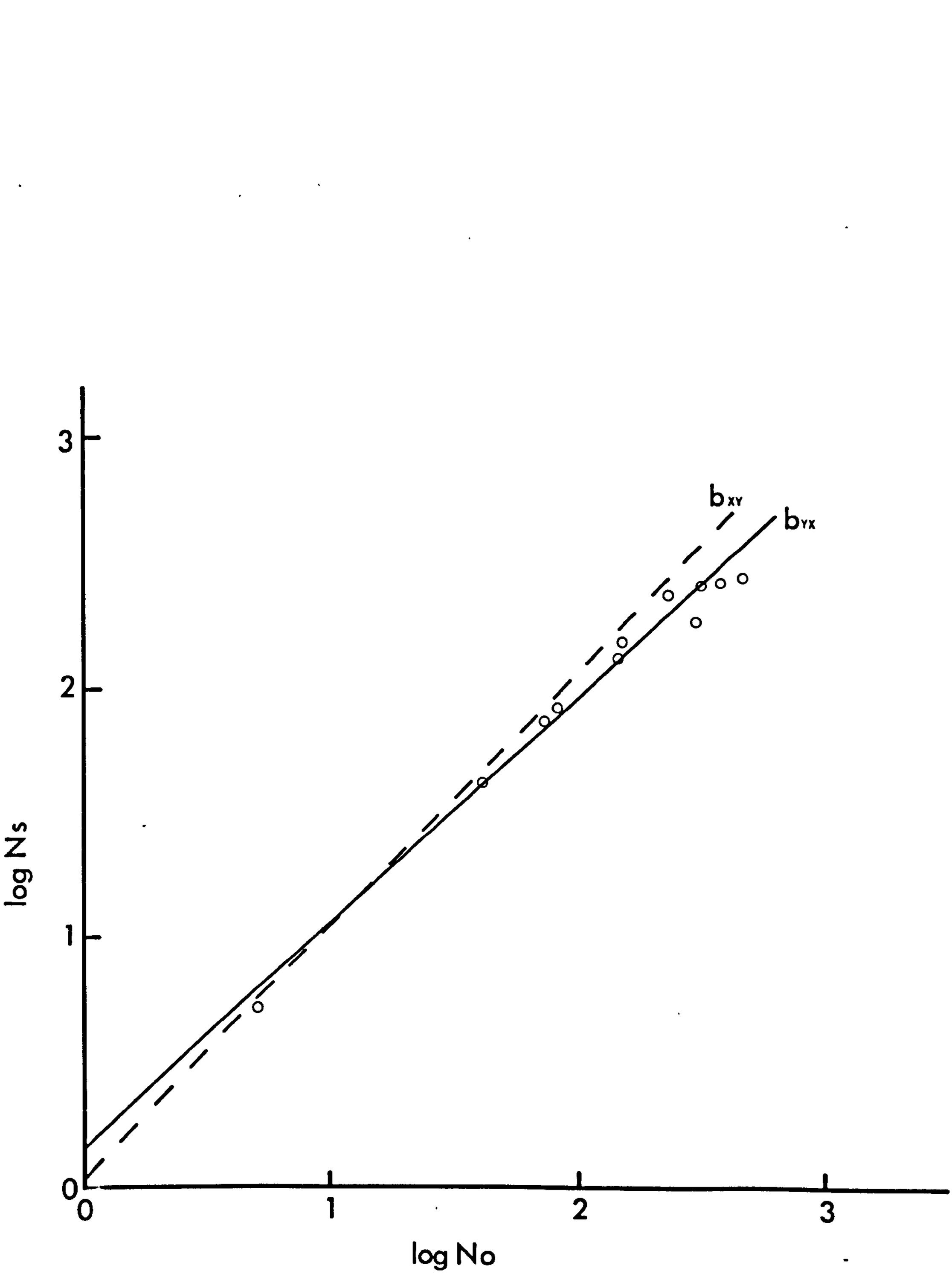

b XY
b YX
log Ns
log No
0
1
2
3
0
1
2
3

FIG. 40 : Logarithmic plots of Ns against No for A.fluviatilis. The raw data was multiplied by 10 prior to transformation.

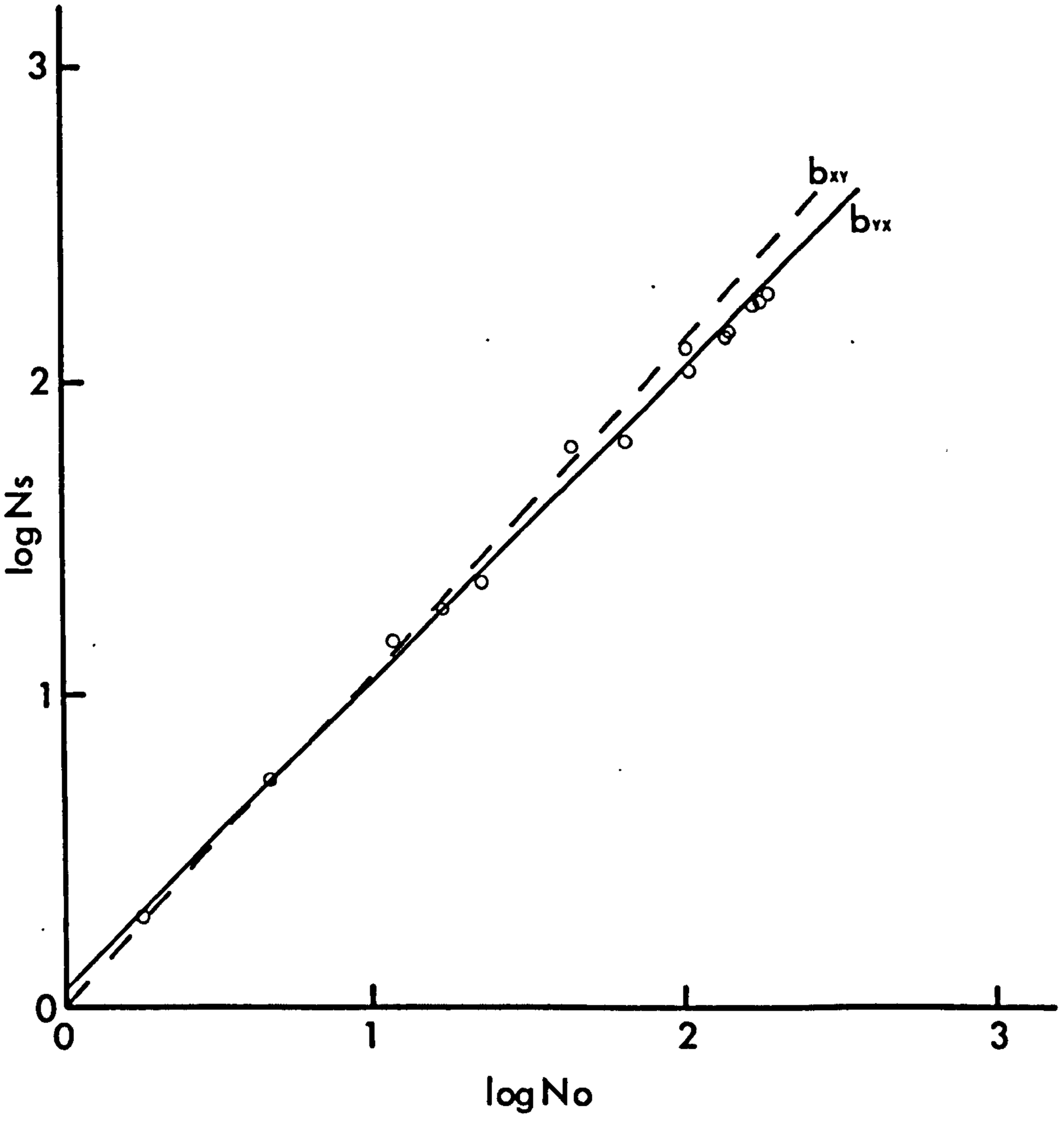

3
2
1
0
log Ns
bxy
byx
0
1
2
3
log No

FIG. 41 : k - plot representation of the egg capsule mortality in P.contortus.

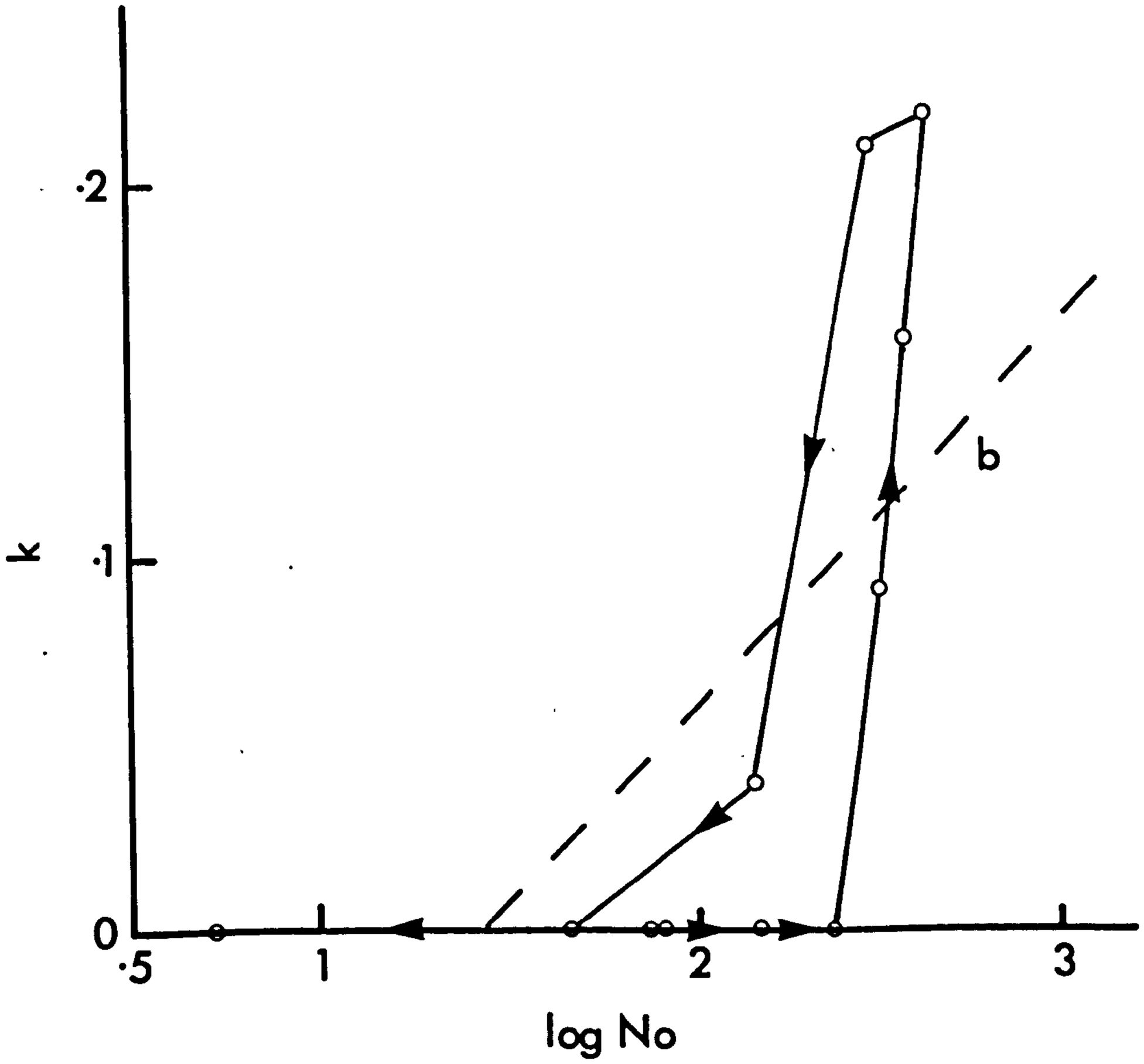

k
·2
·1
0
·5
1
2
3
b
log No

FIG. 42 : k - plot representation of the egg capsule mortality in A.fluviatilis.

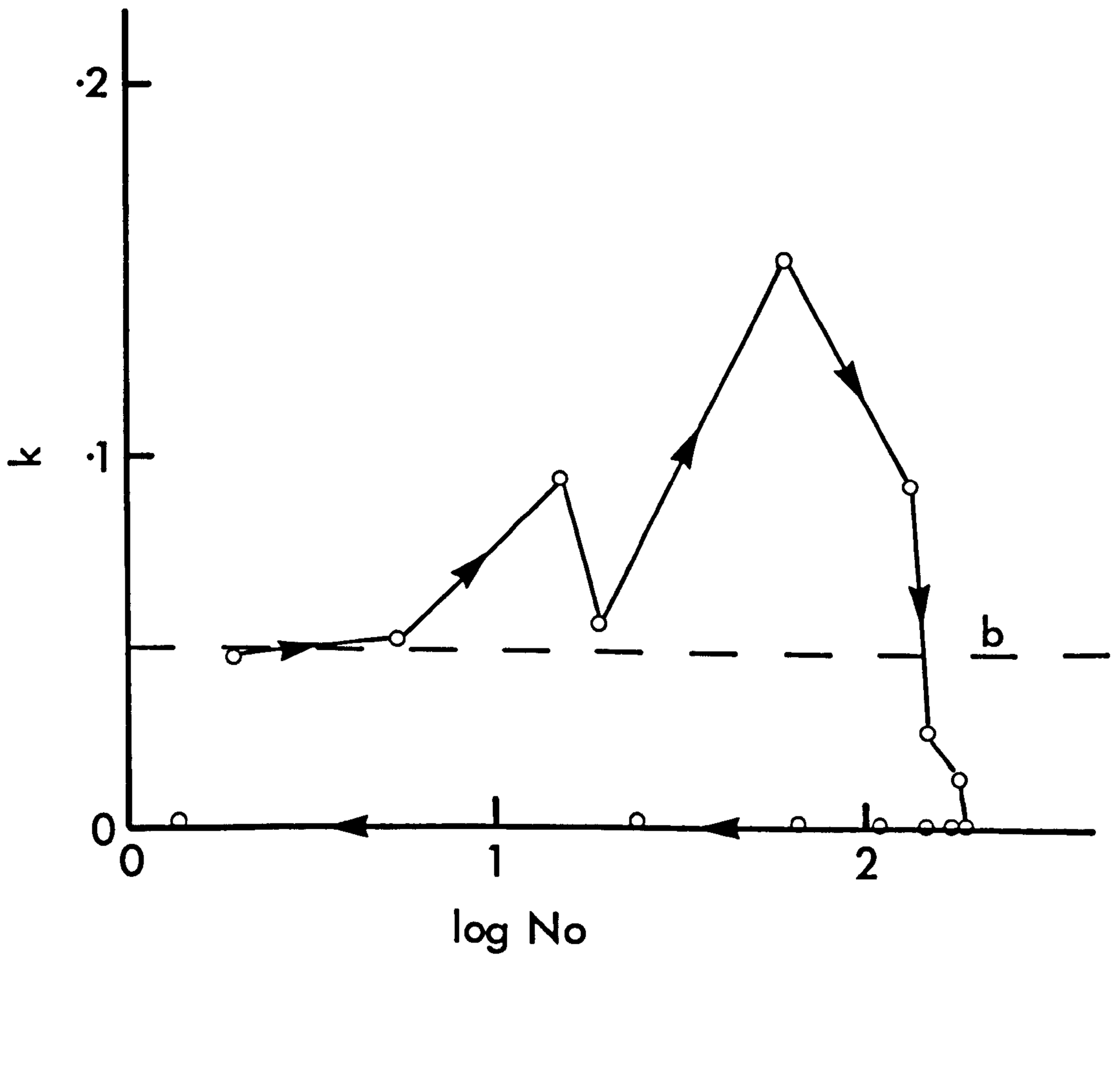
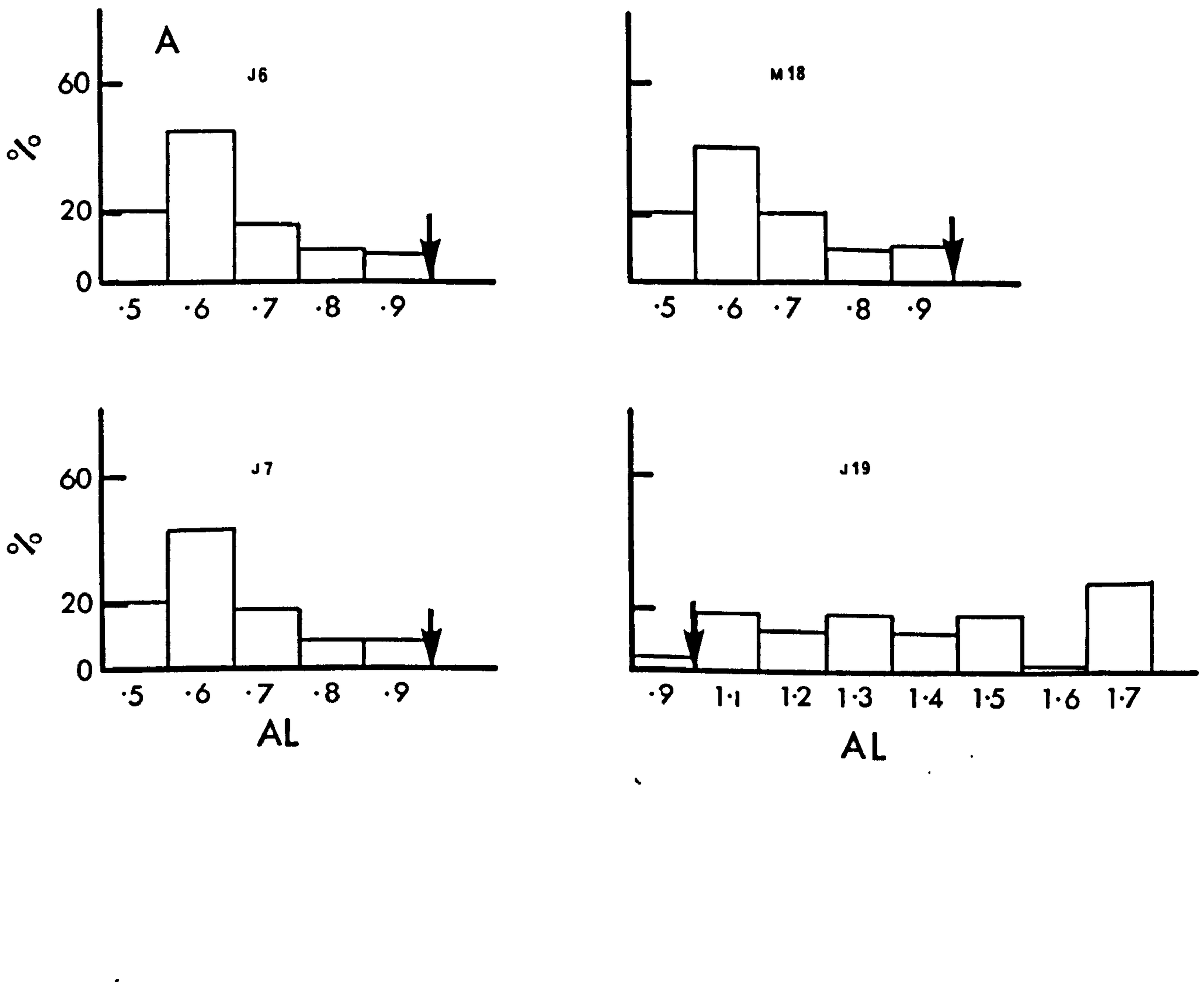

·2
·1
0
K
b
0
1
2
log No

FIG. 43 : The size-frequency distribution of spat produced during the first two months of oviposition.

A = A.fluviatilis

B = P.contortus

Vertical arrows represent the mean size of spat, on eclosion, in the laboratory.


A
J6
M 18
J7
J 19
60
20
0
%
·5
·6
·7
·8
·9
1·1
1·2
1·3
1·4
1·5
1·6
1·7
AL

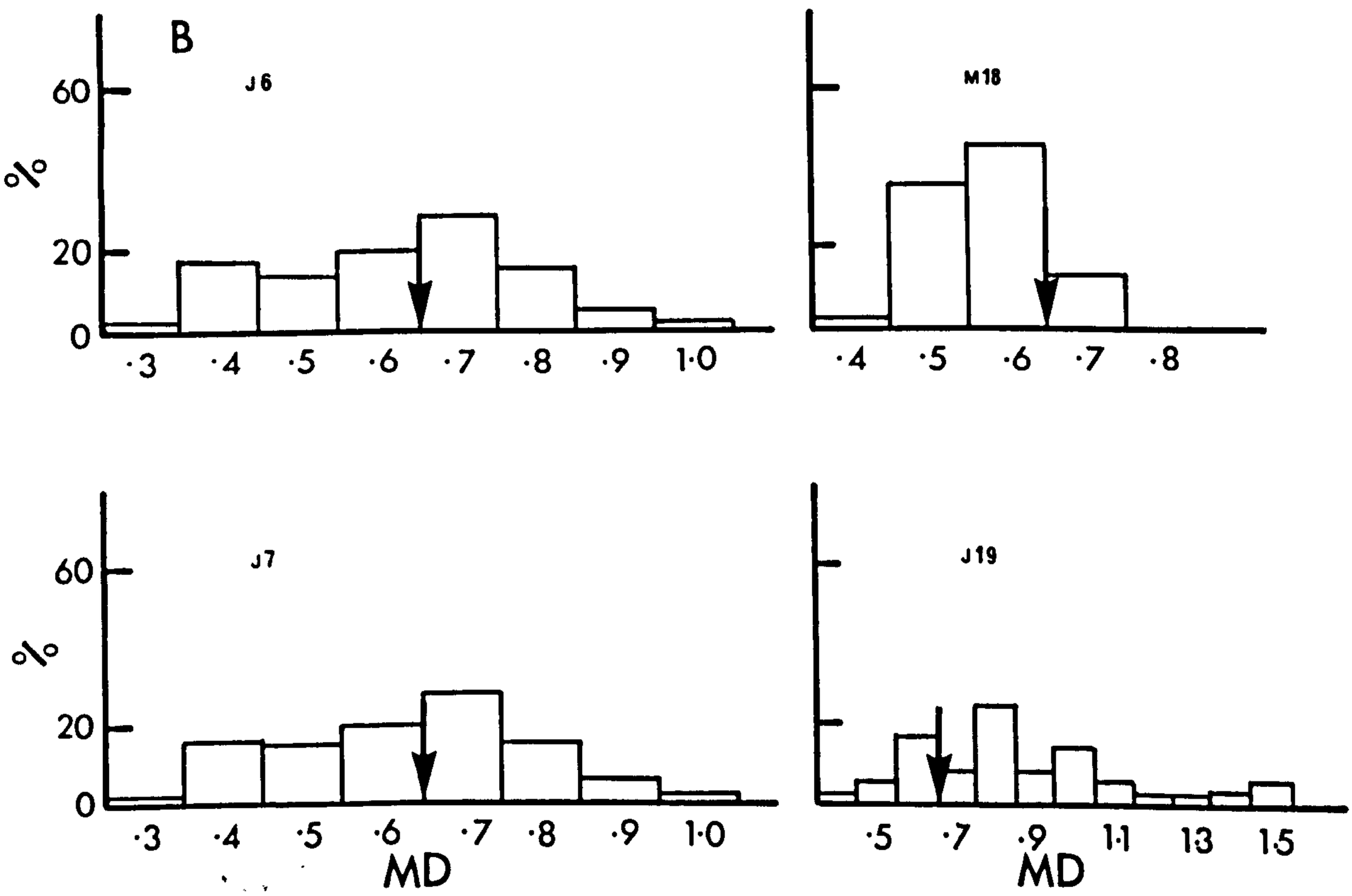
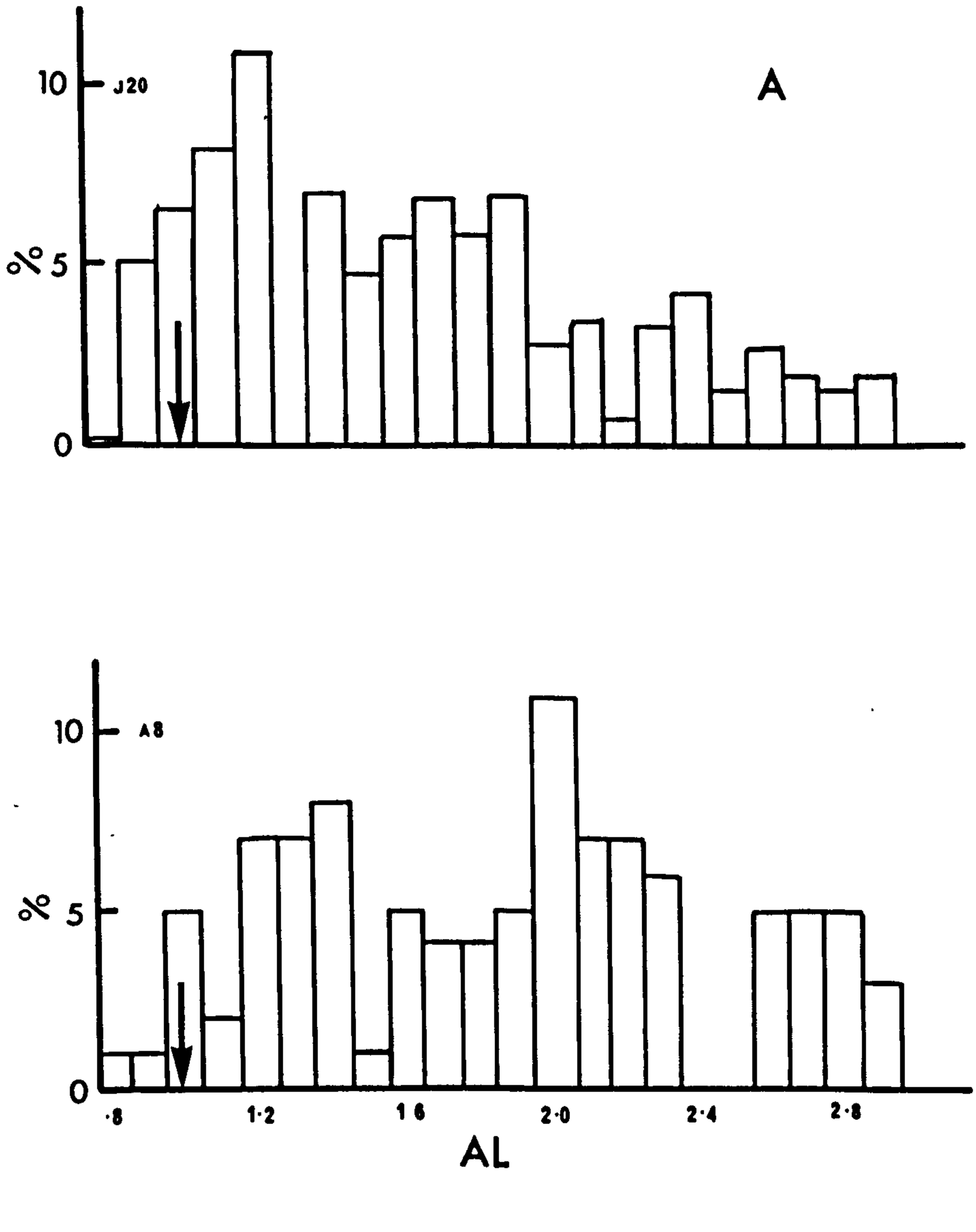

B
J6
M18
J7
J19
60
20
0
%
·3
·4
·5
·6
·7
·8
·9
1·0
·4
·5
·6
·7
·8
·5
·7
·9
1·1
1·3
1·5
MD
MD

FIG. 44 : The size-frequency distribution of spat in the month immediately following oviposition.

A = A.fluviatilis.

B = P.contortus

Vertical arrows represent the mean size of spat, on eclosion, in the laboratory.


10
J20
%
5
0
A
10
A8
%
5
0
·8
1·2
1·6
2·0
2·4
2·8
AL

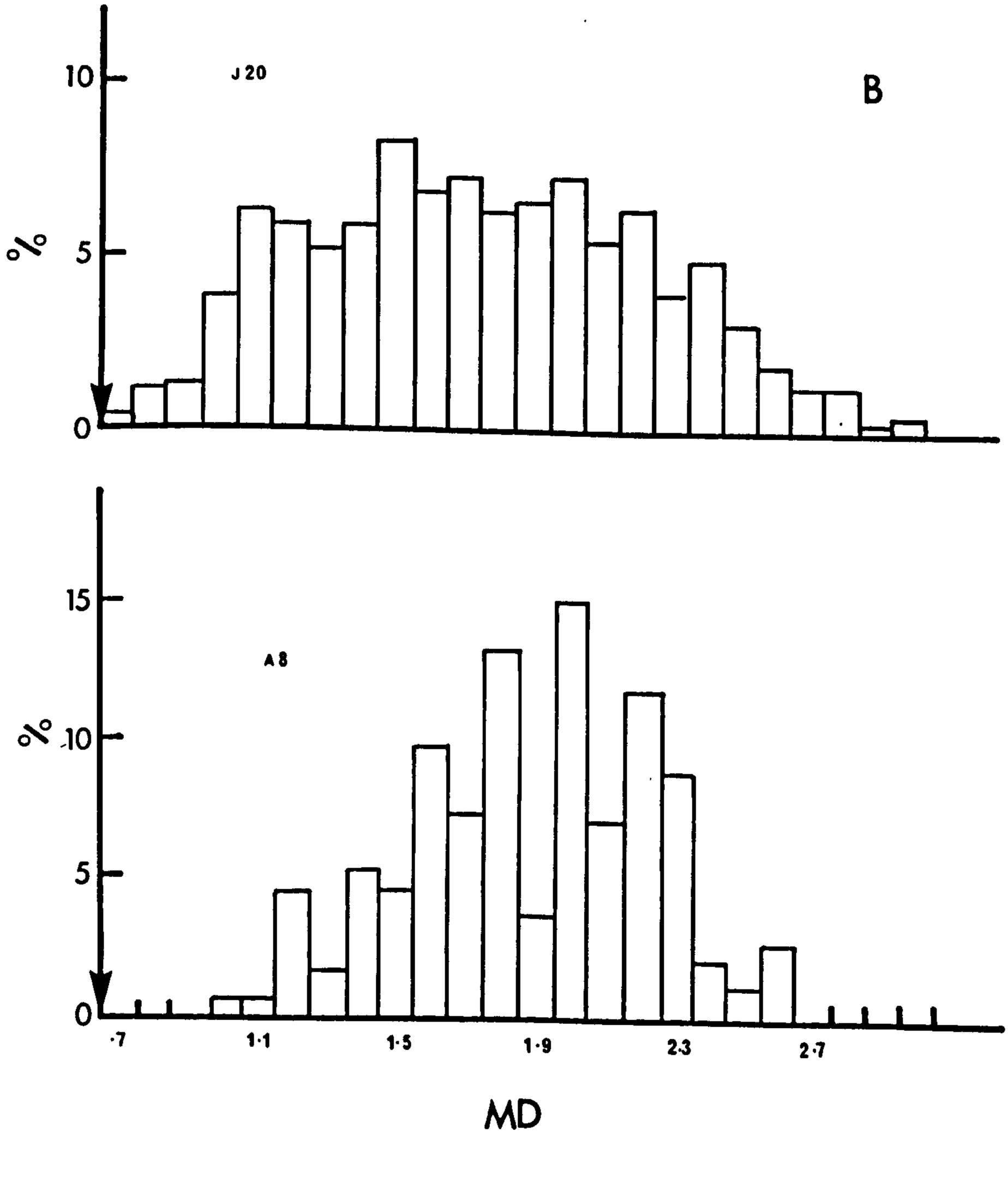

J 20
B
10
5
0
%
A 8
15
10
5
0
%
·7
1·1
1·5
1·9
2·3
2·7
MD

FIG. 45 : The relationship between adult (Na) and resultant spat (Ns) densities in different habitats for A. fluviatilis (A) and P.contortus (B). Both Ns and Na are expressed in nos./10,000LP.

Key

1 - Malham Water (immediately below the Tarn outflow) a

2 - Station 2b

3 - Station 1b

4 - Ha Mire shore

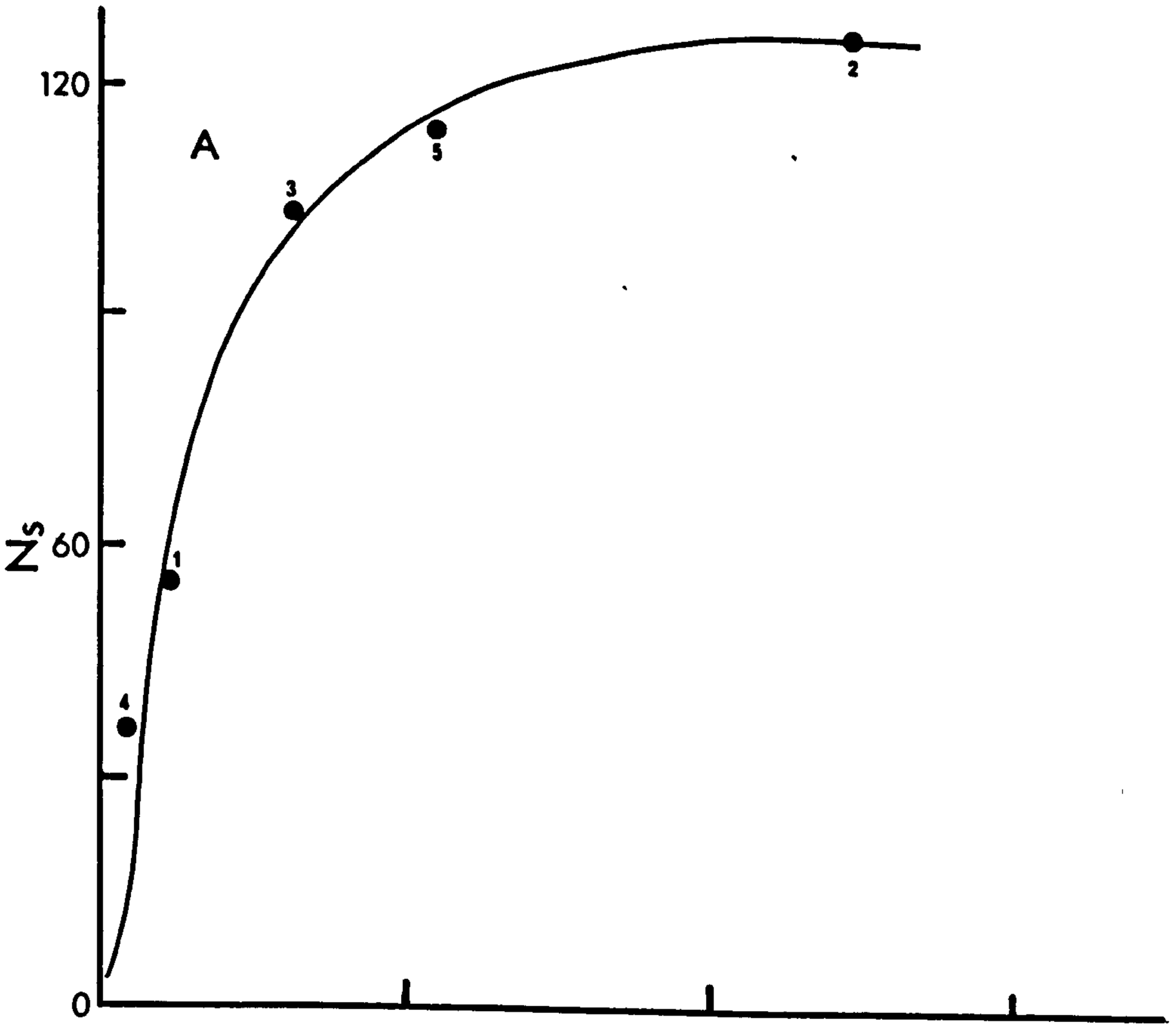
5 - The river Wharfe at Pool c

6 - Station 5b

a - see FIG. 3

b - see FIG. 9

c - see FIG. 1


120
A
60
0
N^s
1
2
3
4
5

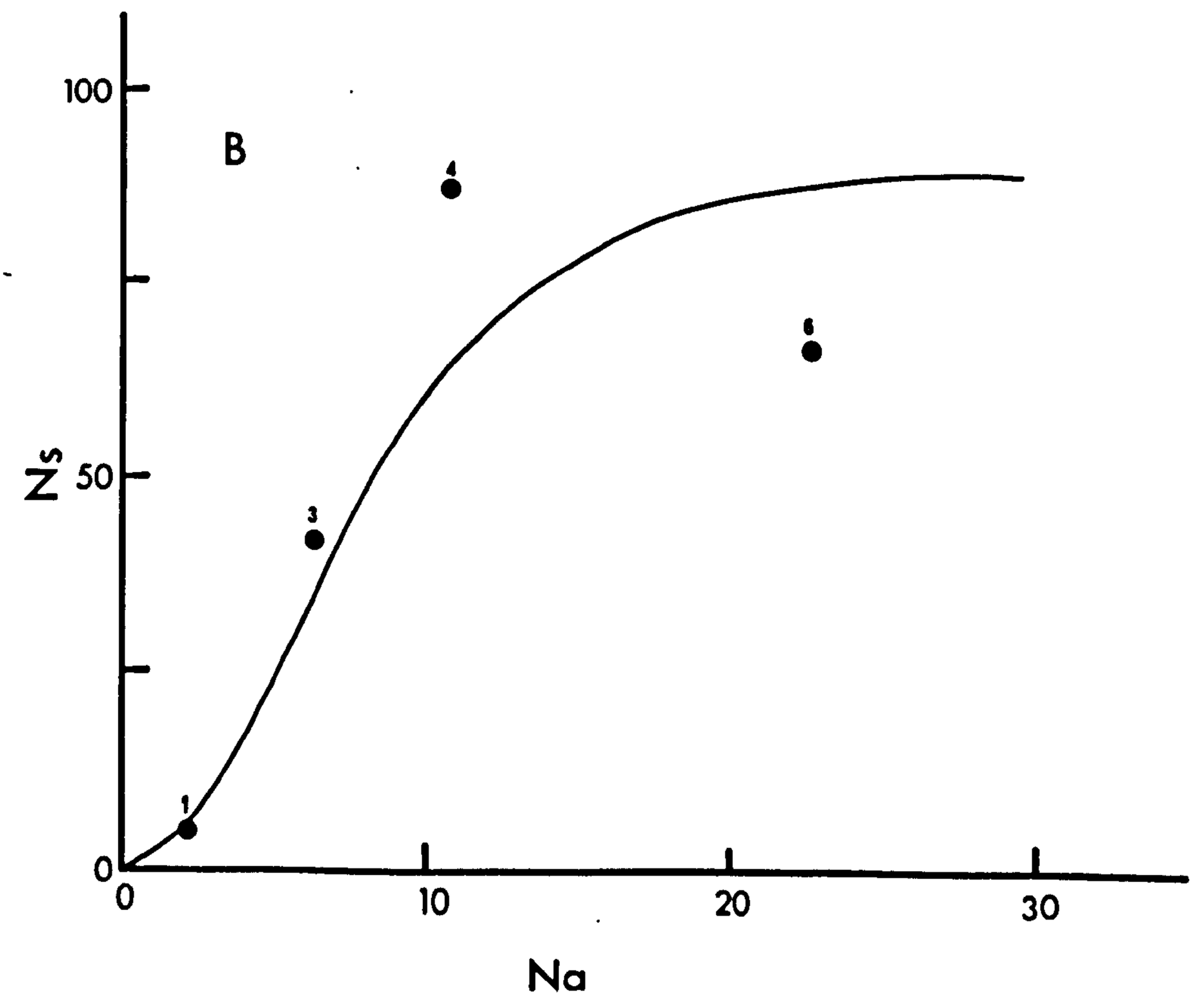

100
B
50
0
N^s
1
3
4
6
0
10
20
30
Na

FIG. 46 : The survivorship curve of P.contortus in GENERATION

2. Lx is in terms of nos./10,000LP.

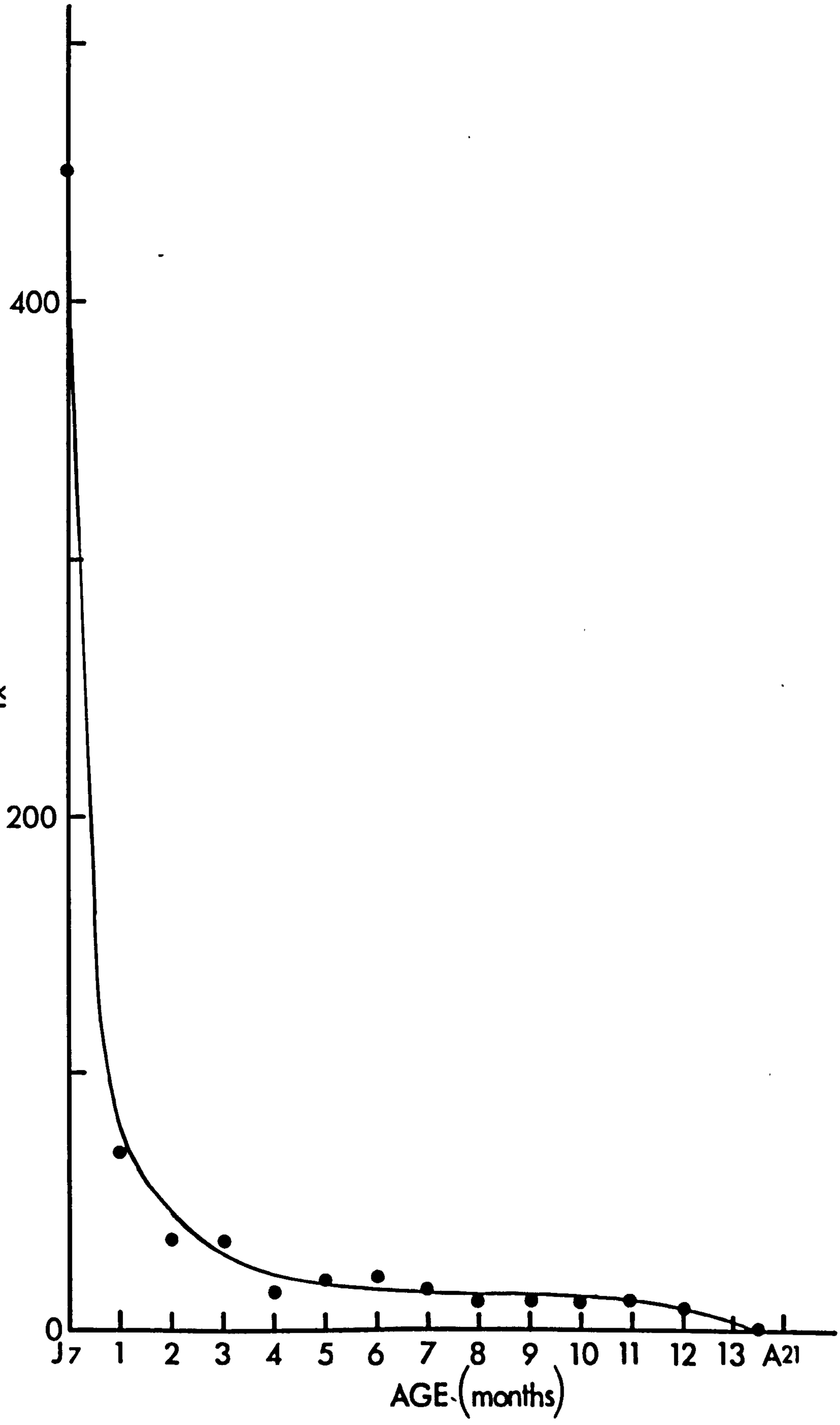

400
200
0
1x
J7
1
2
3
4
5
6
7
8
9
10
11
12
13
A21
AGE (months)

FIG. 47 : The survivorship curve of A.fluviatilis in GENERATION 2. Lx is in terms of nos./10,000LP.

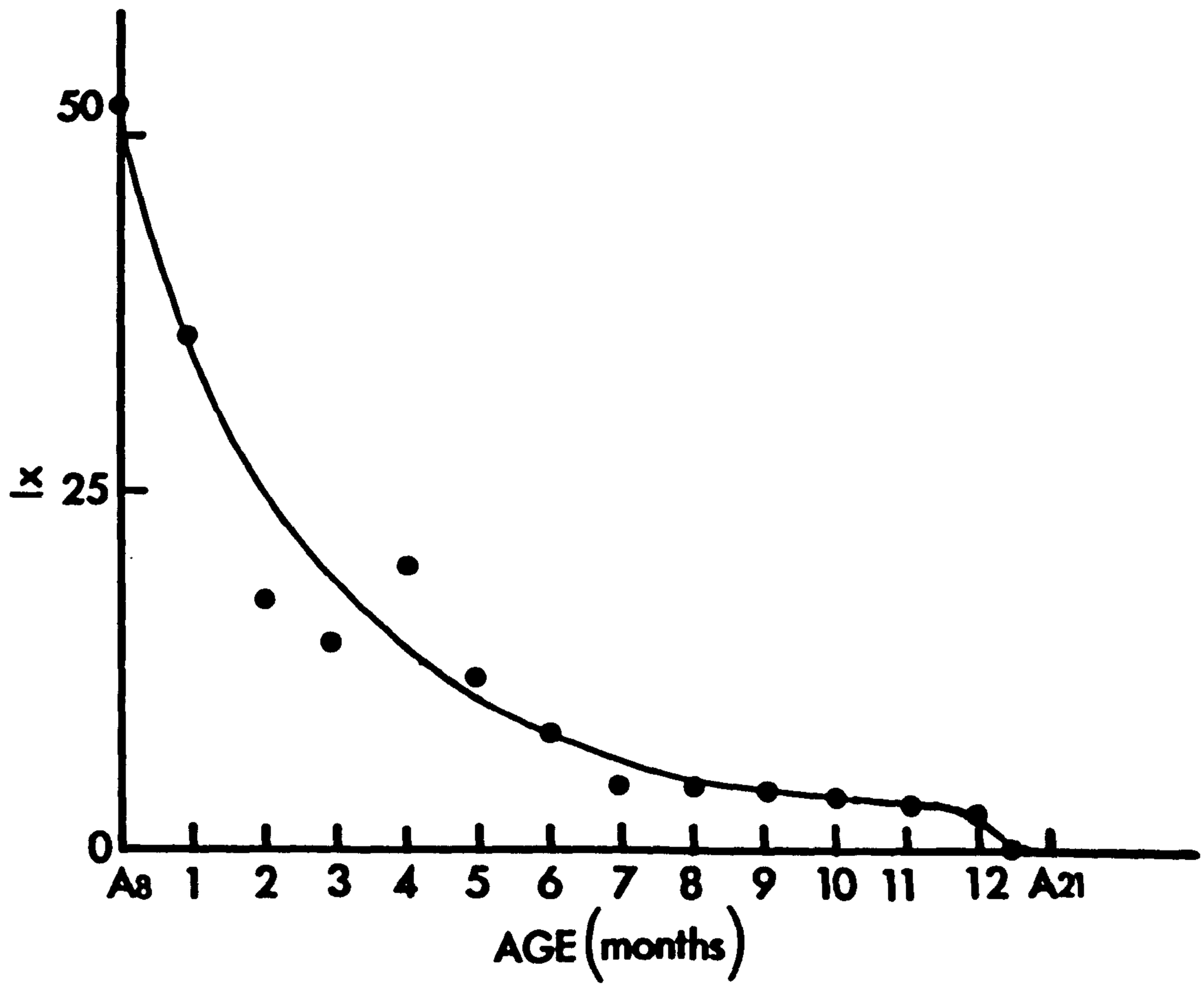

50
25
0
x̄
A8
1
2
3
4
5
6
7
8
9
10
11
12
A21
AGE (months)

FIG. 48 : A semi-logarithmic plot of Lx against time for P.contortus in GENERATION 2.

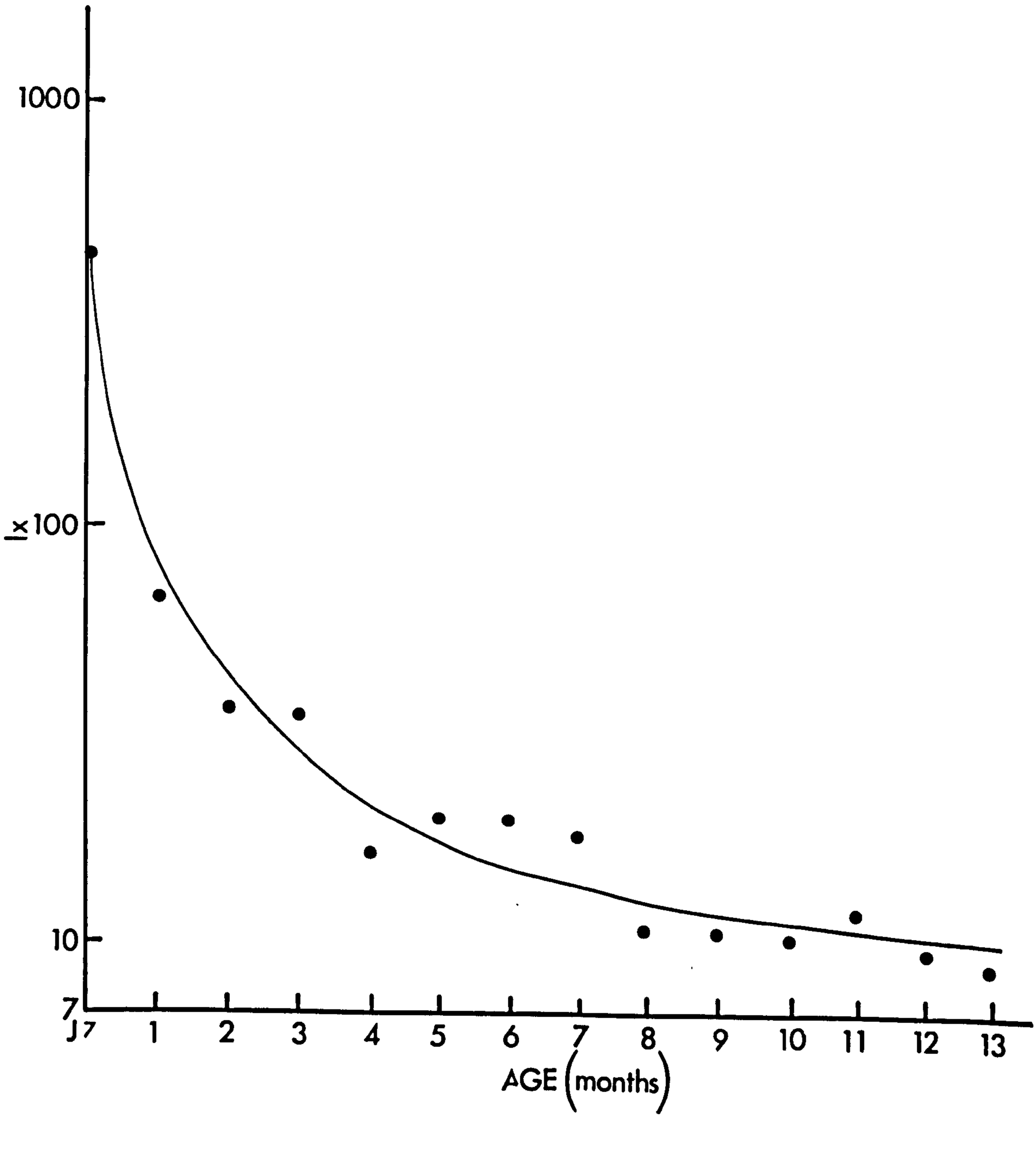

1000
×100
10
7
J7
1
2
3
4
5
6
7
8
9
10
11
12
13
AGE (months)

FIG. 49 : A semi-logarithmic plot of Lx against time for A.fluviatilis in GENERATION 2. The data can be represented either by a single regression line (solid line) or two separate lines (broken line). See text for further explanation.

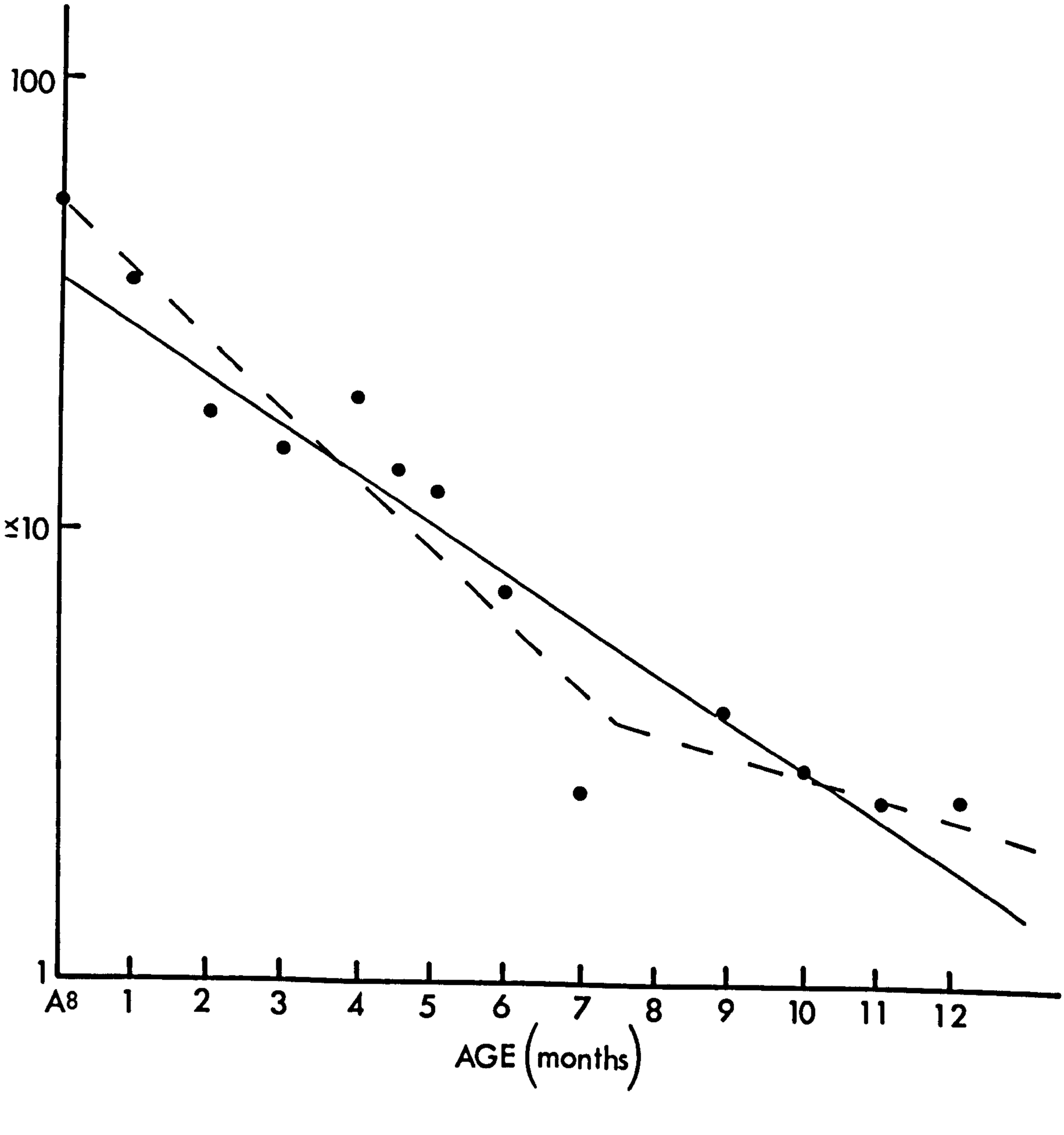

100
≤10
1
A8
1
2
3
4
5
6
7
8
9
10
11
12
AGE (months)

FIG. 50 : A double-logarithmic plot of snail density (Lx) against time for P.contortus in GENERATION 2.

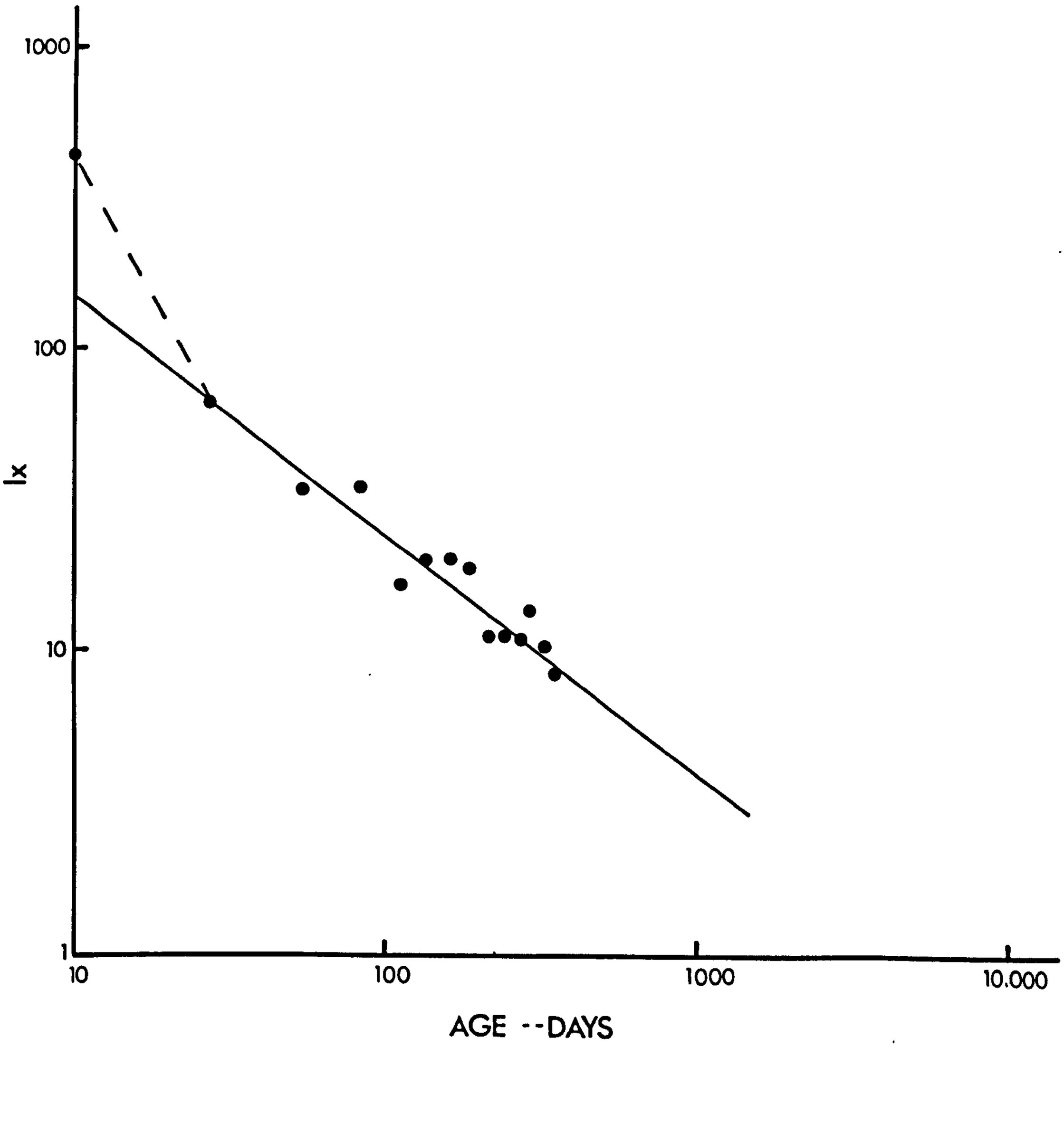

1000
100
10
1
lx
10
100
1000
10.000
AGE --DAYS

FIG. 51 : Phenological information on Ha Mire populations of leeches and flatworms between February, 1970 and July, 1971.

Key

B = breeding period

L = lag between egg laying and the appearence of larvae.

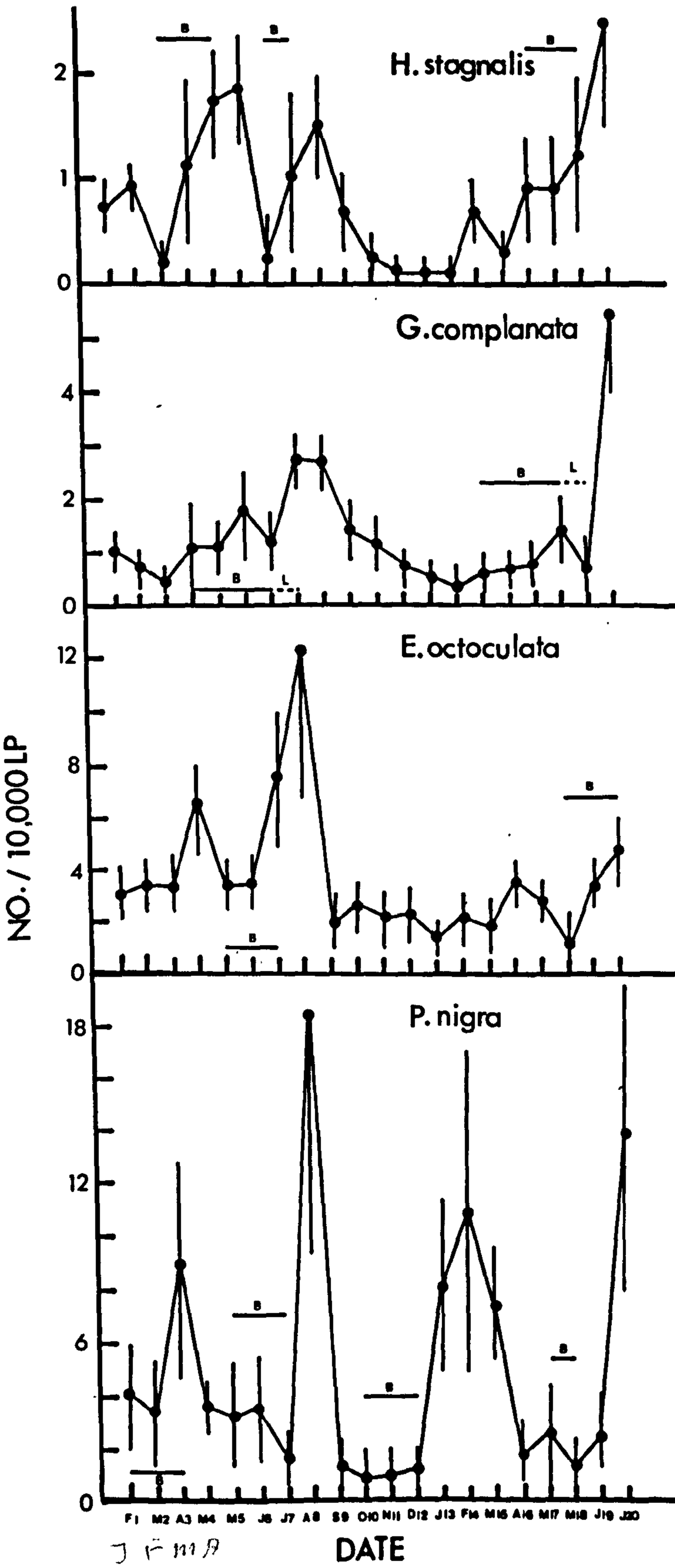

H. stagnalis
G. complanata
E. octoculata
P. nigra
NO. / 10,000 LP
DATE
F1 M2 A3 M4 M5 J6 J7 A8 S9 O10 N11 D12 J13 F14 M15 A16 M17 M18 J19 J20

FIG. 52 : The relationship between shell-free, tissue, dry weight and shell length (AL) for A.fluviatilis in February.

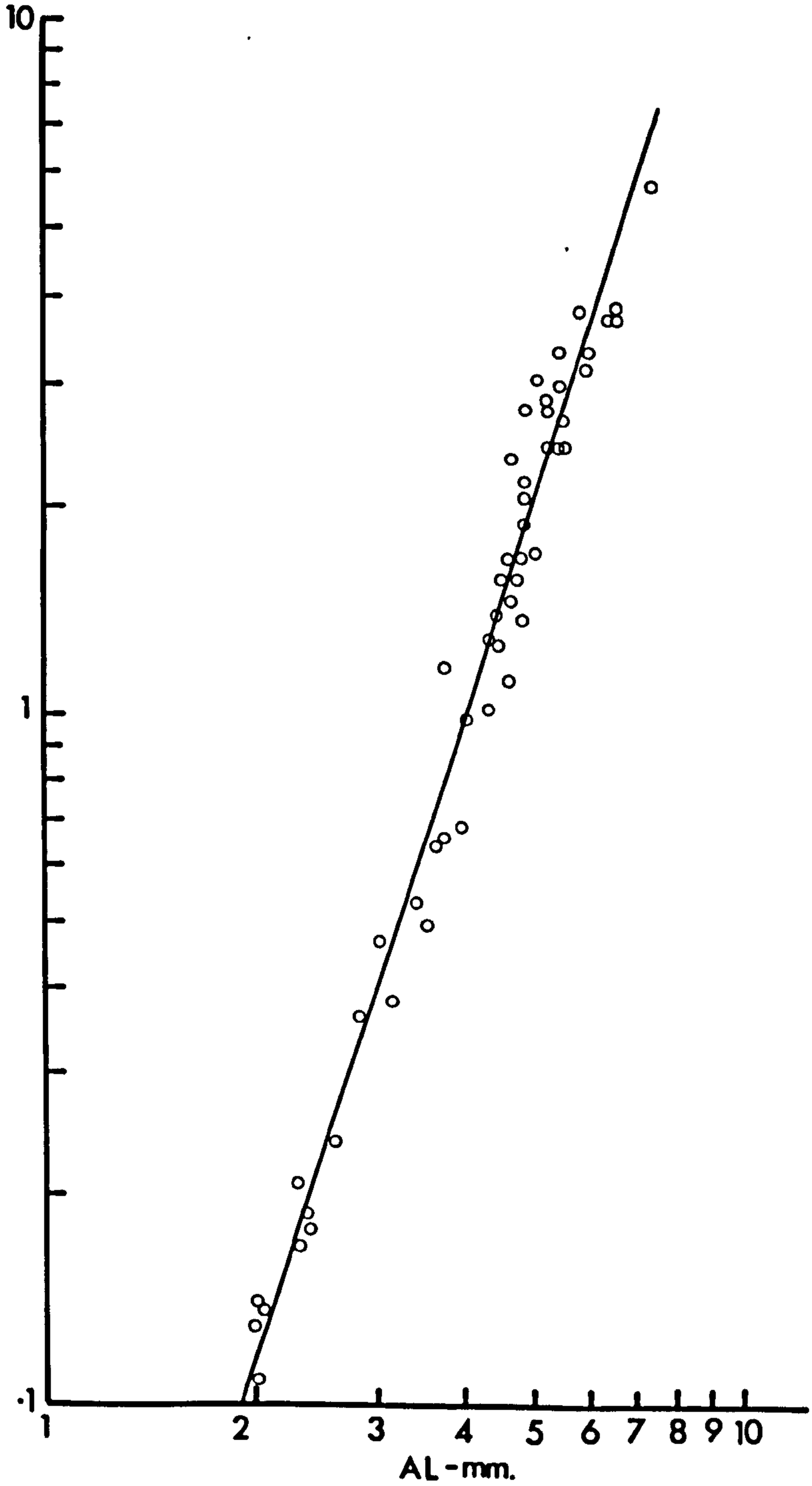

10
1
·1
WEIGHT- mg.
1
2
3
4
5
6
7
8
9
10
AL - mm.

FIG. 53 : The relationship between shell-free, tissue, dry weight and shell length (MD) for P.contortus in February.

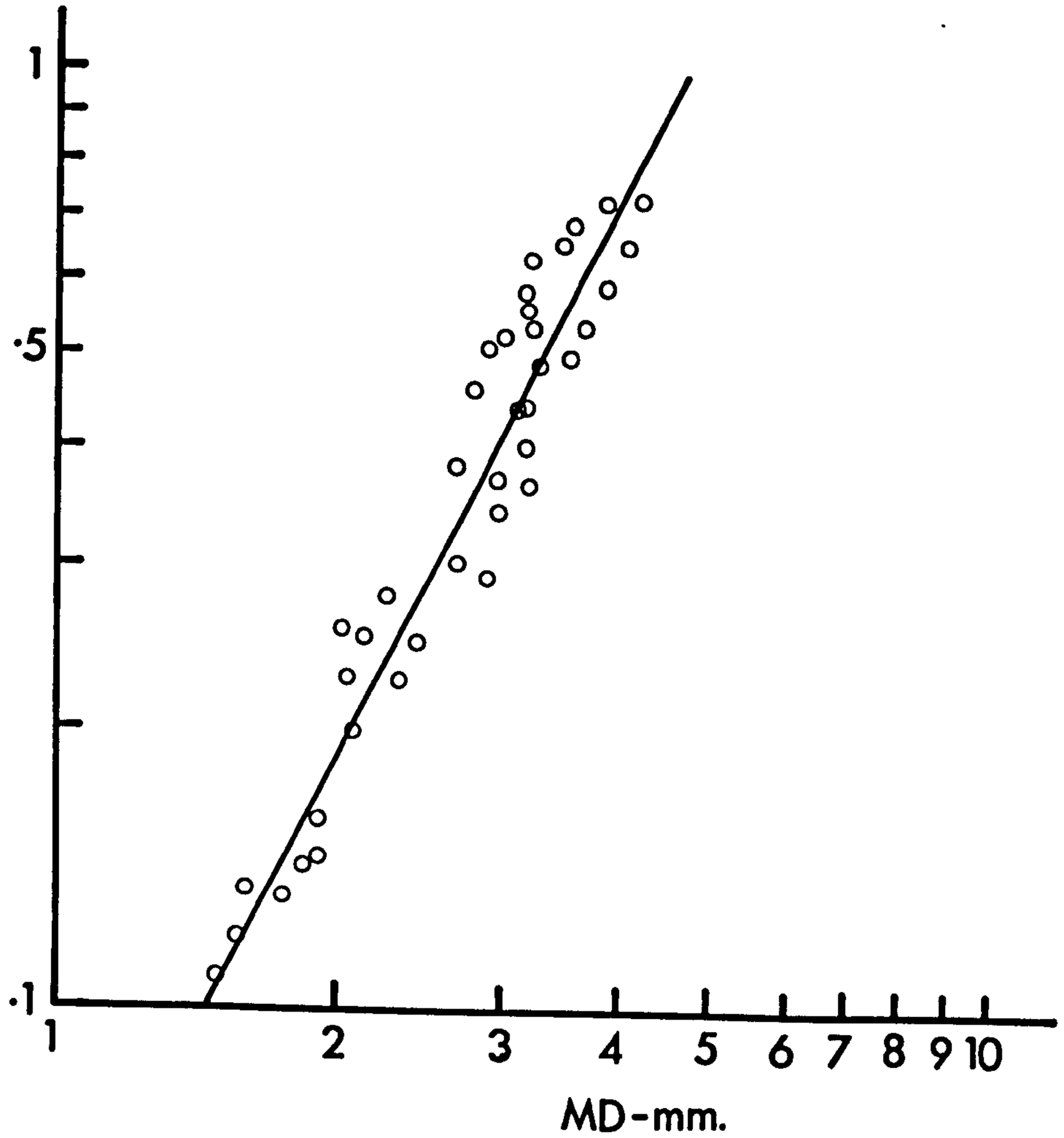

WEIGHT-mg.
1
·5
·1
1
2
3
4
5
6
7
8
9
10
MD-mm.

FIG. 54 : The definitive length-dry weight relationship for A.fluviatilis in February (with 95% confidence limits) and a comparison with values obtained at other times of the year.

Key

1 - September

2 - November

3 - January

4 - April

5 - May

6 - June

7 - July

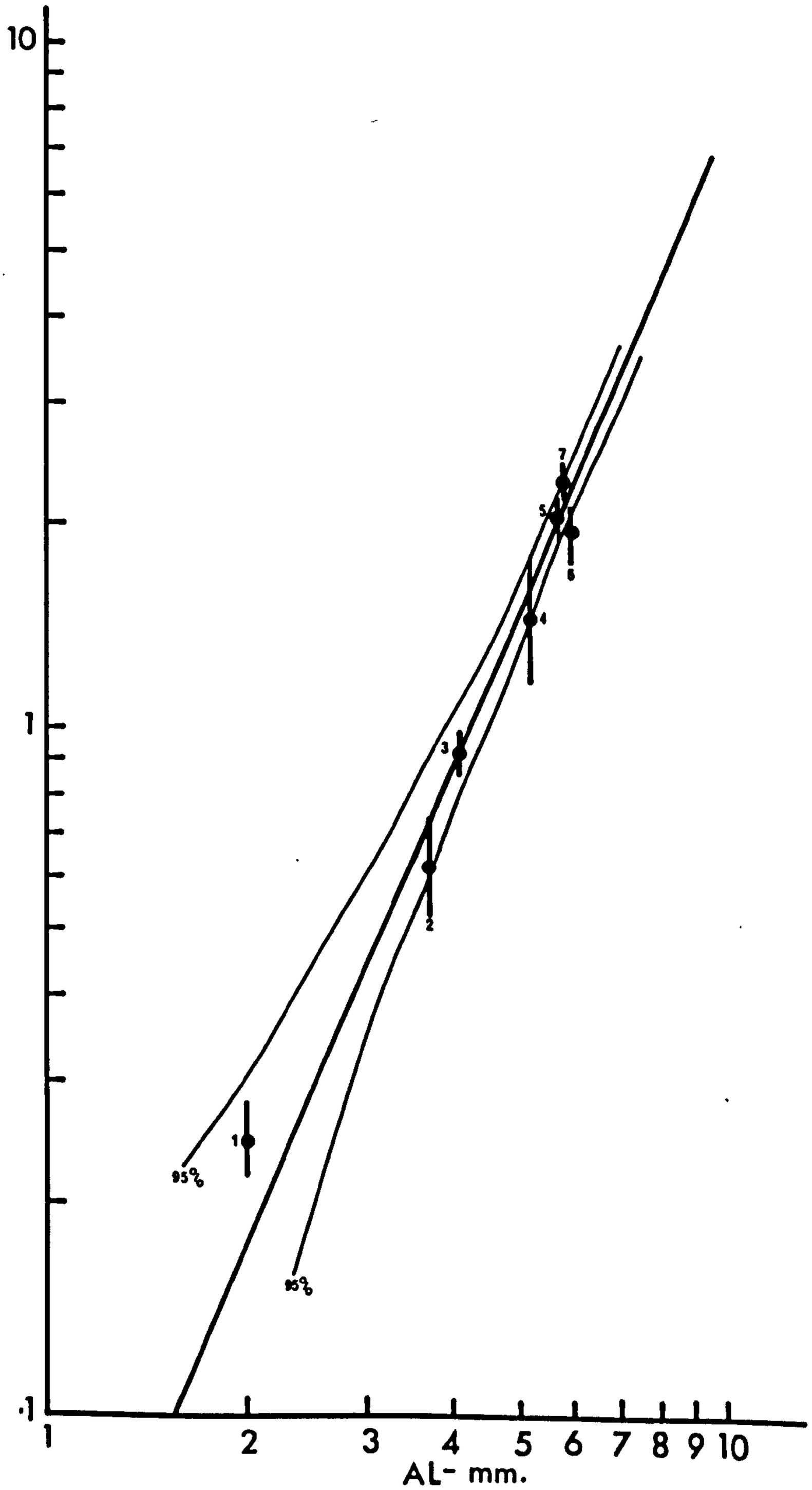

10
1
.1
WEIGHT - mg.
95%
95%
1
2
3
4
5
6
7
1
2
3
4
5
6
7
8
9
10
AL- mm.

FIG. 55 : The definitive length-dry weight relationship for P.contortus in February (with 95% confidence limits) and a comparison with values obtained at other times of the year.

Key

1 - September

2 - November

3 - January

4 - April

5 - May

6 - June

7 - July

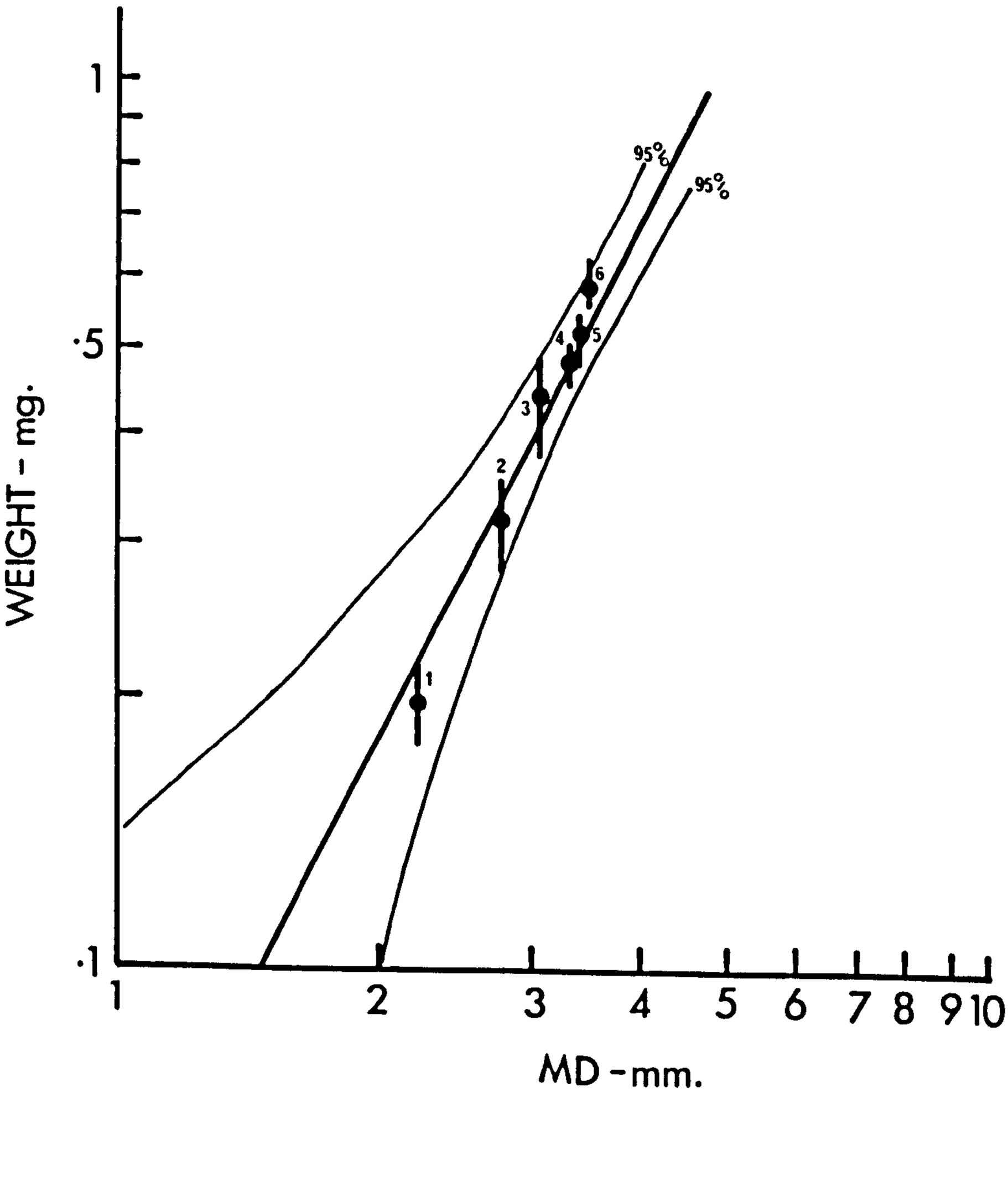

WEIGHT - mg.
1
·5
·1
95%
95%
1
2
3
4
5
6
1
2
3
4
5
6
7
8
9
10
MD - mm.

FIG. 56 : The relationship between shell length and shell dry weight in A.fluviatilis.

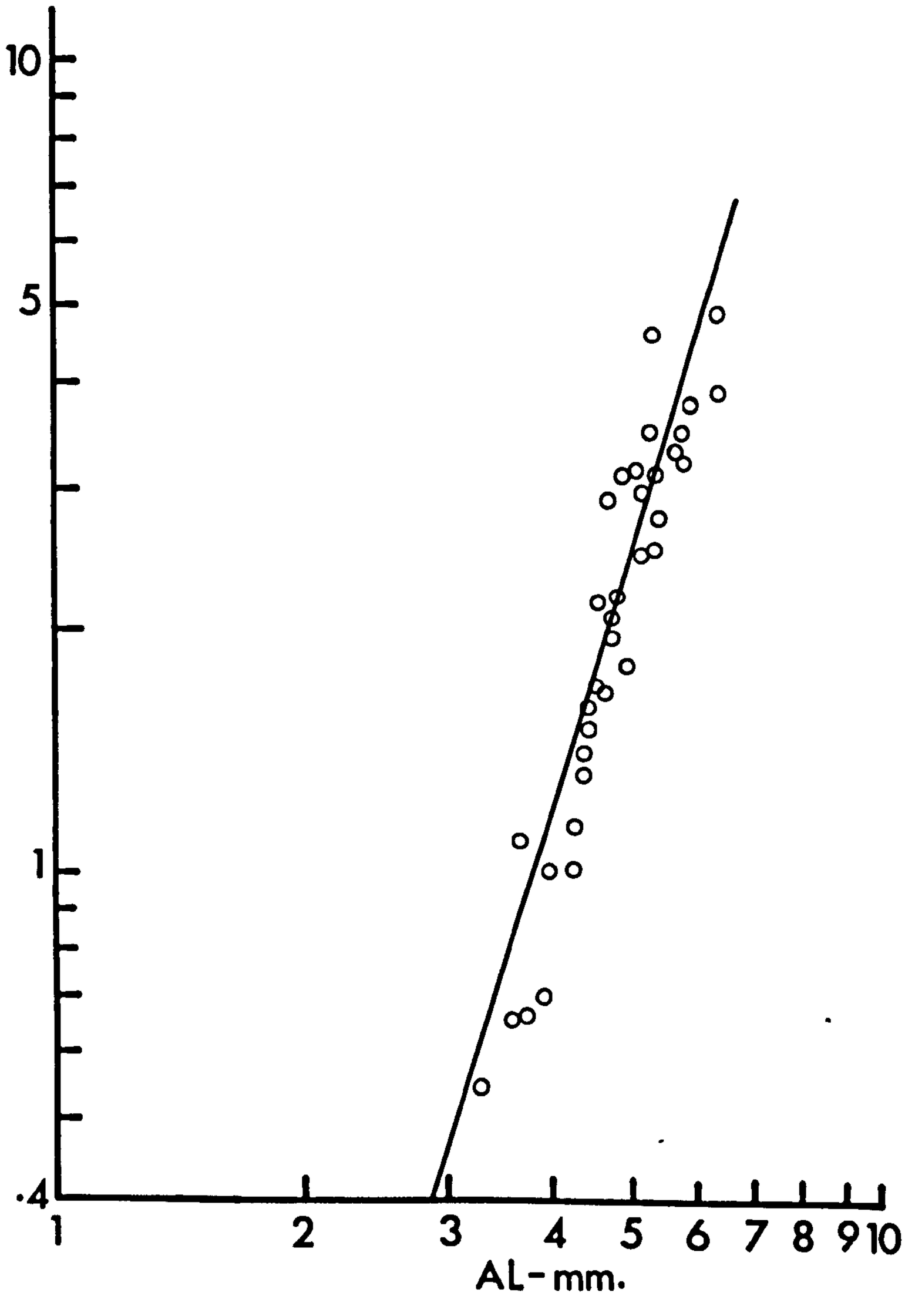

10
5
1
.4
WEIGHT - mg.
1
2
3
4
5
6
7
8
9
10
AL - mm.

FIG. 57 : The relationship between shell length and shell dry weight in P.contortus.

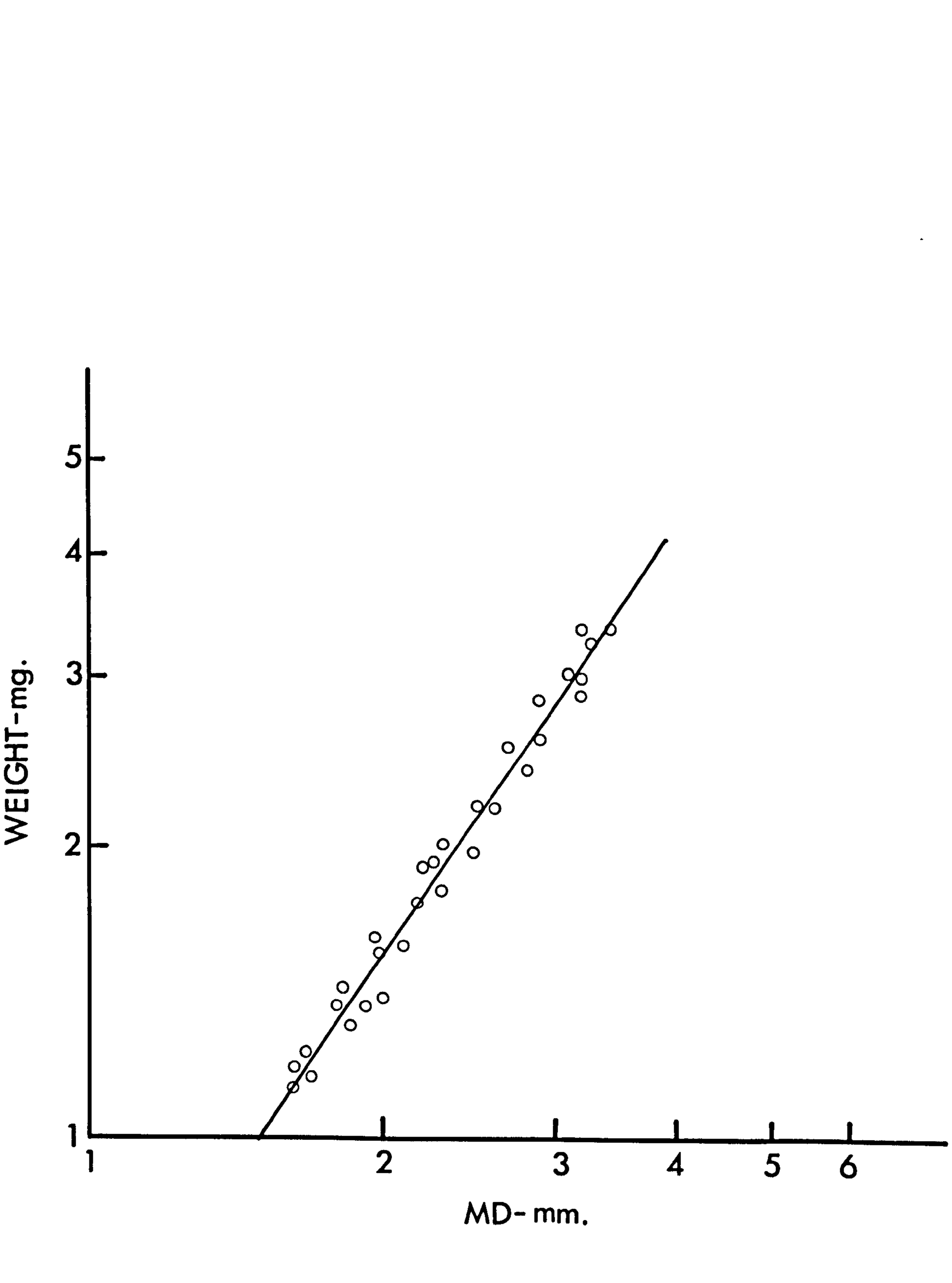

WEIGHT-mg.
5
4
3
2
1
1
2
3
4
5
6
MD- mm.

FIG. 58 : The relationship of various measurable, linear shell-parameters (defined by Hunter, 1961b) to in-tact (A, B, & C) and conceptually uncoiled (D) shell geometries.

Key

A - patelloid case

B - turbinate case

C - discoidal case

AL - aperture length

SL - shell length

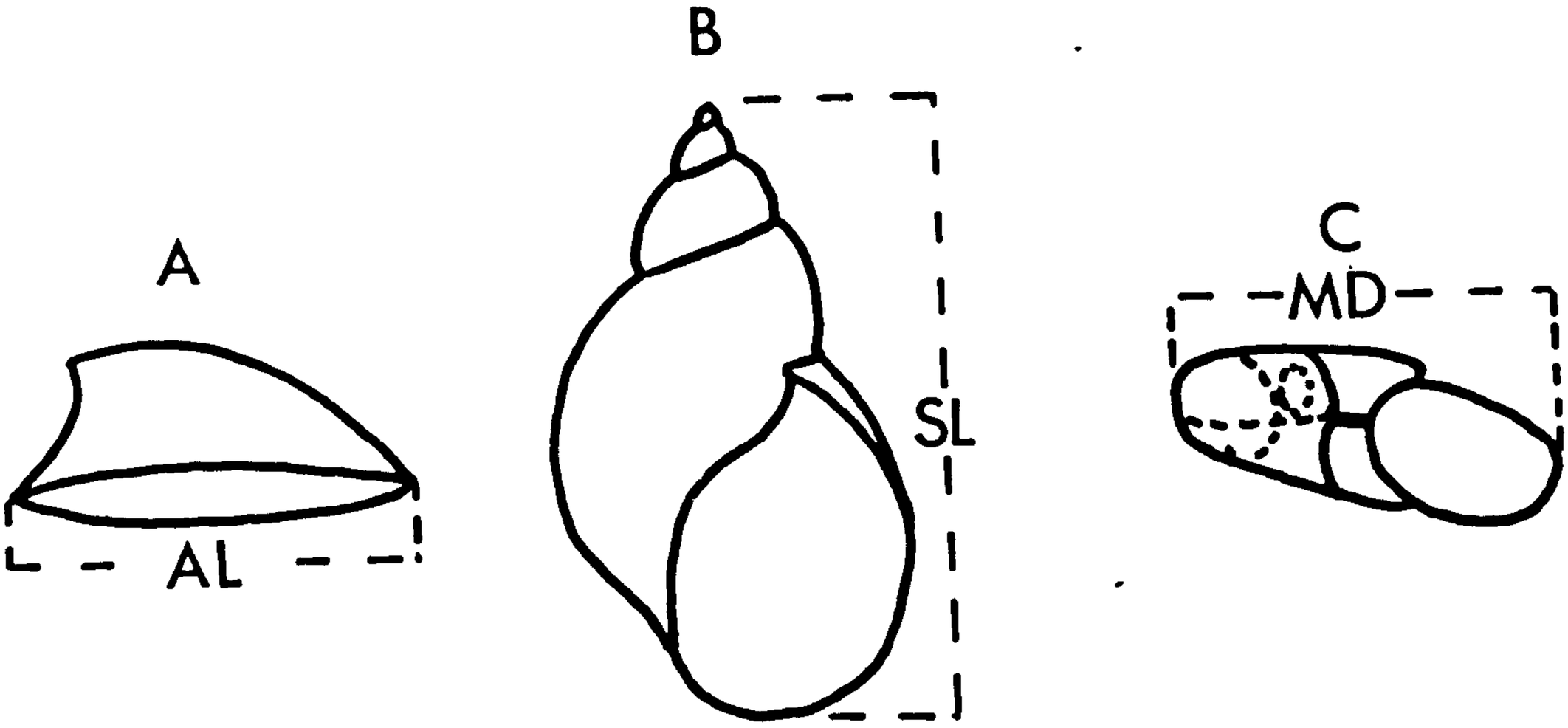
MD - maximum diameter

AL = d

MD(SL) = a + b + c + d

Q = degrees turned by the shell generating vector before the next component of MD or SL cuts the cone

= 180°


B
A
AL
SL
C
MD

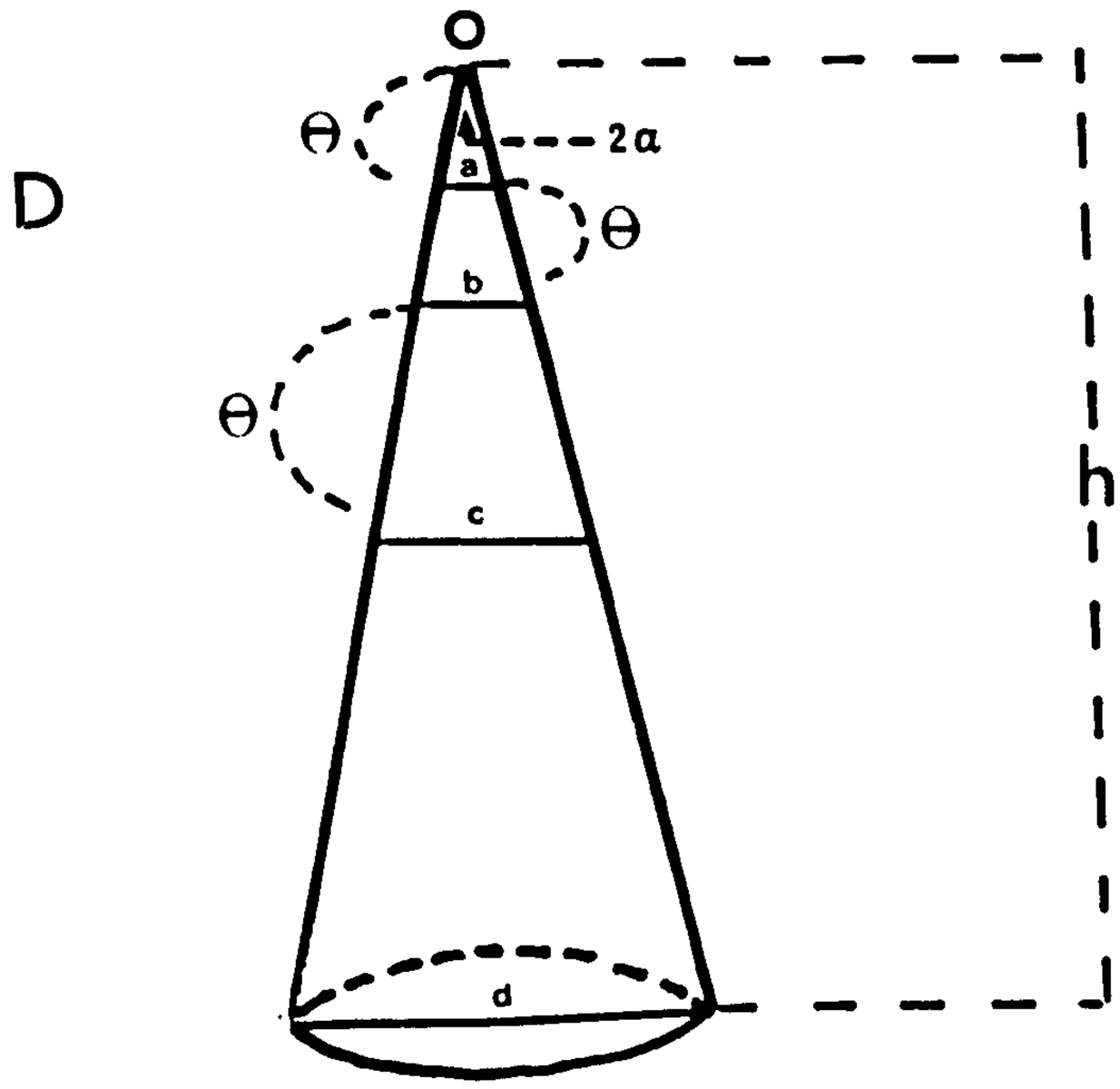

D
O
θ
2α
a
θ
b
θ
c
d
h

FIG. 59 : The size of successive whorl radii (r) and cumulative widths (Σw) plotted against shell turns in P.contortus.

Key

A - the expected behaviour of r in an equiangular spire
B - " " " " r in an archimedes spire (starting from whorl 2)
C - " " " " r in an archimedes spire (starting from whorl 1)
D - " " " " Σw in an equiangular spire

■ - the actual behaviour of r

▲ - the actual behaviour of Σw

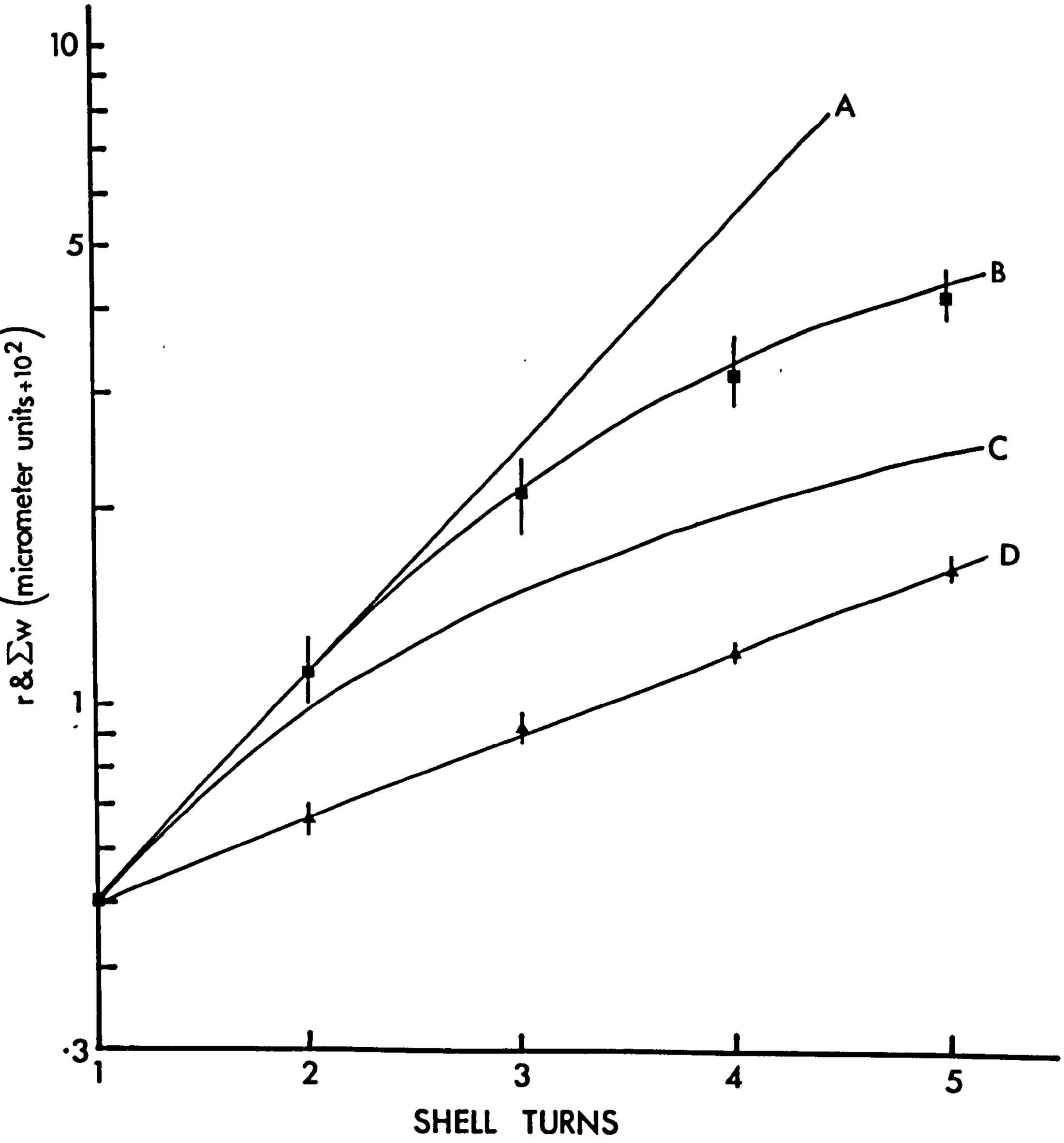

10
5
1
·3
r&Σw (micrometer units+10²)
A
B
C
D
1
2
3
4
5
SHELL TURNS

FIG. 60 : The geometry of the shell of P.contortus.

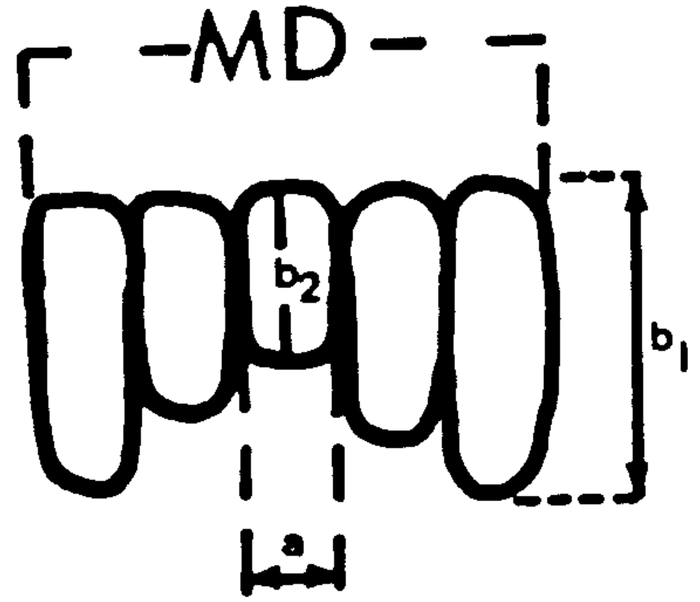
Key

A - a hypothetical cross-section taken from the centre of the shell to its aperture and based on the truncated, ellipsoidal cone model.

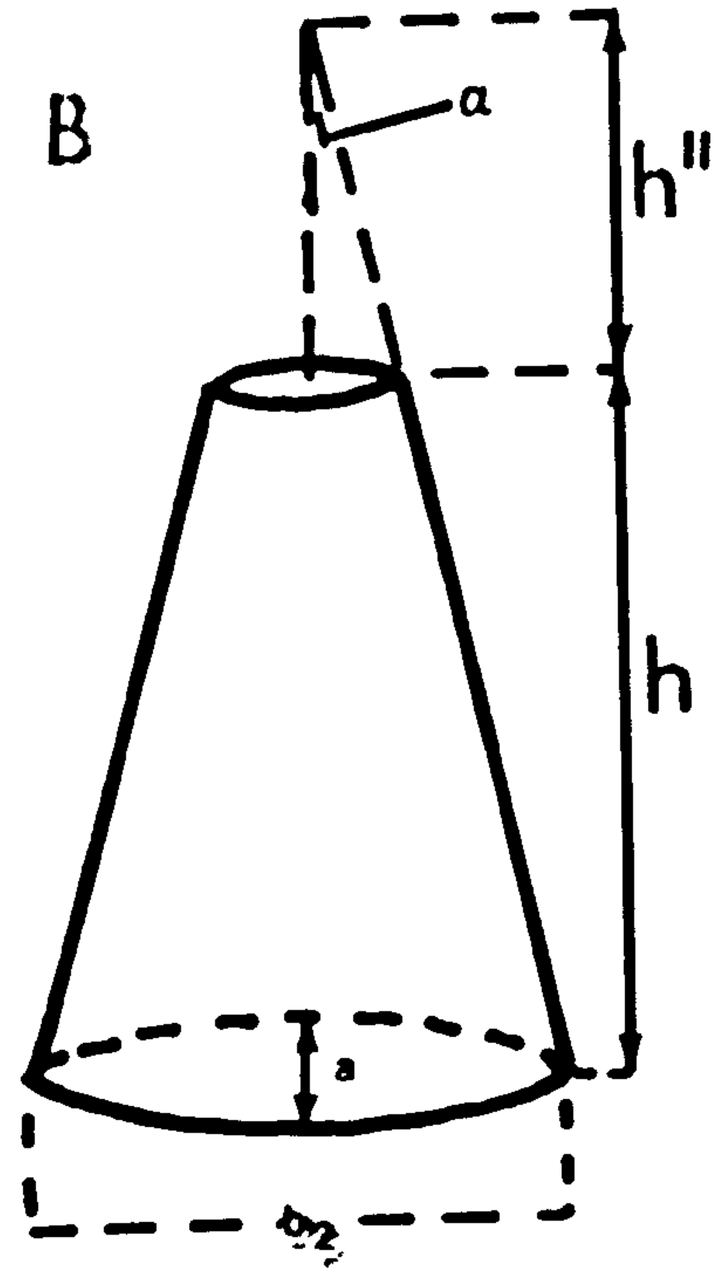
C - actual cross-section of the shell of P.contortus.

B - a conceptually unrolled shell.

A



B



C

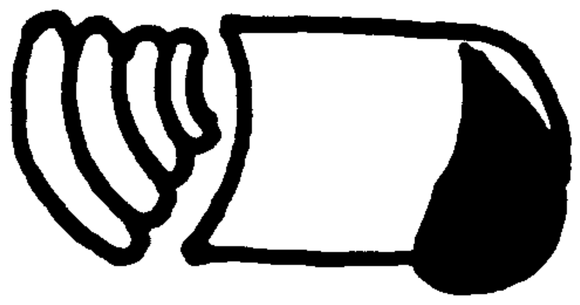


FIG. 61 : Seasonal fluctuations in the caloric density of P.contortus (A) and A.fluviatilis (B)

Key

ovip. - oviposition

a.f.d.w.- ash-free dry weight

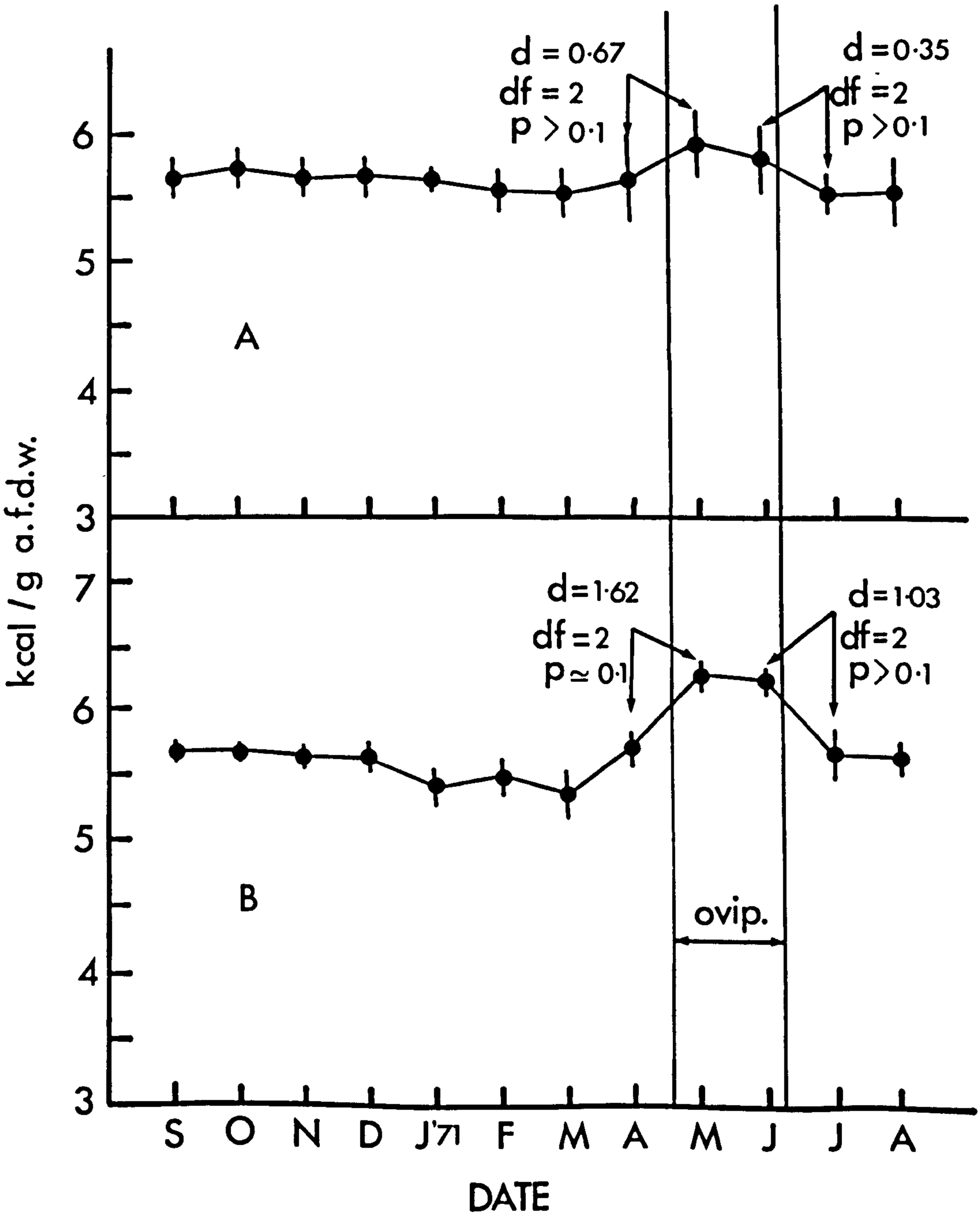

kcal / g a.f.d.w.
7
6
5
4
3
A
d = 0·67
df = 2
p > 0·1
d = 0·35
df = 2
p > 0·1
B
d = 1·62
df = 2
p ≃ 0·1
d = 1·03
df = 2
p > 0·1
ovip.
S
O
N
D
J'71
F
M
A
M
J
J
A
DATE

FIG. 62 : The growth curves of P.contortus as determined in the laboratory under 3 different temperature regimens. Broken lines show the pattern of growth after a temperature change, the extent and direction of which is indicated by the vertical arrows.

Key

▲ - determined in August, 1970.

■ - determined in January, 1971.

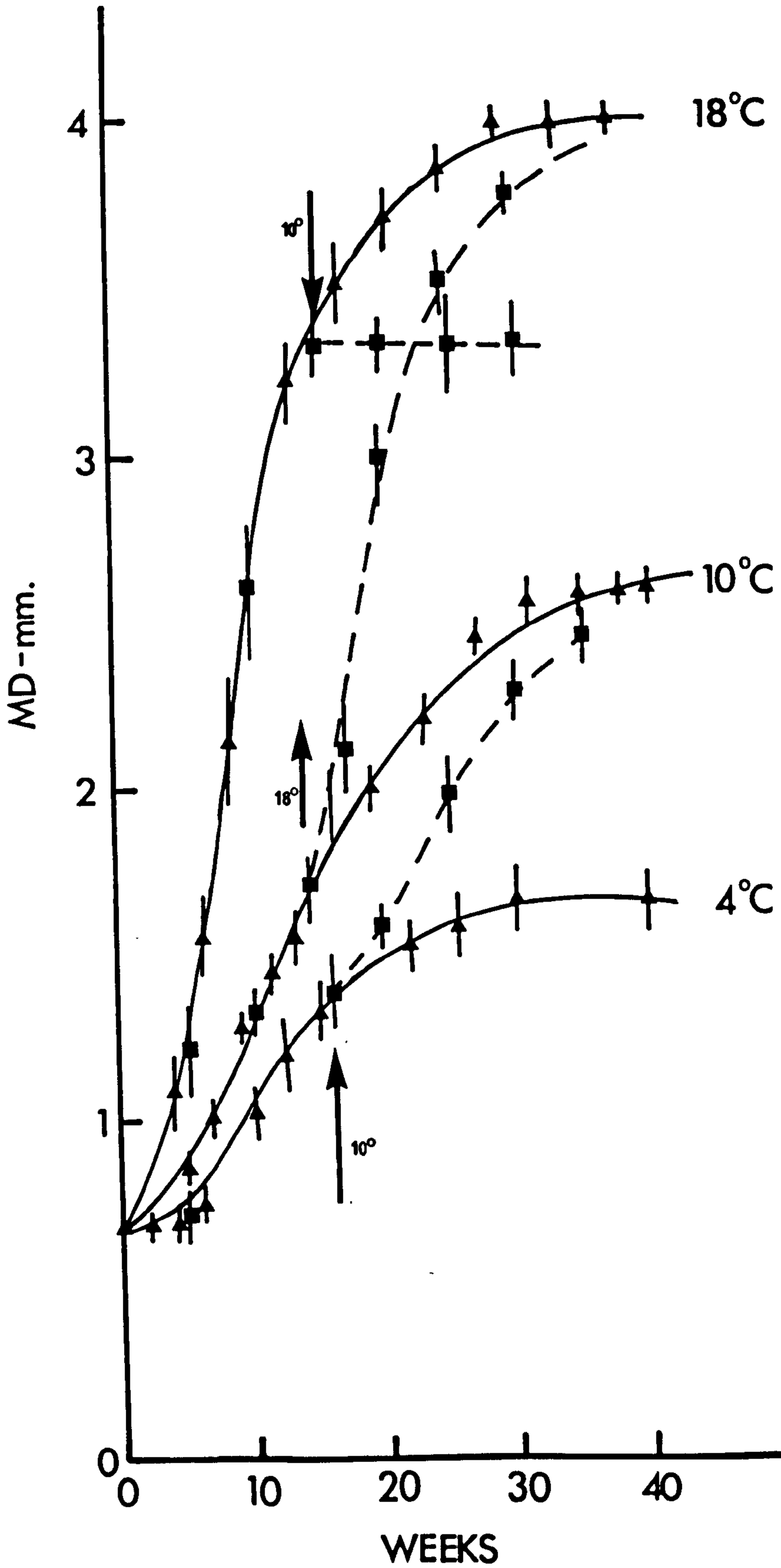

4
3
2
1
0
MD-mm.
18°C
10°C
4°C
16°
18°
10°
0
10
20
30
40
WEEKS

FIG. 63 : A semi-logarithmic plot showing the relationship between log. MD and time in P.contortus. The data are derived from FIG. 62. L_∞ represents a crude estimation of the asymptotic size.

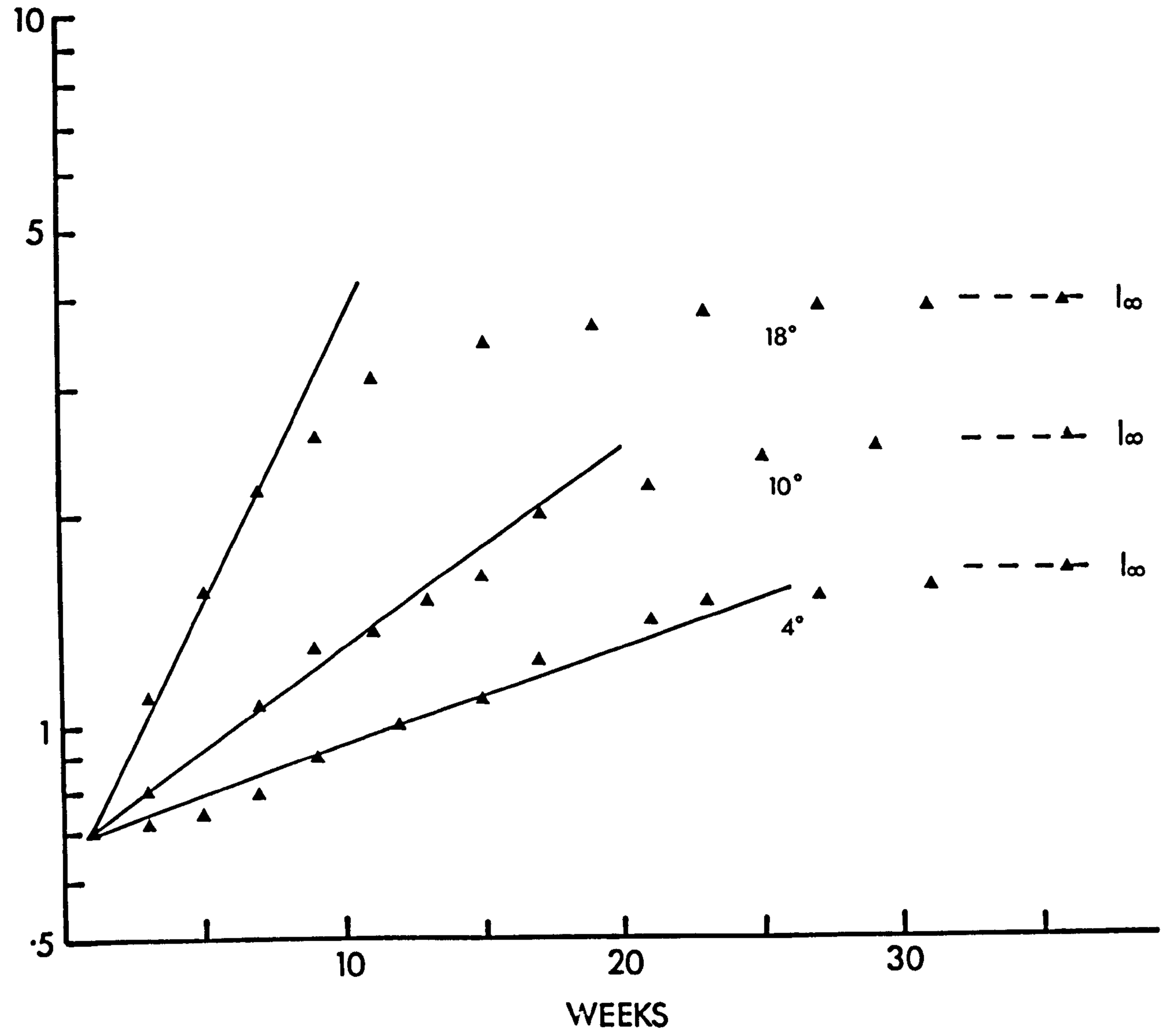
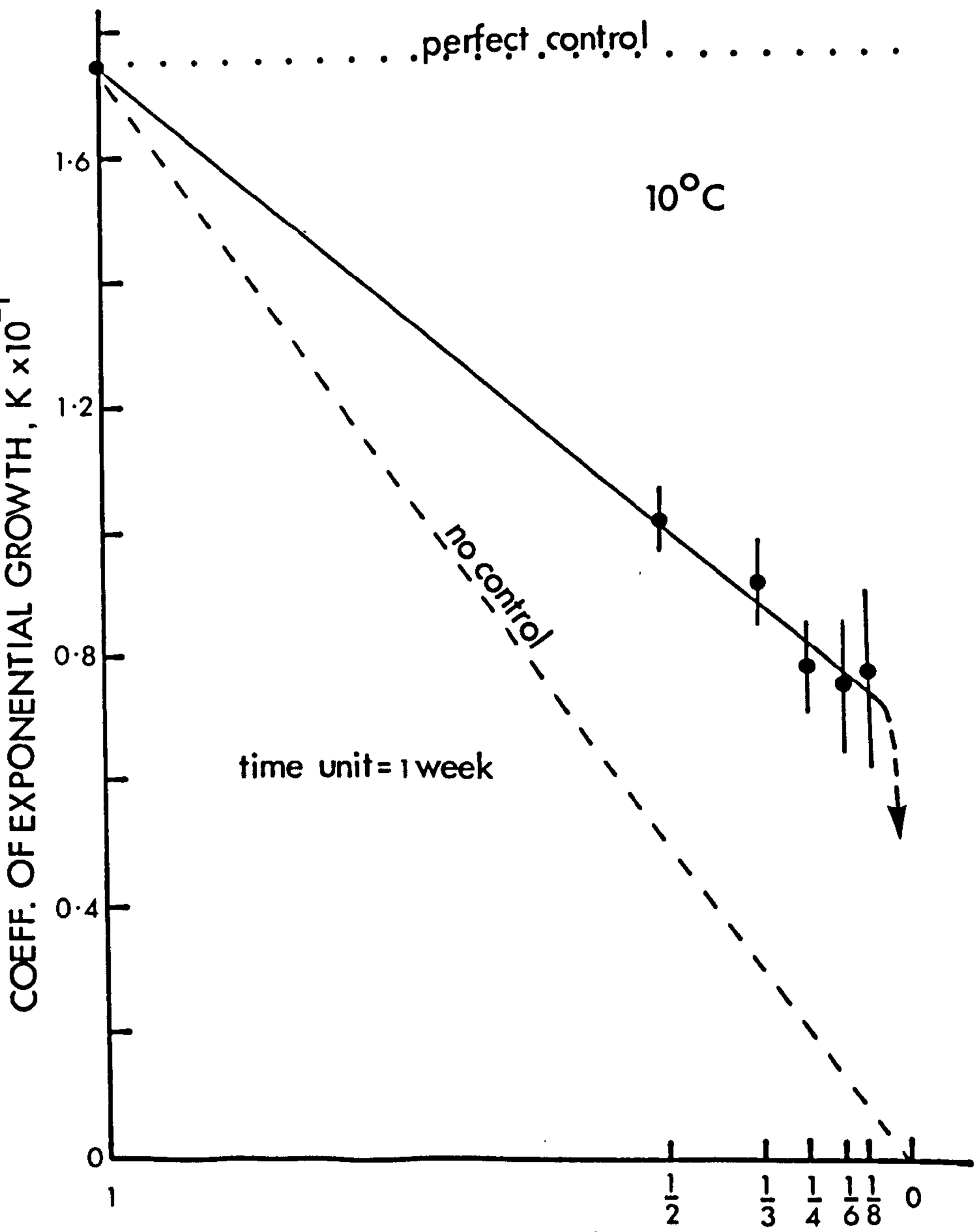

10
5
1
·5
MD-mm.
18°
10°
4°
I_∞
I_∞
I_∞
10
20
30
WEEKS

FIG. 64 : The relationship between the coefficient of exponential growth at 10°C (caloric) and the fractional amount of time (in days) snails were exposed to food. The straight, broken line indicates growth rate coefficients which would be expected if snails grow at a rate simply proportional to the fraction of time they were exposed to food. The dotted line indicates the condition of perfect control and the solid line indicates the actual response.



TEMPORAL FOOD AVAILIBILITY

FIG. 65 : A systems representation of energy flow within the individual, (modified from Hubbell, 1971, and represented in the complex frequency (S) domain).

Key

AG(S) = actual growth rate
DG(S) = desired growth rate
KDG = desired growth rate generating subsystem
KAE = error correction constant of anabolism
KRE = error correction constant of catabolism
KAP = size component constant of anabolism
KRP = size component constant of catabolism

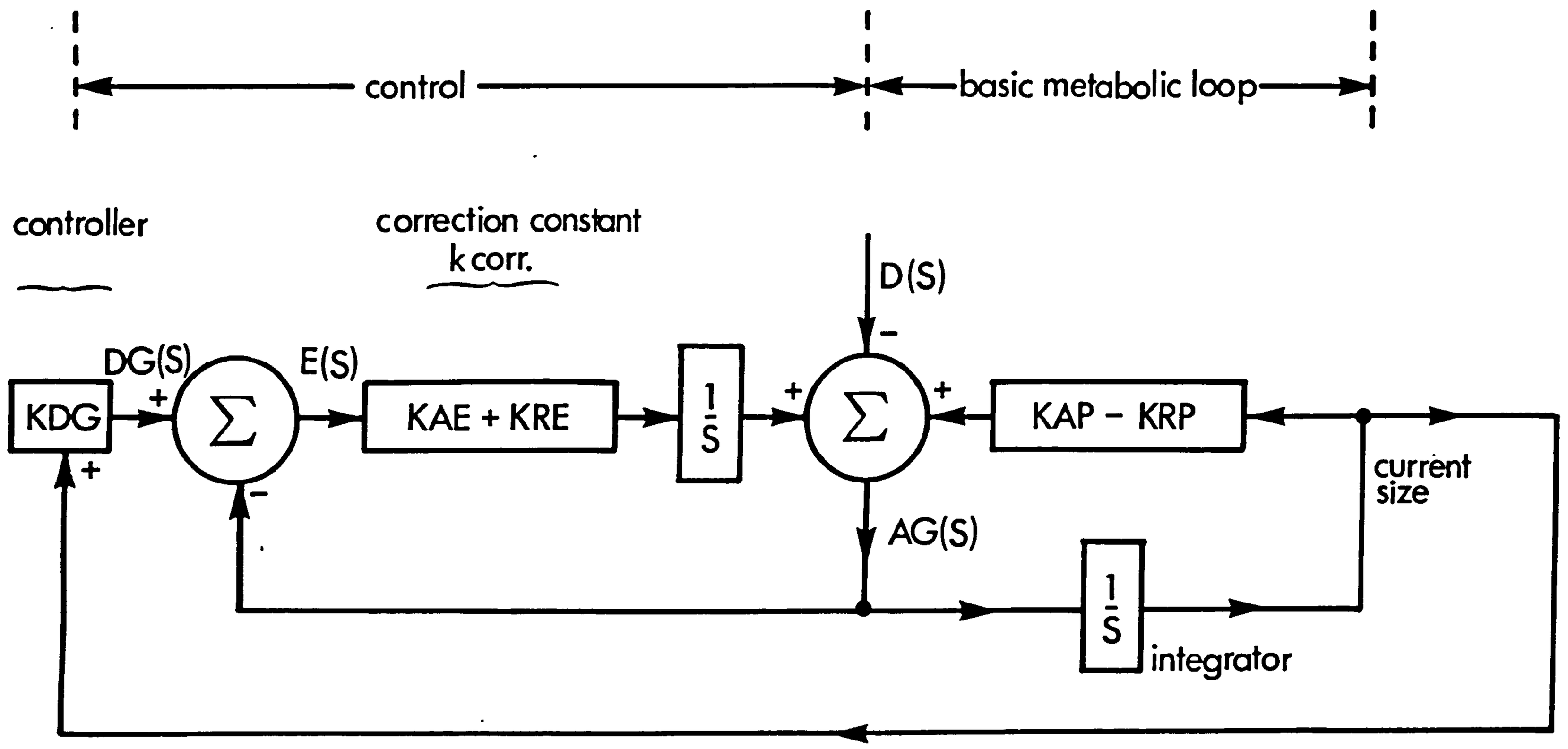

control
basic metabolic loop
controller
correction constant
k corr.
D(S)
DG(S)
E(S)
KDG
KAE + KRE
KAP – KRP
AG(S)
current
size
integrator

FIG. 66 : Plots showing the relationship between the "need for control", (E(S)) and observed control in P. contortus (A) and A.vulgare (B). Data for the isopod were derived from Hubbell (1971).

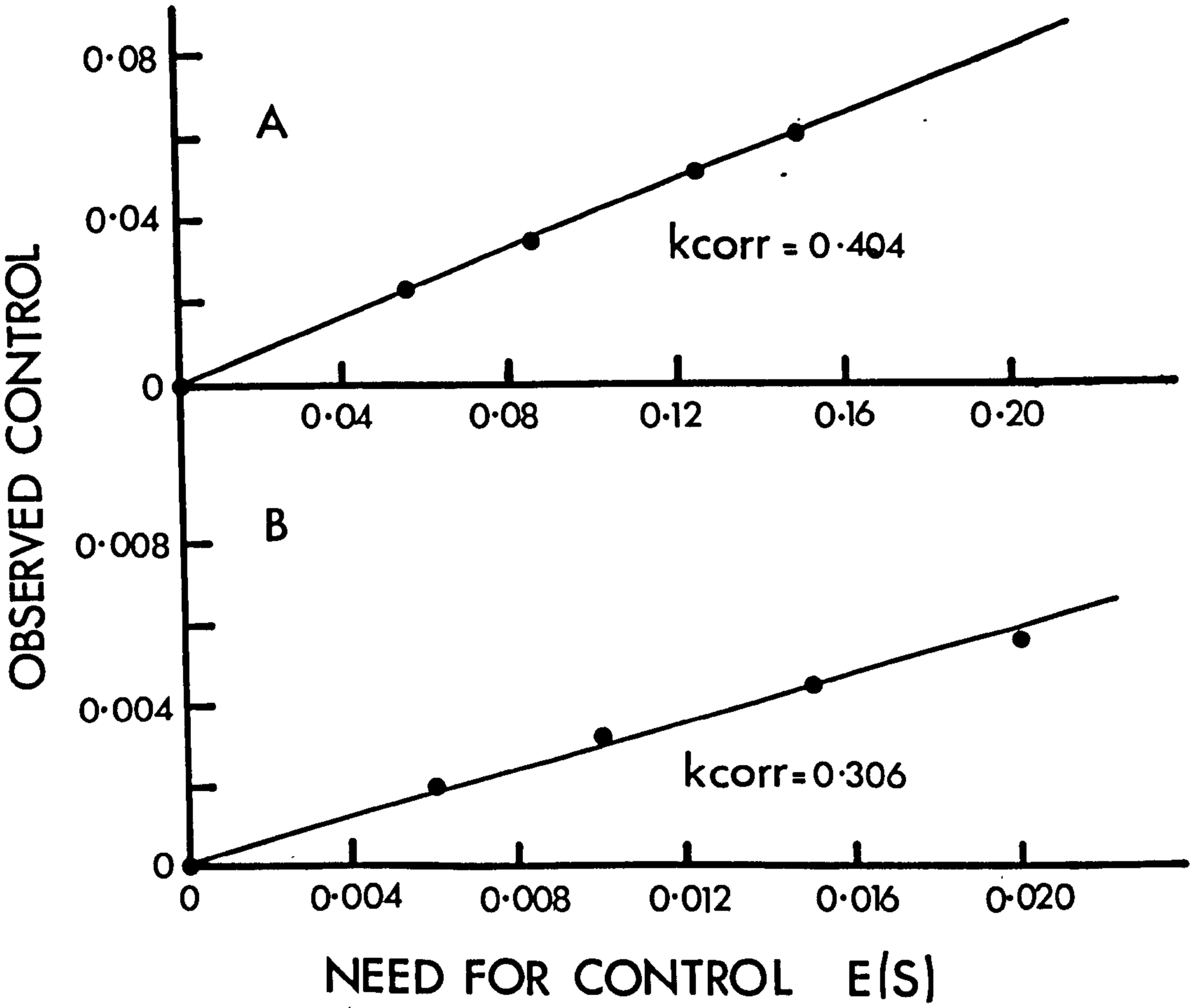

A
0·08
0·04
0
kcorr = 0·404
0·04
0·08
0·12
0·16
0·20
B
0·008
0·004
0
kcorr=0·306
0
0·004
0·008
0·012
0·016
0·020
OBSERVED CONTROL
NEED FOR CONTROL E(S)

FIG. 67 : The coefficient of exponential growth (caloric) in cohorts of P.contortus subjected to various, prior nutritional histories (i.e. 1 - 1/8 temporal food availability), but then transferred to a continuous food regimen :

A - over the first week after transference.

B - " " second " " ".

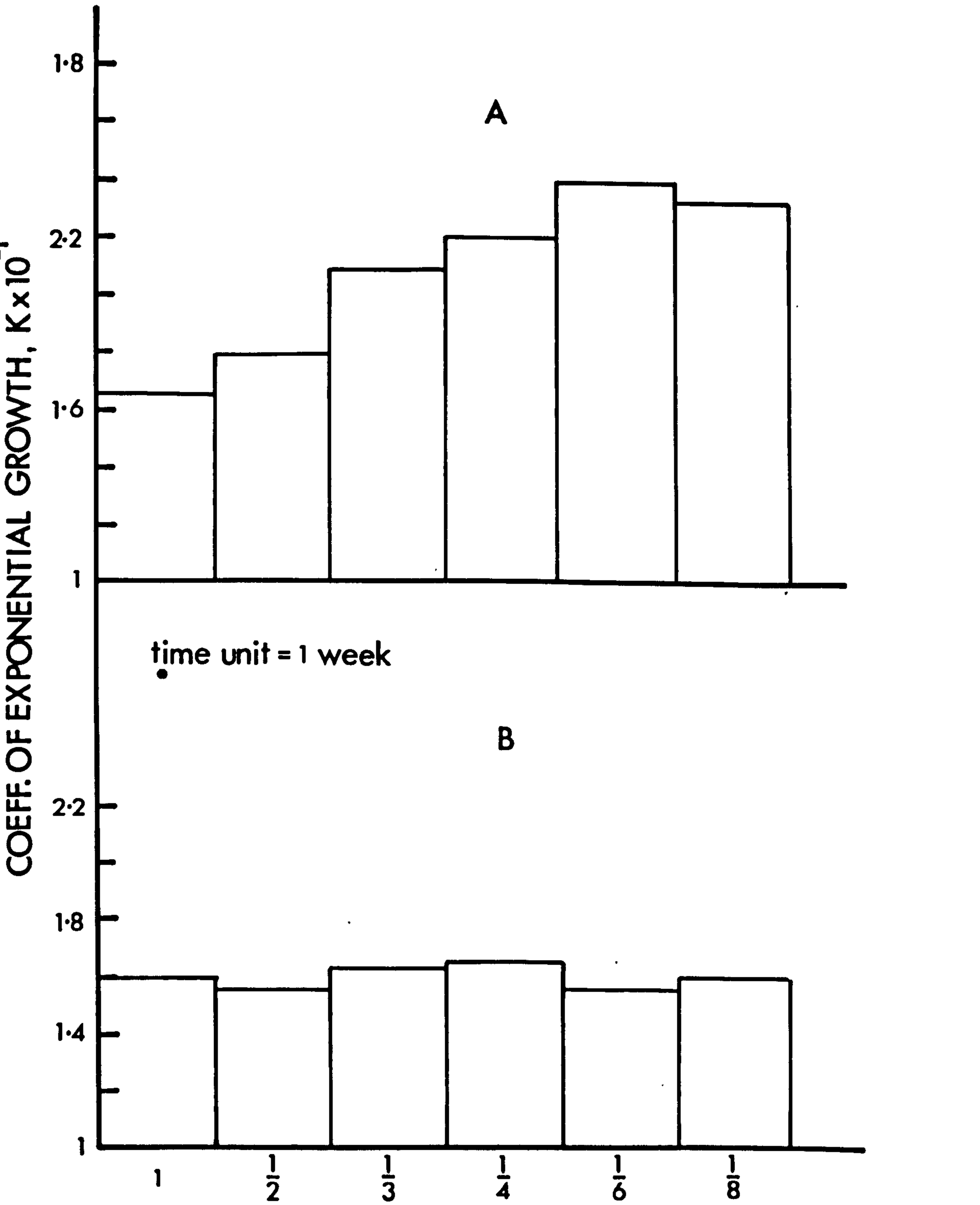

A
1·8
2·2
1·6
1
time unit = 1 week
B
2·2
1·8
1·4
1
1
1/2
1/3
1/4
1/6
1/8
COEFF. OF EXPONENTIAL GROWTH, K x 10⁻¹
TEMPORAL FOOD AVAILIBILITY - DAYS

FIG. 68 : Growth curves of individuals in the GENERATION 2, population of A.fluviatilis on Ha Mire shore, expressed in terms of length (A), ash-free dry weight (B) and potential energy (C).

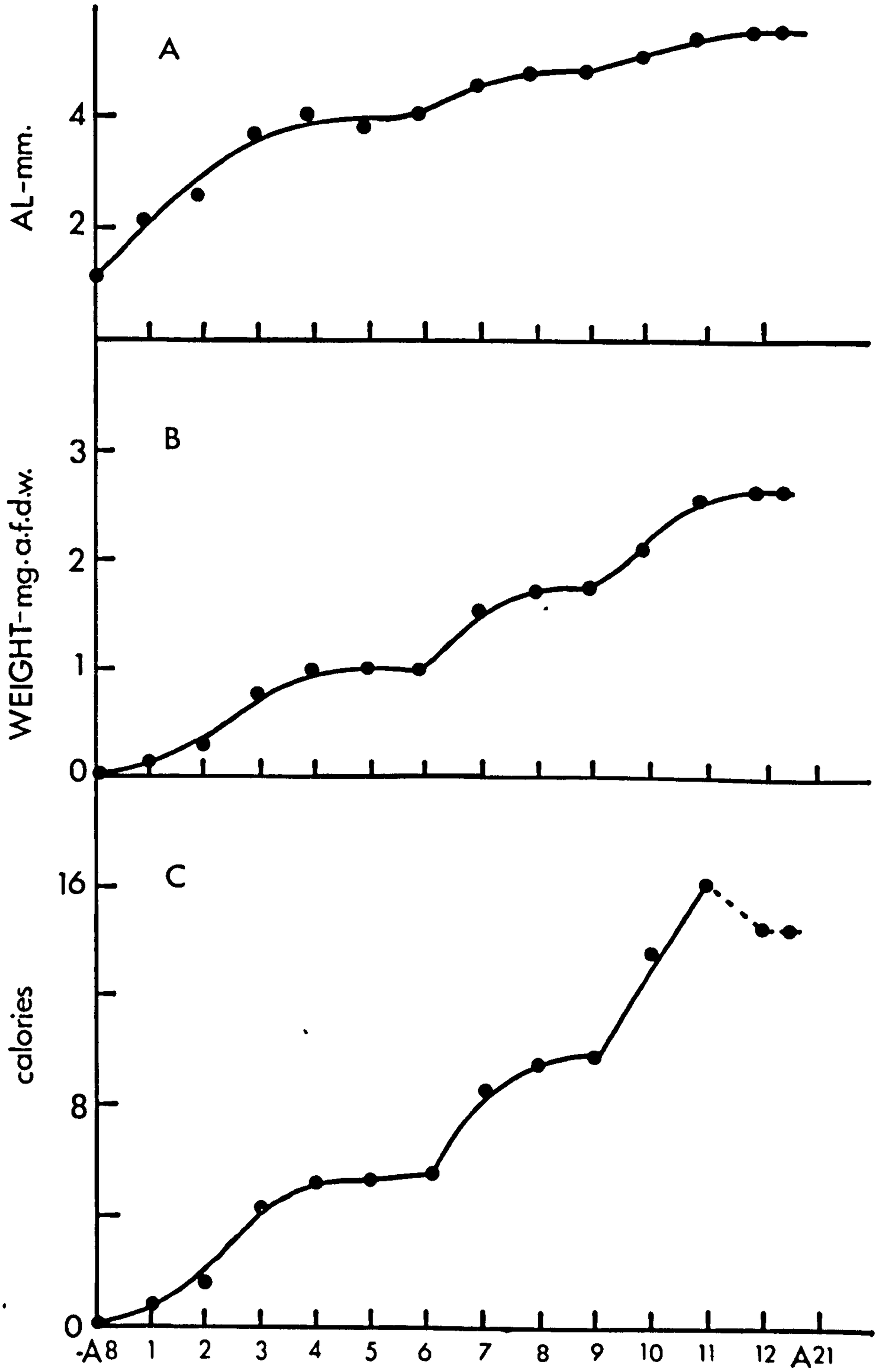

A
AL-mm.
4
2
B
WEIGHT-mg.a.f.d.w.
3
2
1
0
C
calories
16
8
0
-A8
1
2
3
4
5
6
7
8
9
10
11
12
A21
AGE - months

FIG. 69 : Growth curves of individuals in the GENERATION 2, population of P.contortus on Ha Mire shore, expressed in terms of length (A), ash-free dry weight (B) and potential energy (C).

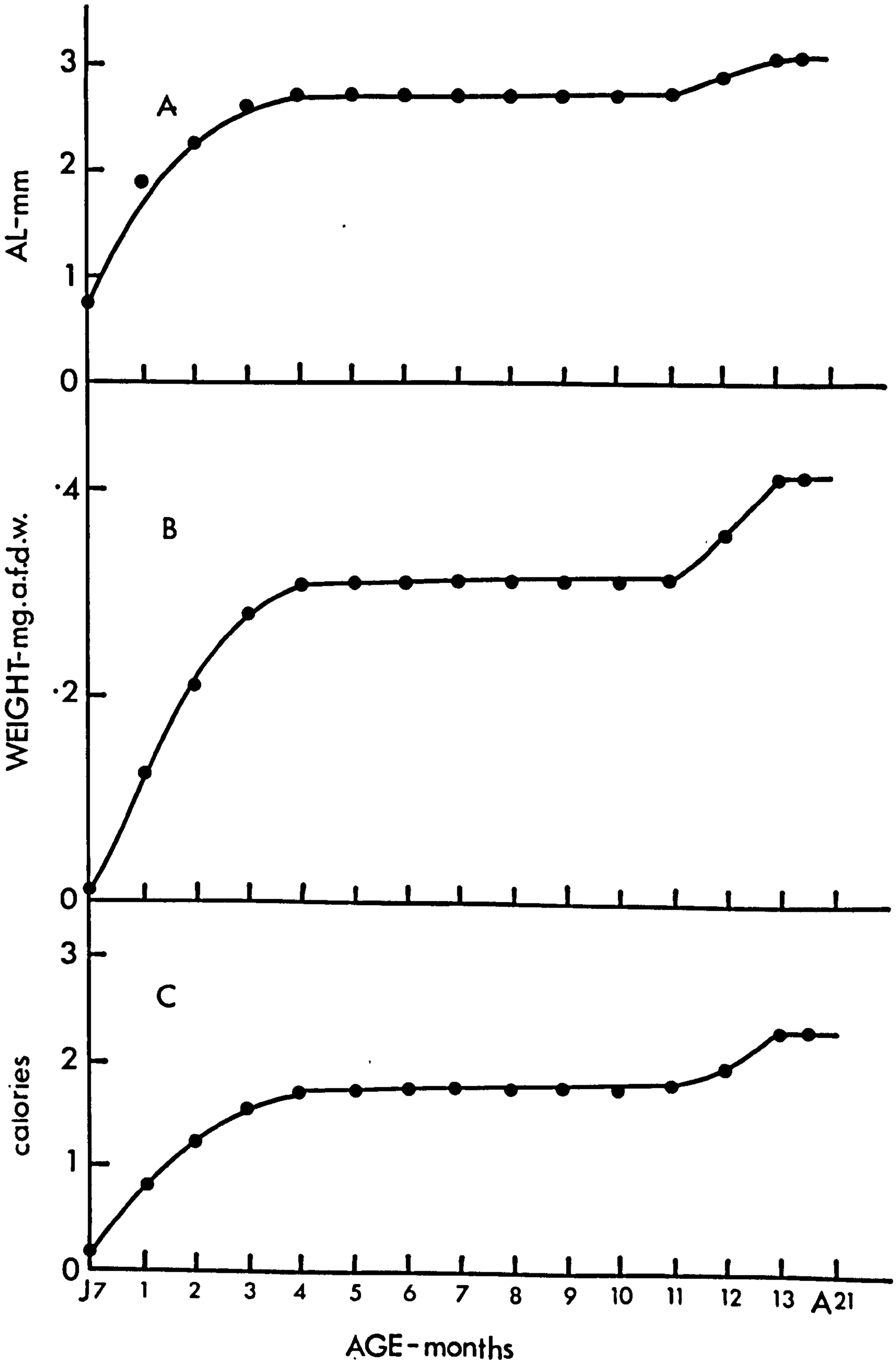

AL-mm
3
2
1
0
A
WEIGHT-mg.a.f.d.w.
·4
·2
0
B
calories
3
2
1
0
C
J7
1
2
3
4
5
6
7
8
9
10
11
12
13
A21
AGE-months

FIG. 70 : A cross-section of the apparatus used for investigating food-preferences in snails.

Key

1 - plankton net

2 - perspex, cylindrical chamber (dia. = 10cm.)

3 + 6 - filter-paper semi-circles carrying the food-choices

4 - enamel tank

5 - polythene washer

7 - baffle around the aerator

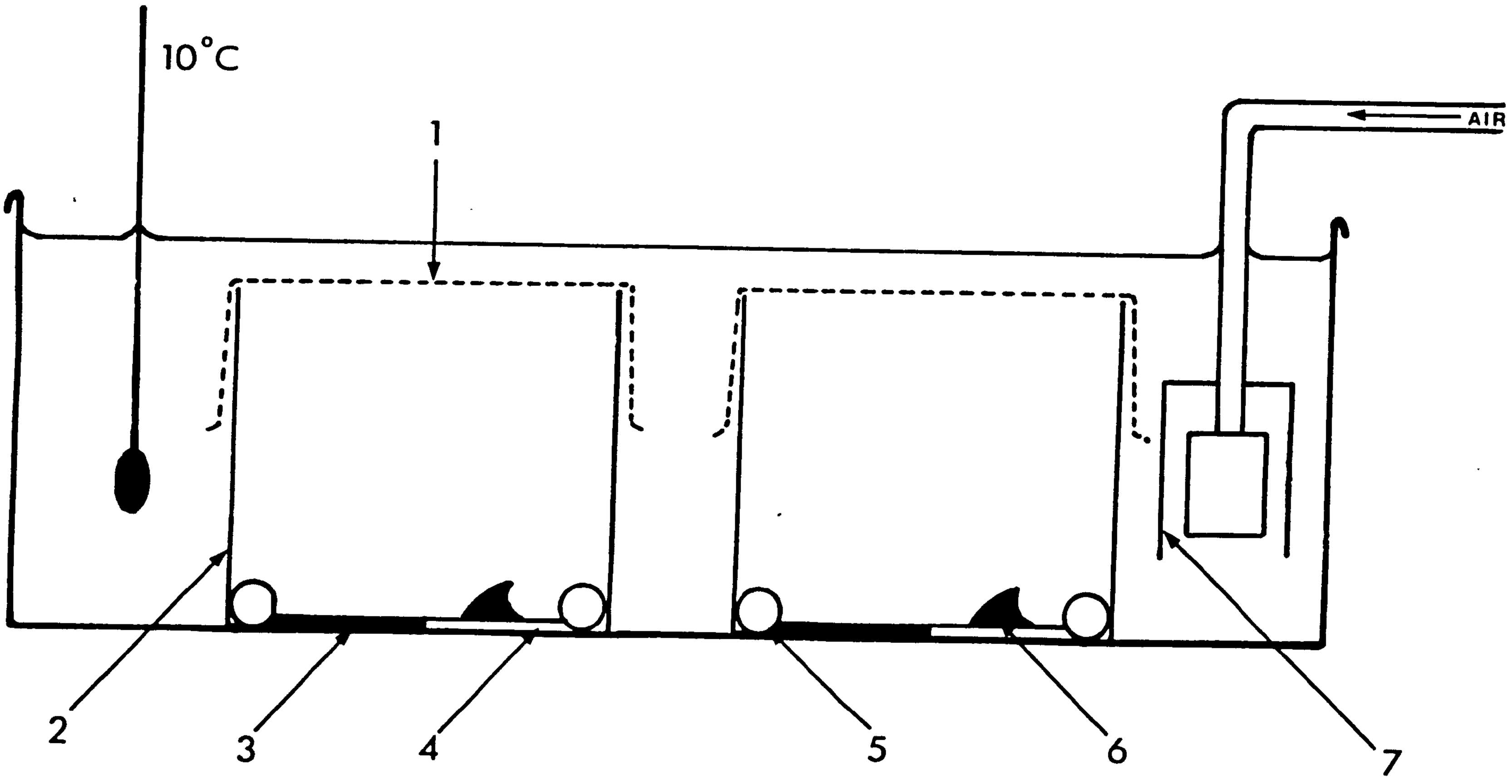

10°C
1
AIR
2
3
4
5
6
7

FIG. 71 : The relationship between the relative abundance (%) of algal types found on the sides of snail-bearing stones (Ssn) and in snails' guts.

Key

△ - diatoms

□ - blue-green algae

○ - green algae and rest

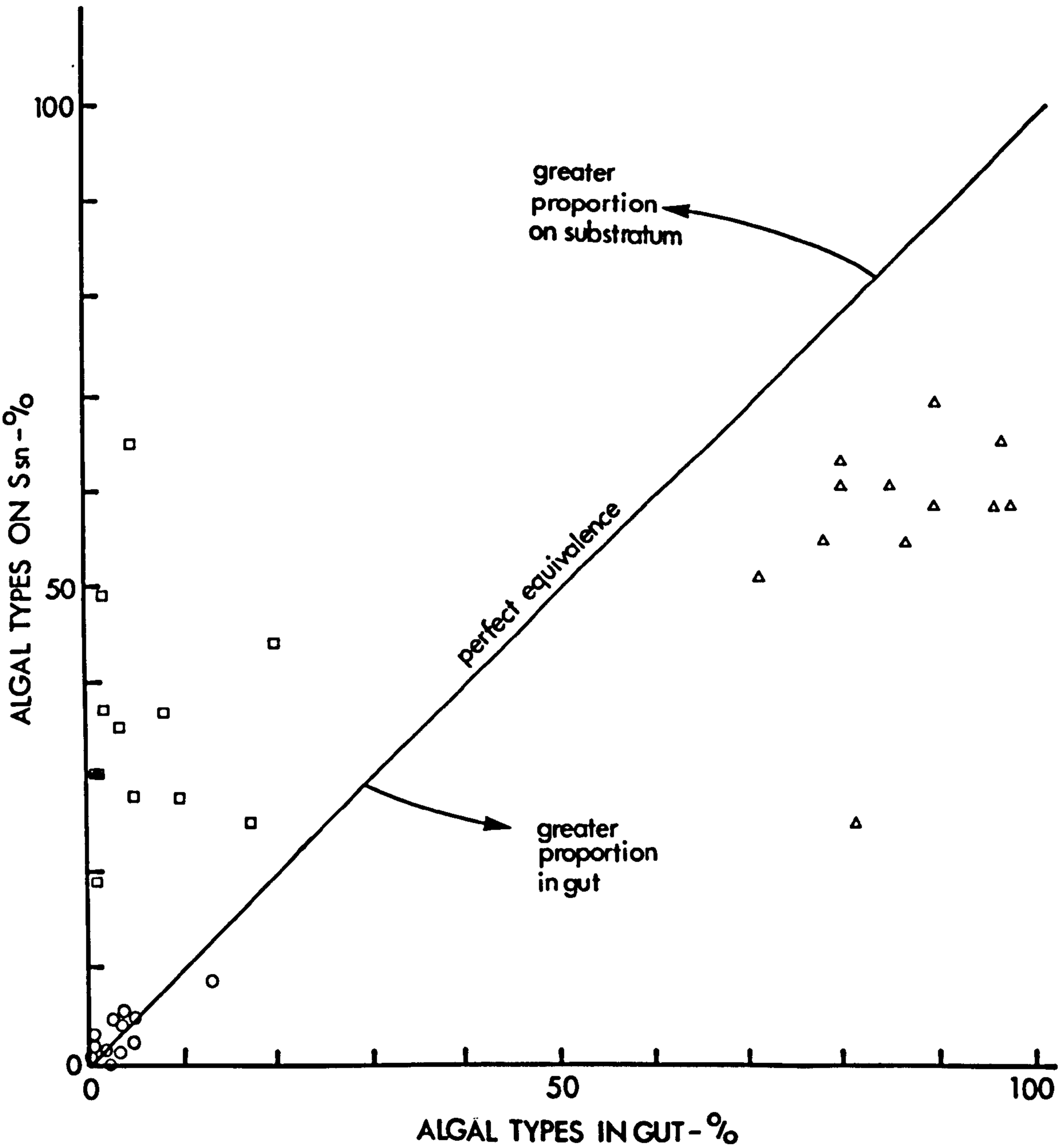

100
50
0
0
50
100
ALGAL TYPES ON Sn - %
ALGAL TYPES IN GUT - %
greater proportion on substratum
perfect equivalence
greater proportion in gut

FIG. 72 : The relationship between the relative abundance (%) of diatom genera on the sides of snail-bearing stones (Ssn) and in snails' guts.

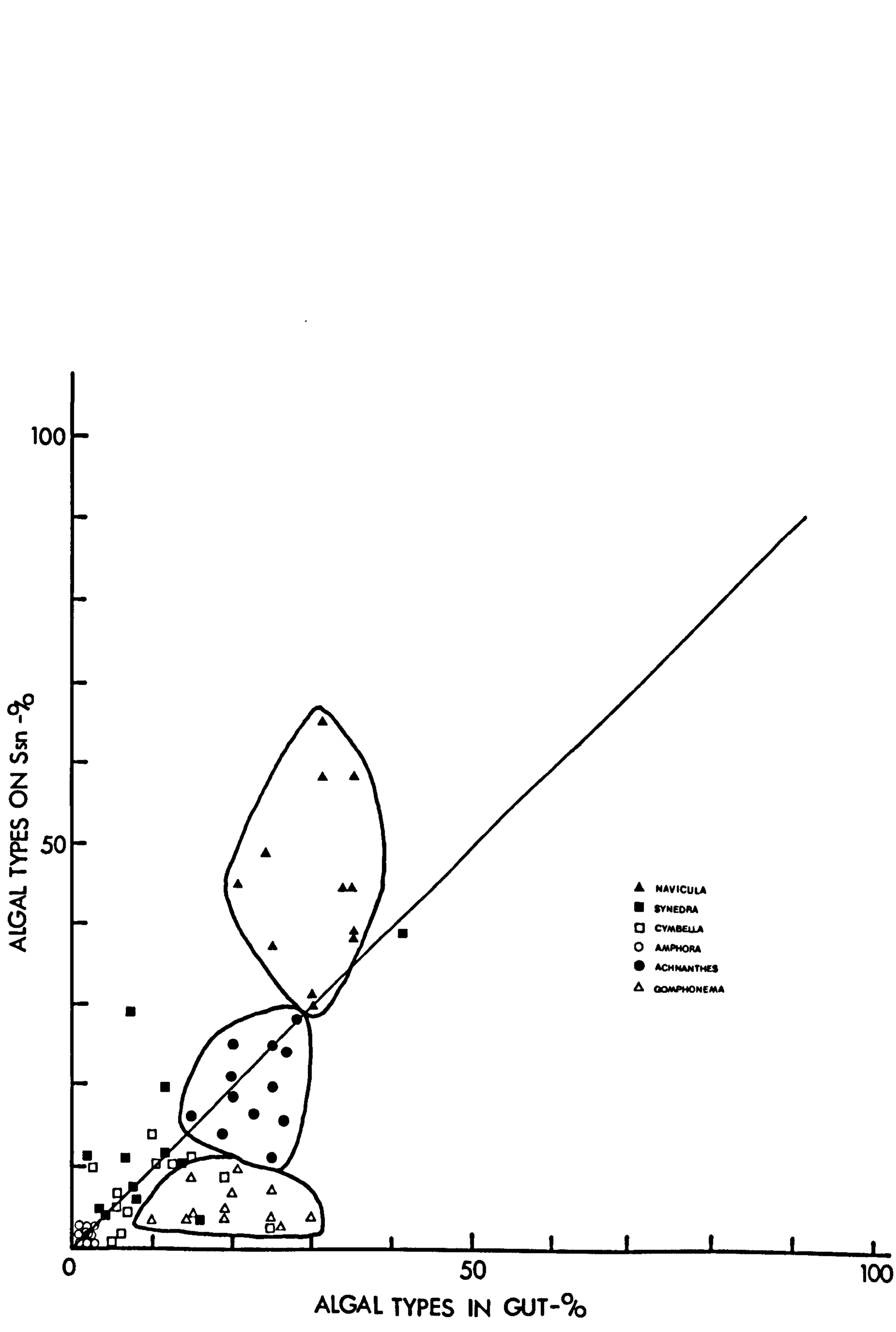

100
50
0
50
100
ALGAL TYPES ON Ssn -%
ALGAL TYPES IN GUT-%
NAVICULA
SYNEDRA
CYMBELLA
AMPHORA
ACHNANTHES
GOMPHONEMA

FIG. 73 : The relationship between the relative abundance of algal-types found on stones with (Ssn) and without (Sns) snails (for key, see FIG. 71).

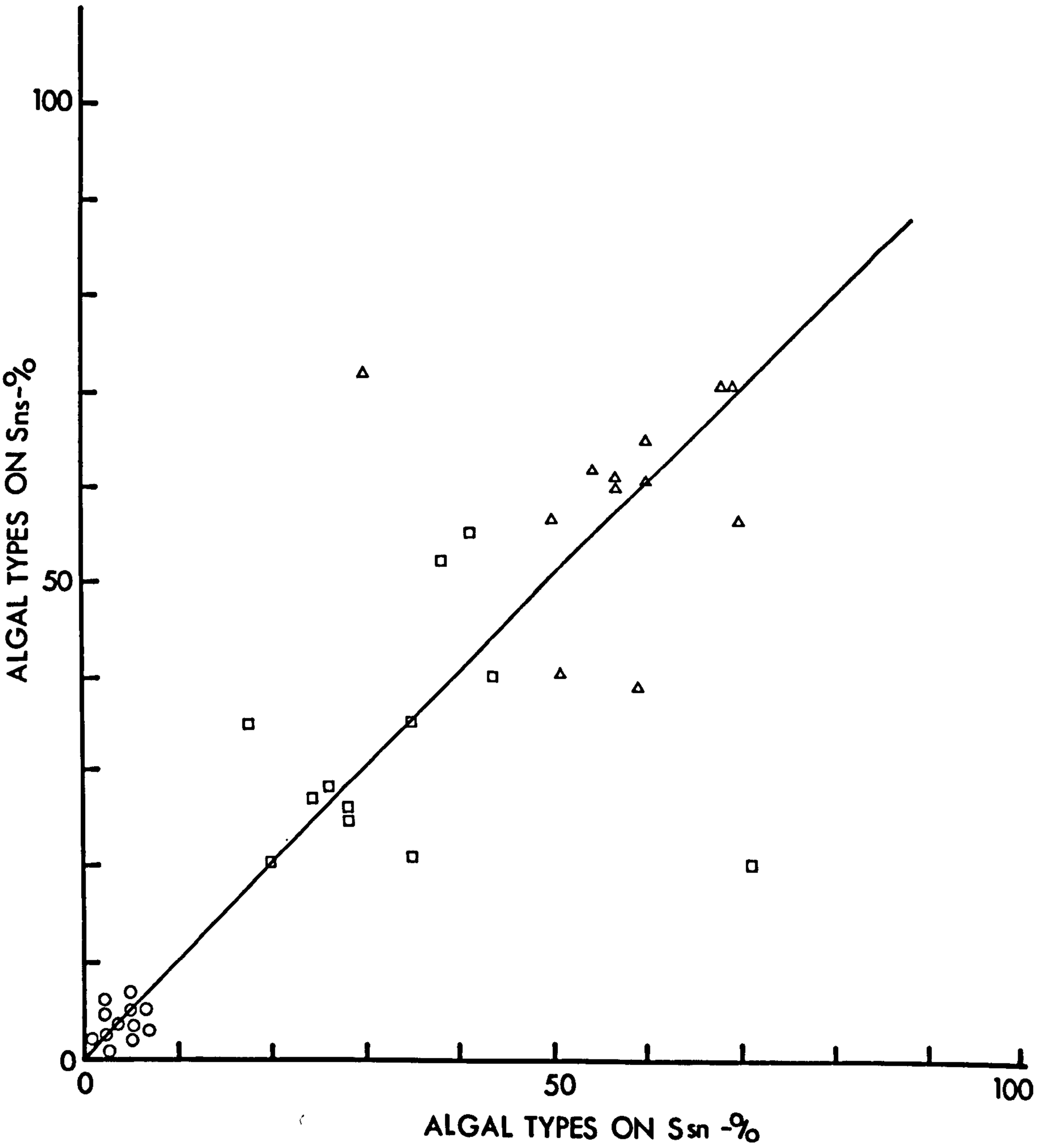

100
50
0
0
50
100
ALGAL TYPES ON Sns-%
ALGAL TYPES ON Ssn -%

FIG. 74 : The relationship between the relative abundance of diatom genera found on stones with (Ssn) and without (Sns) snails (for key, see FIG. 72).

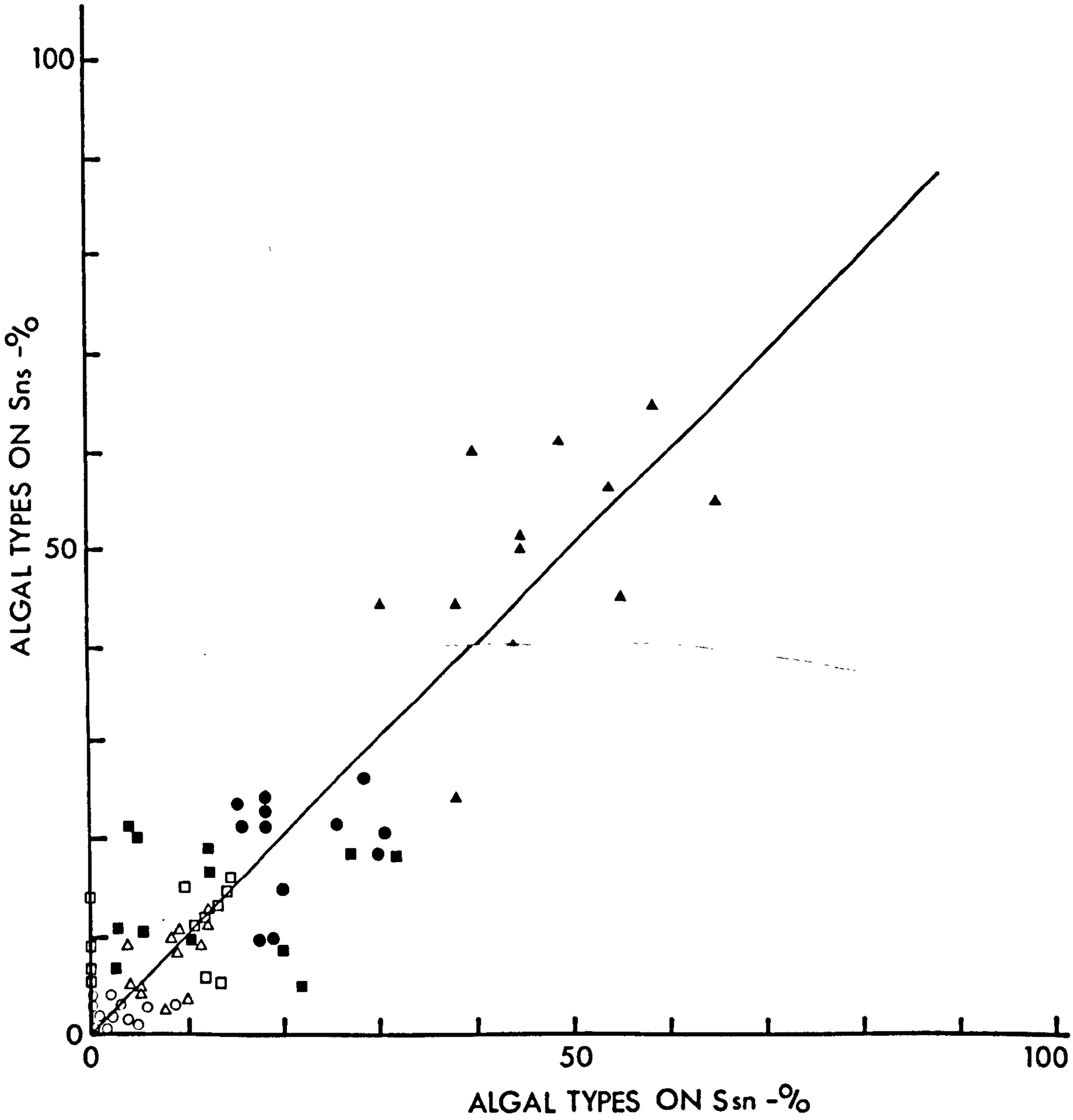

100
50
0
0
50
100
ALGAL TYPES ON Sns -%
ALGAL TYPES ON Ssn -%

FIG. 75 : The dispersion patterns (% of total no. involved on each choice) of A.fluviatilis,in a multiple choice feeding experiment, after 12 contact-hours. The snails had been deprived of food for 1 (A), 3 (B), and 7 (C) days prior to use.

Key

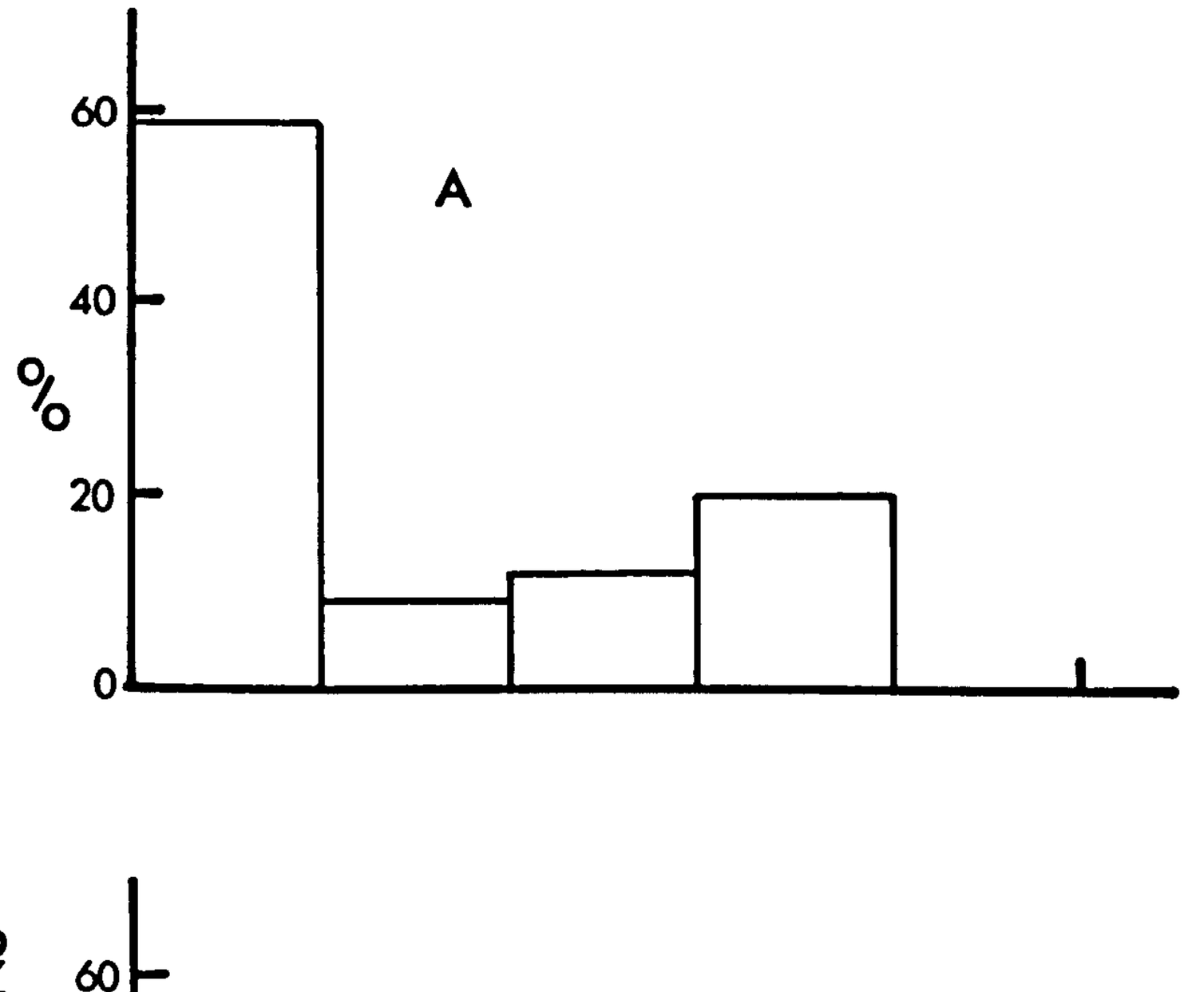
D - diatoms

BG - blue-green algae

GF - green filamentous algae

GU - green unicellular algae

C - control (no food)


A
60
40
20
0
%

B
SNAIL POSITIONS
%
60
40
20
0

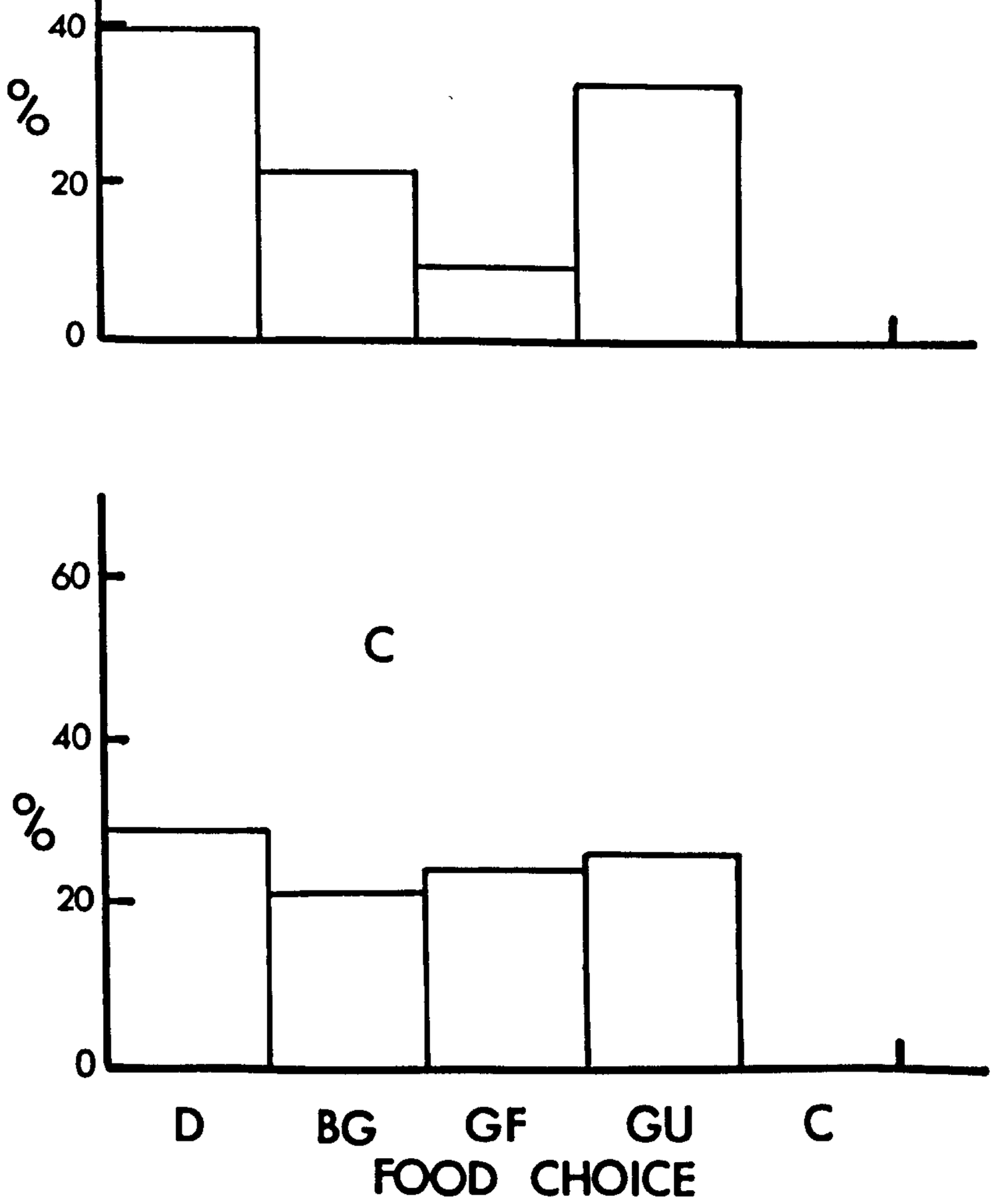

C
60
40
20
0
%
D
BG
GF
GU
C
FOOD CHOICE

FIG. 76 : The seasonal variation of algal cell volumes on the sides of snail-bearing stones. Confidence limits are not depicted, but were no more than 12% of the mean values shown.

Key

For A (groups other than diatoms)

O - blue-green algae

X - filamentous green algae

★ - unicellular green algae

For B (diatoms)

■ - Synedra

△ - Cymbella

▲ - Navicula

○ - Gomphonema

□ - Achnanthes

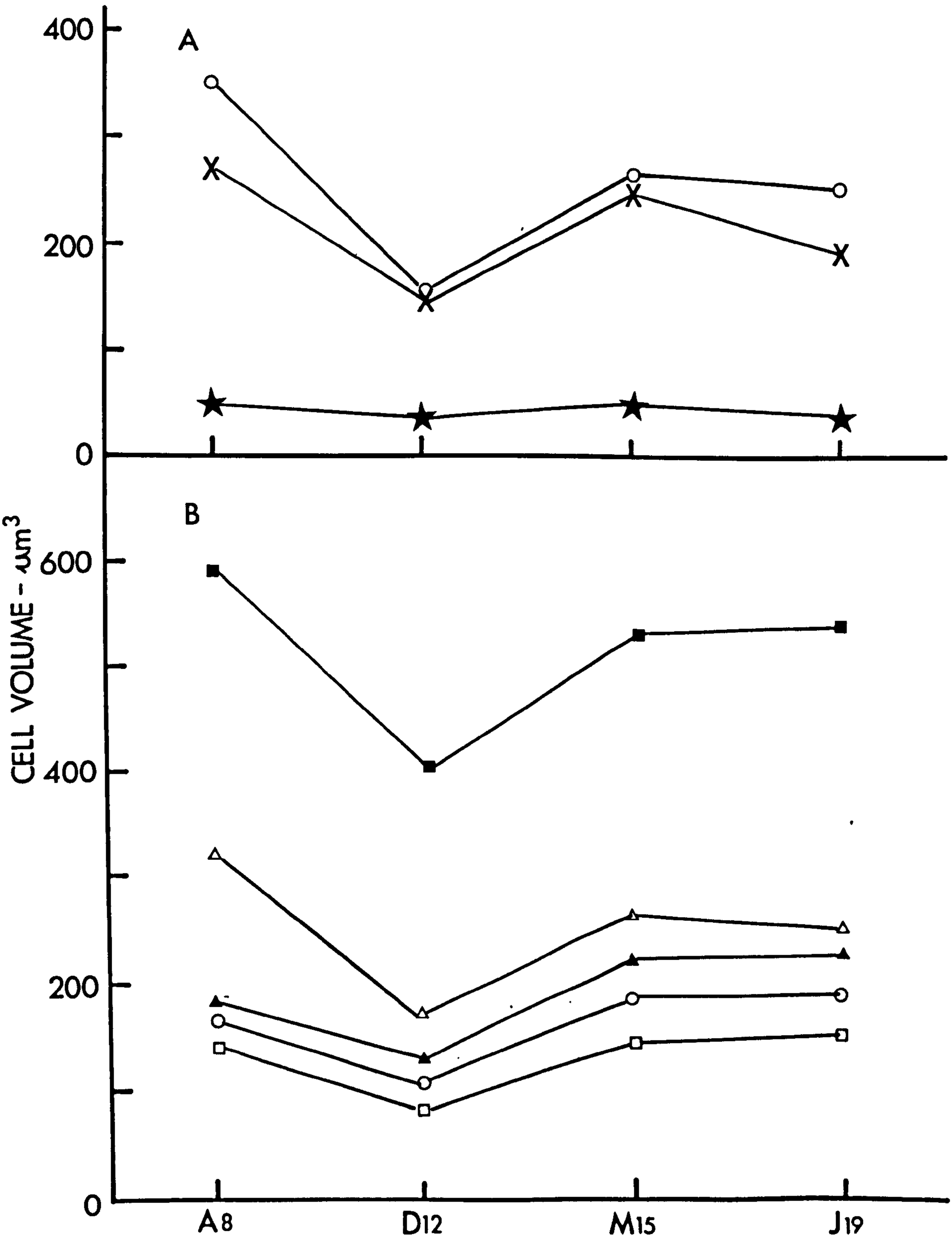

400
A
X
200
0
B
CELL VOLUME - μm^3
600
400
200
0
A8
D12
M15
J19
DATE

FIG. 77 : The seasonal variation of algal cell volumes found in the crop-gizzard apparatus of A.fluviatilis. Confidence limits are not depicted but were no more than 10% of the mean values shown (for key see FIG. 76).

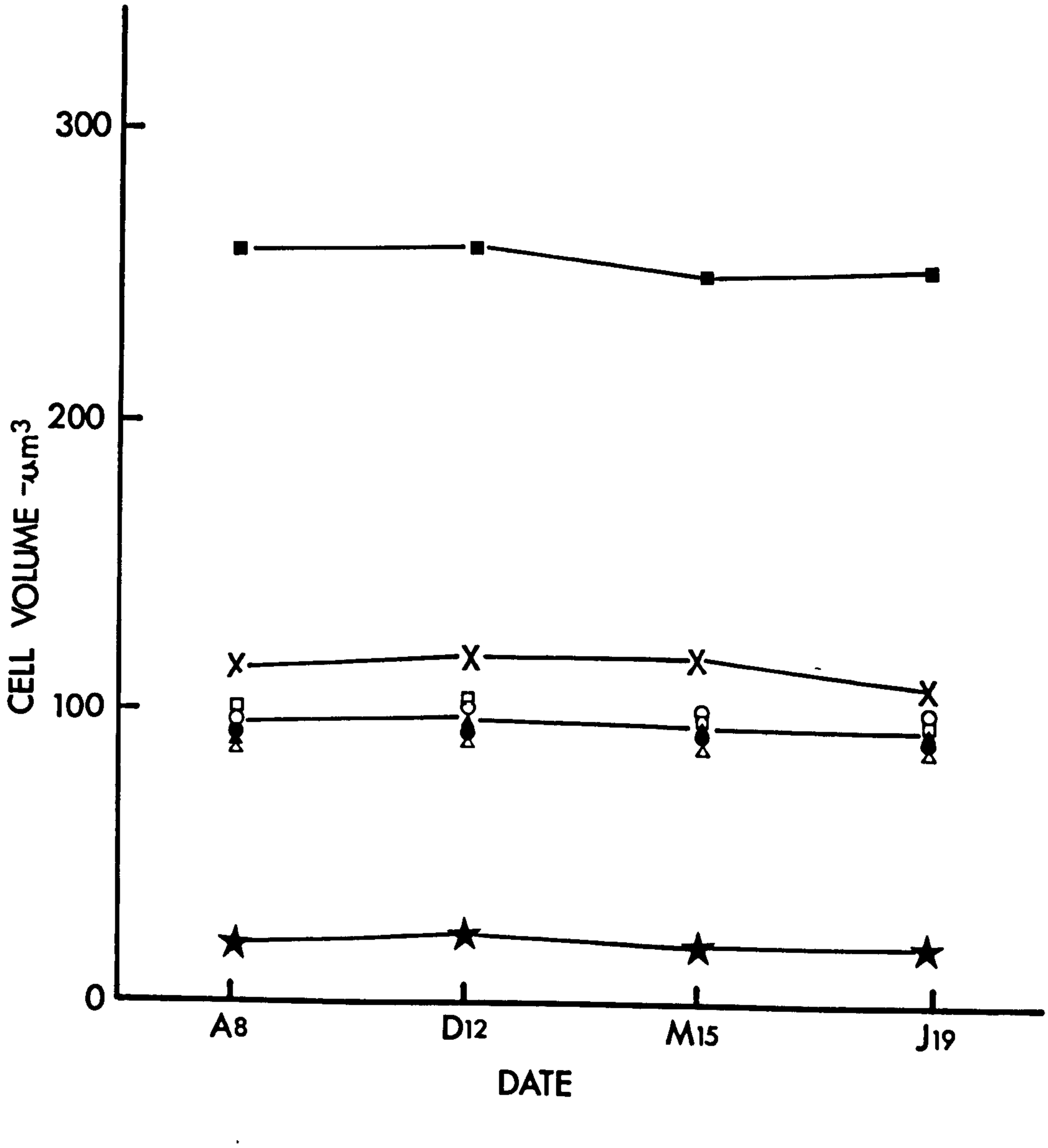

300
200
100
0
CELL VOLUME -um3
A8
D12
M15
J19
DATE

FIG. 78 : Seasonal variations in the relative proportions (% - based on cell numbers) of algal food consumed by A.fluviatilis. Blocks at the end of the figure are the whole-year means, calculated after arcsine transformation, and retransformed for presentation.

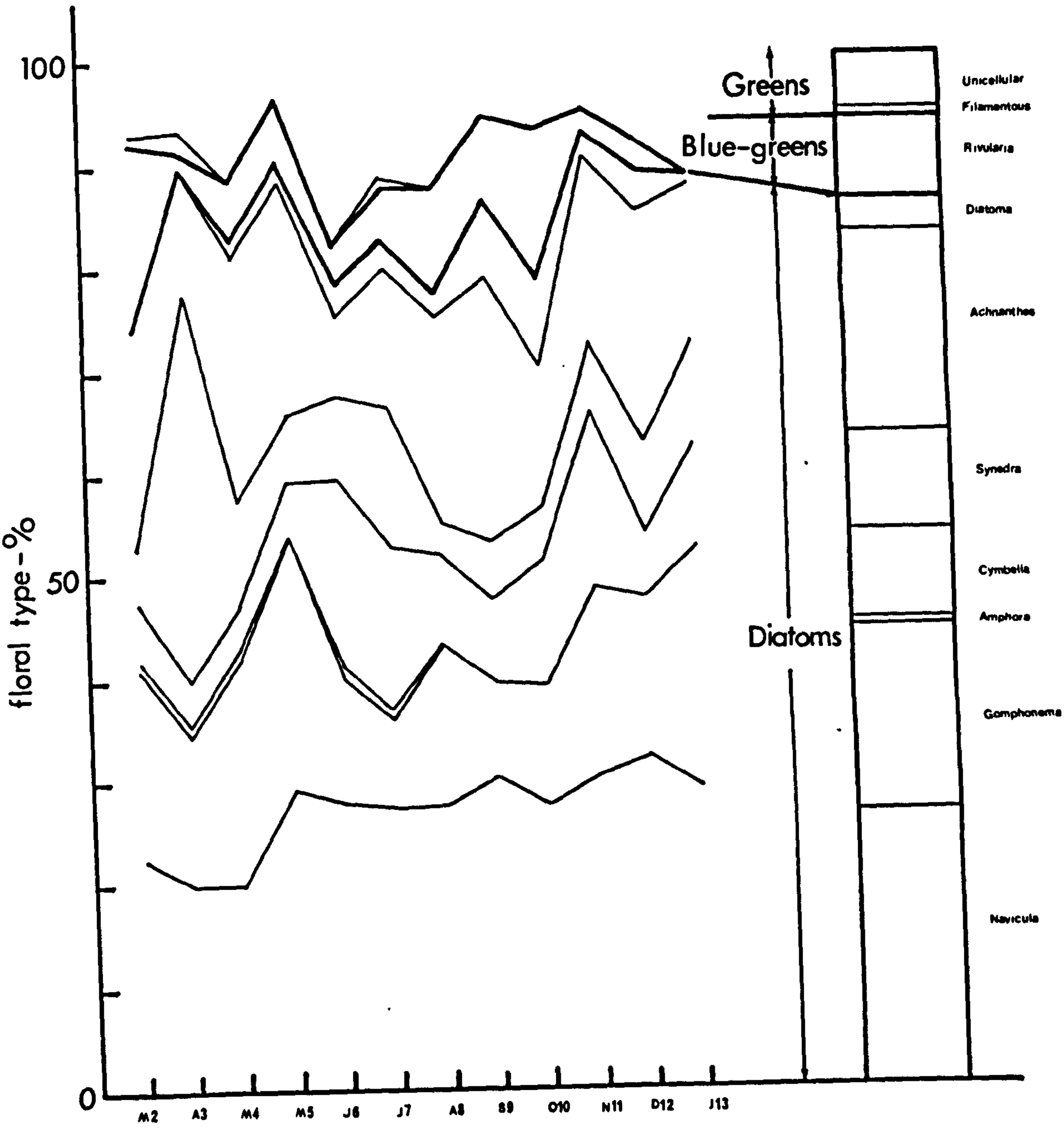

100
50
0
floral type-%
Greens
Blue-greens
Diatoms
Unicellular
Filamentous
Rivularia
Diatoms
Achnanthes
Synedra
Cymbella
Amphora
Gomphonema
Navicula
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
Date

FIG. 79 : Seasonal variations in the relative proportions (% based on biomass- cell vol. x cell nos.) of algal food consumed by A.fluviatilis. Blocks at the end of the figure are as defined in FIG. 78.

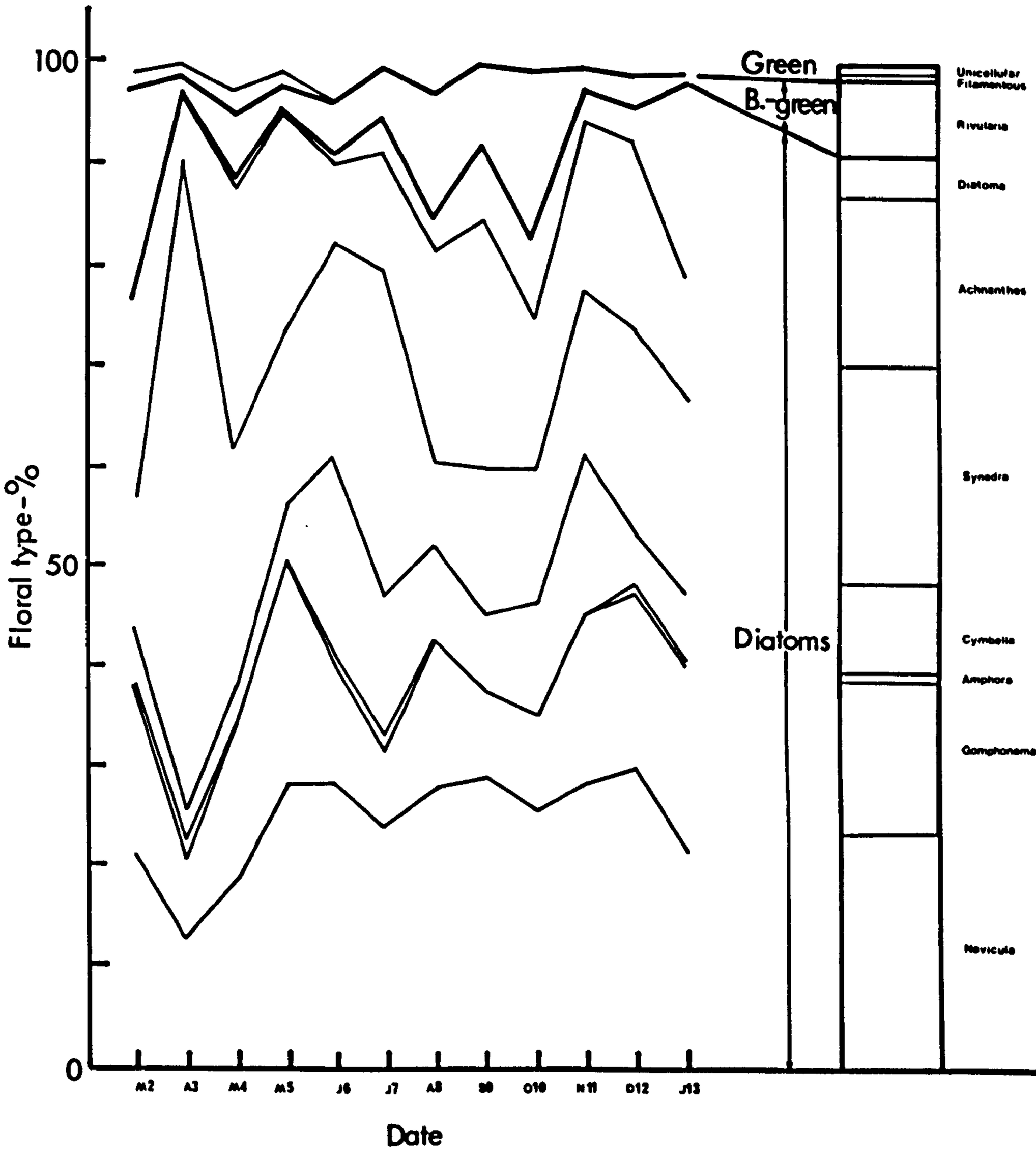

Floral type-%
100
50
0
Green
B.-green
Diatoms
Unicellular Filamentous
Rivularia
Diatoms
Achnanthes
Synedra
Cymbella
Amphora
Gomphonema
Navicula
M2
A3
M4
M5
J6
J7
A8
S9
O10
N11
D12
J13
Date

FIG. 80 : Seasonal variations in the biochemical constitution of epilithic detritus expressed in terms of the relative proportions (%) of the various constituents.

FIG. 81 : Seasonal variations in the caloric density (kcals./g. ash-free dry weight) and ash content (%) of epilithic detritus.

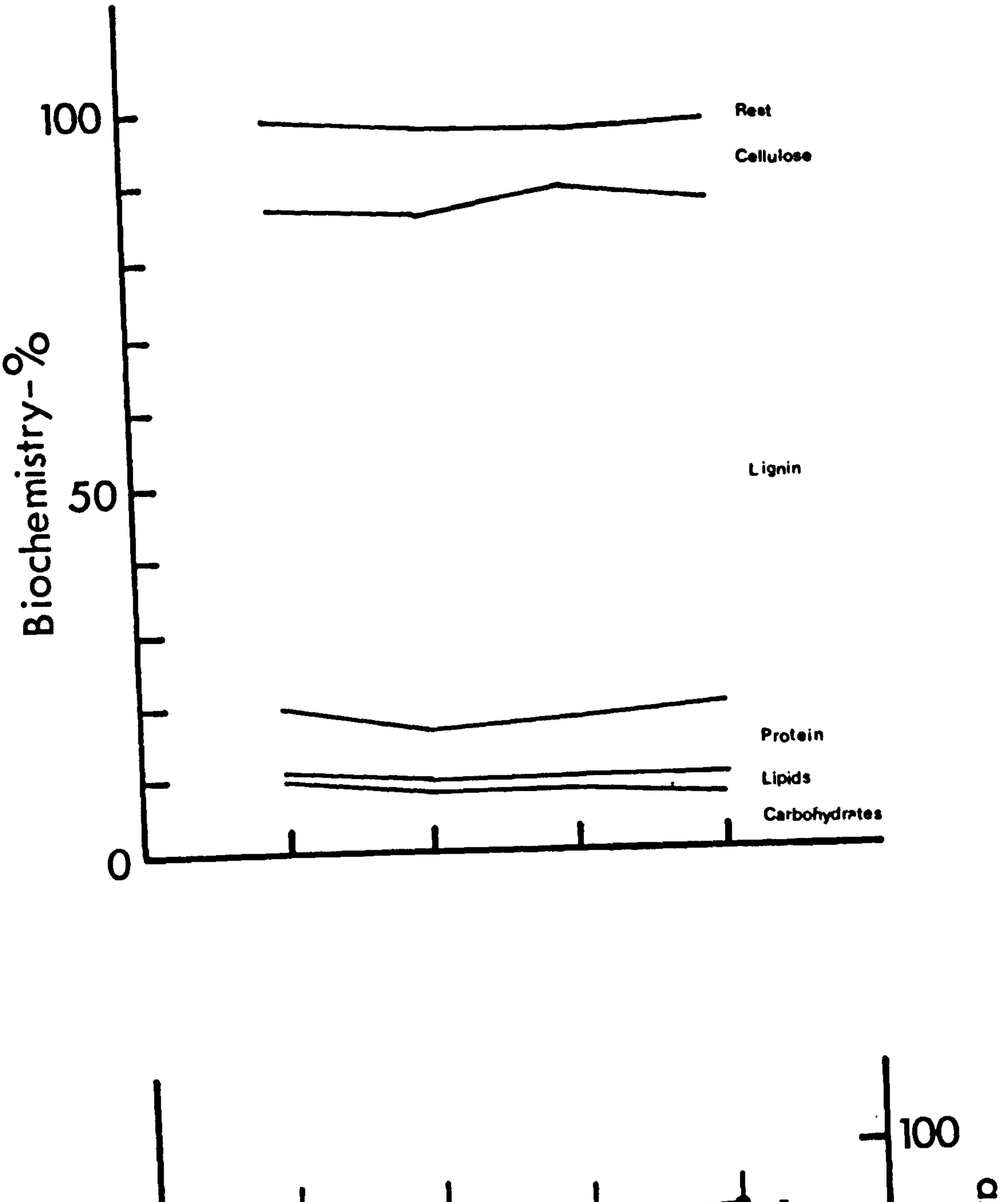

100
50
0
Biochemistry-%
Rest
Cellulose
Lignin
Protein
Lipids
Carbohydrates
4
2
0
kcals.
Energy
Ash
100
50
0
%-ash
D'70
M'70
J'71
S'71
Date

FIG. 82 : Seasonal variations in the quality of epilithic, bacterial communities (i.e. the relative abundance of different bacterial types - %) which developed on cover-slips suspended in the littoral region of Ha Mire shore in 1971.

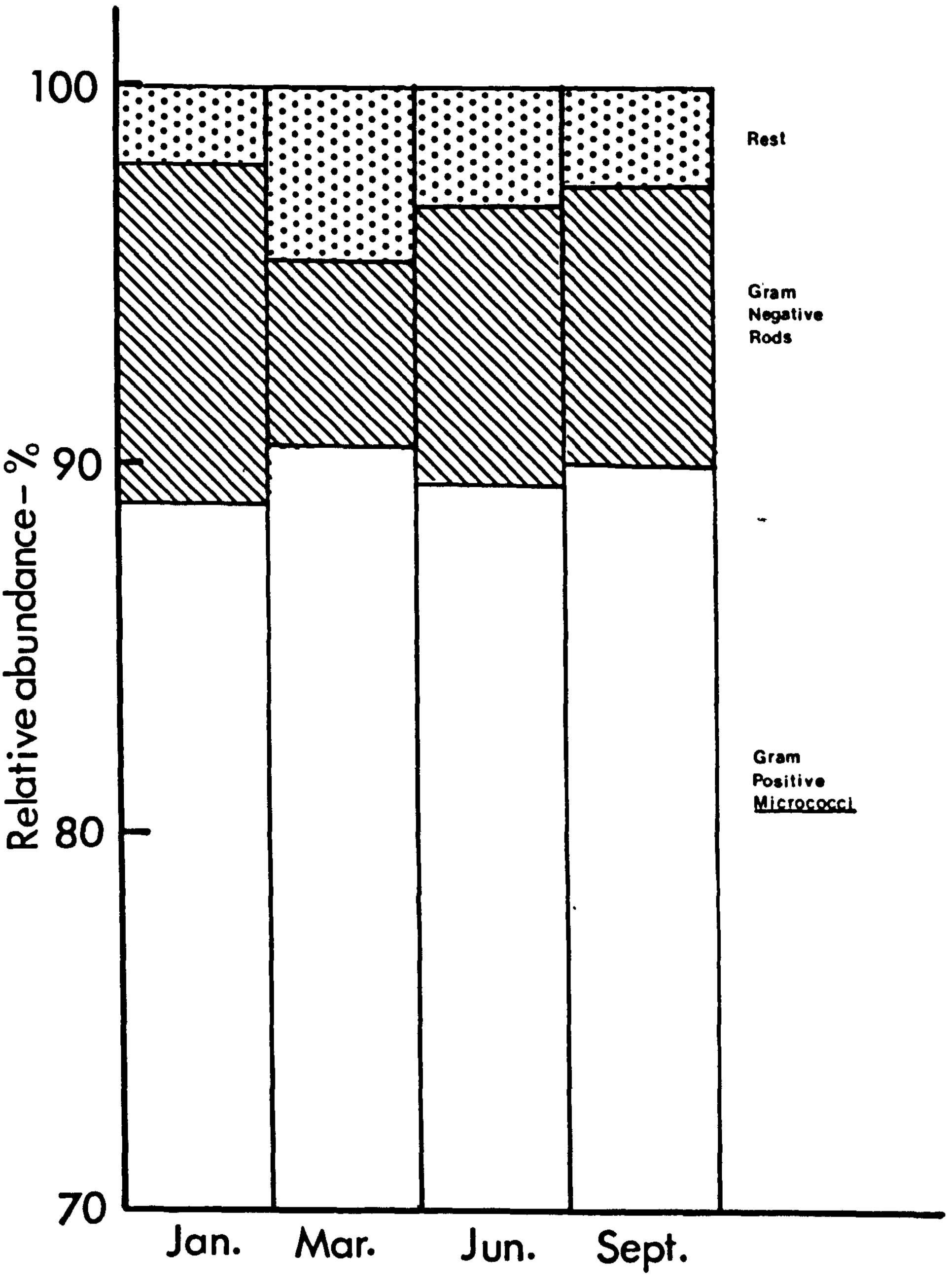
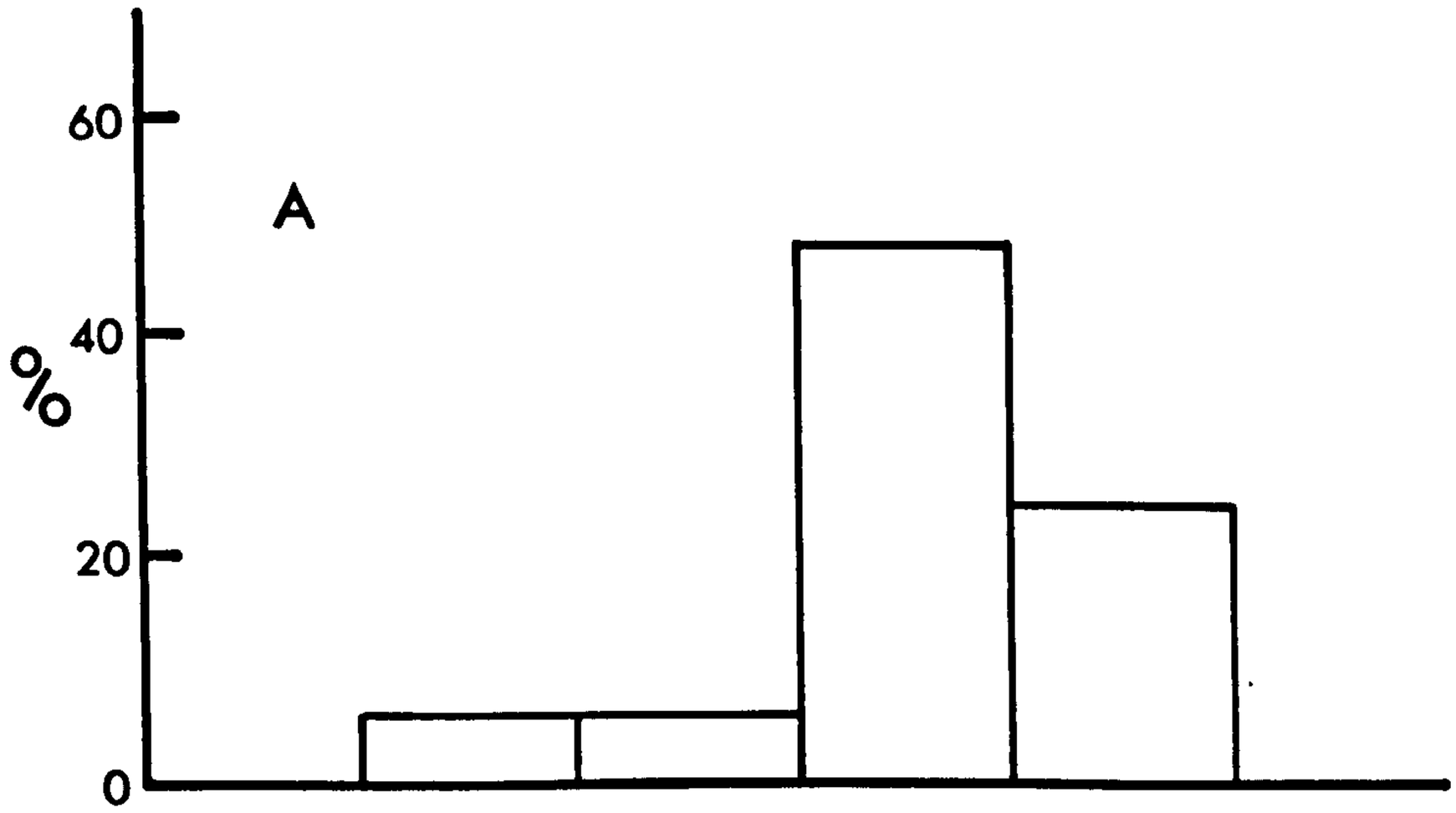
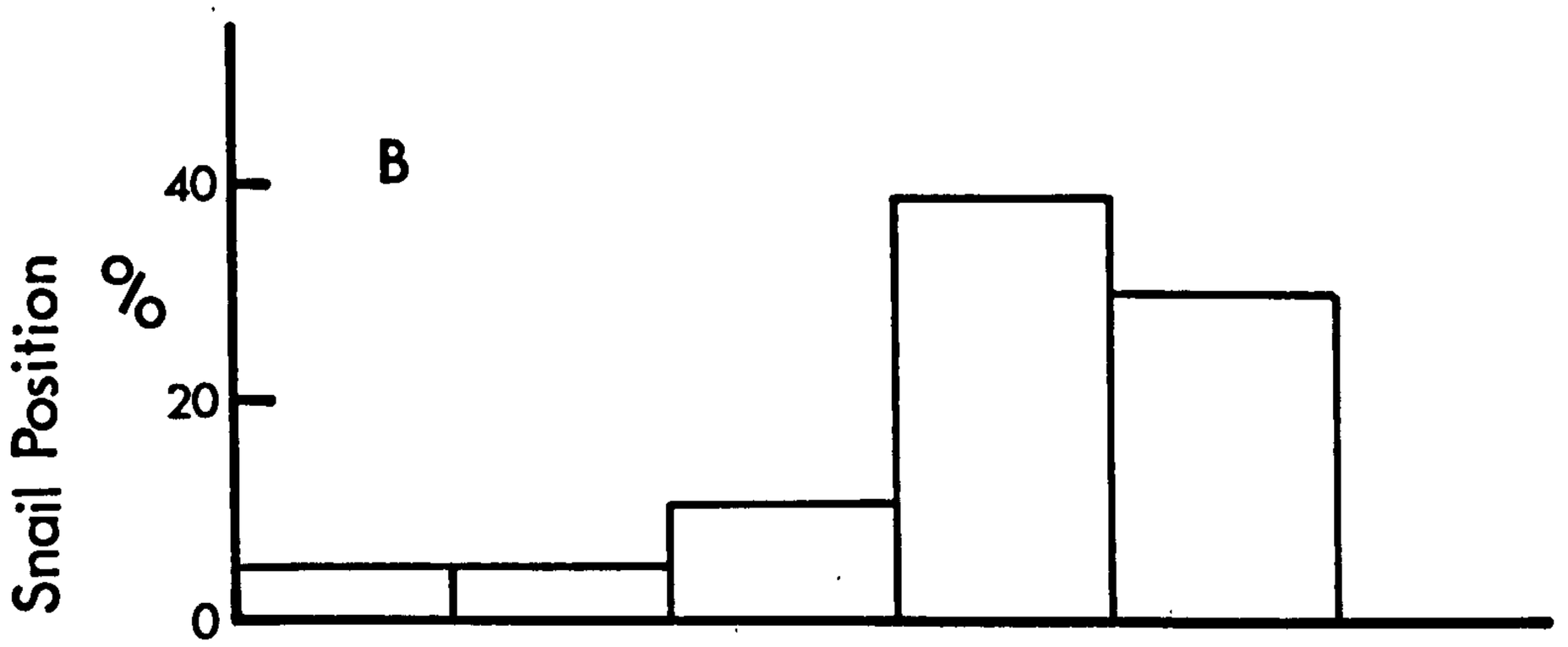

100
90
80
70
Relative abundance - %
Rest
Gram Negative Rods
Gram Positive Micrococci
Jan.
Mar.
Jun.
Sept.
Date

FIG. 83 : The dispersion patterns (% of total no. involved in each case) of P.contortus, in multiple-choice feeding experiments, after 6 contact-hours. The snails were deprived of food for 1(A), 3(B), and 7(C) days prior to use.


A
60
40
%
20
0


B
40
20
%
0
Snail Position

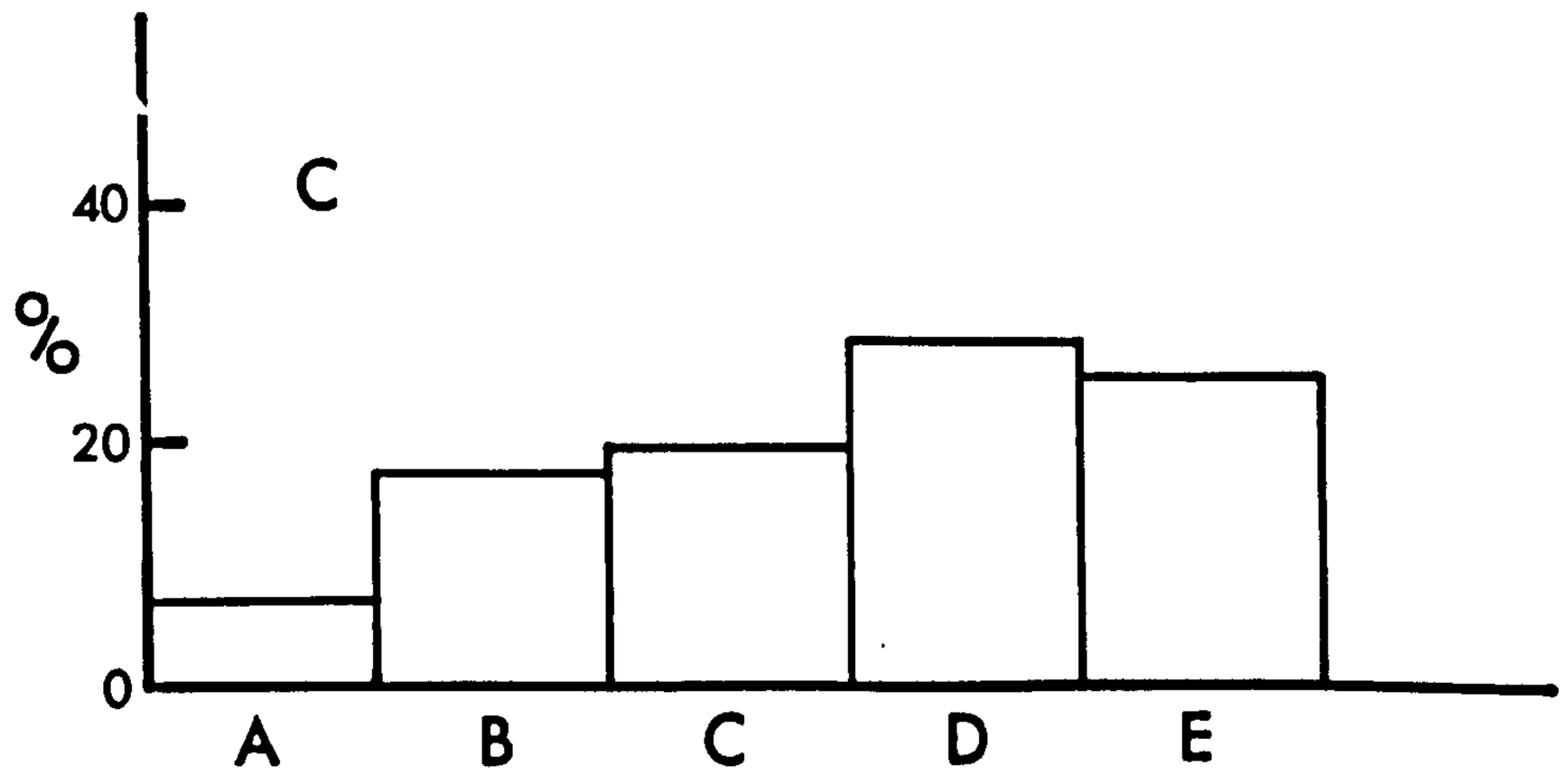

C
40
20
%
0
A
B
C
D
E
Bacterial Choice

FIG. 84 : The effect of food deprivation on the ingestion rate (appetite) and assimilation efficiency of Achnanthes by A.fluviatilis.

Key

■ - ingestion rate

△ - assimilation efficiency

The vertical bars indicate 95% confidence limits.

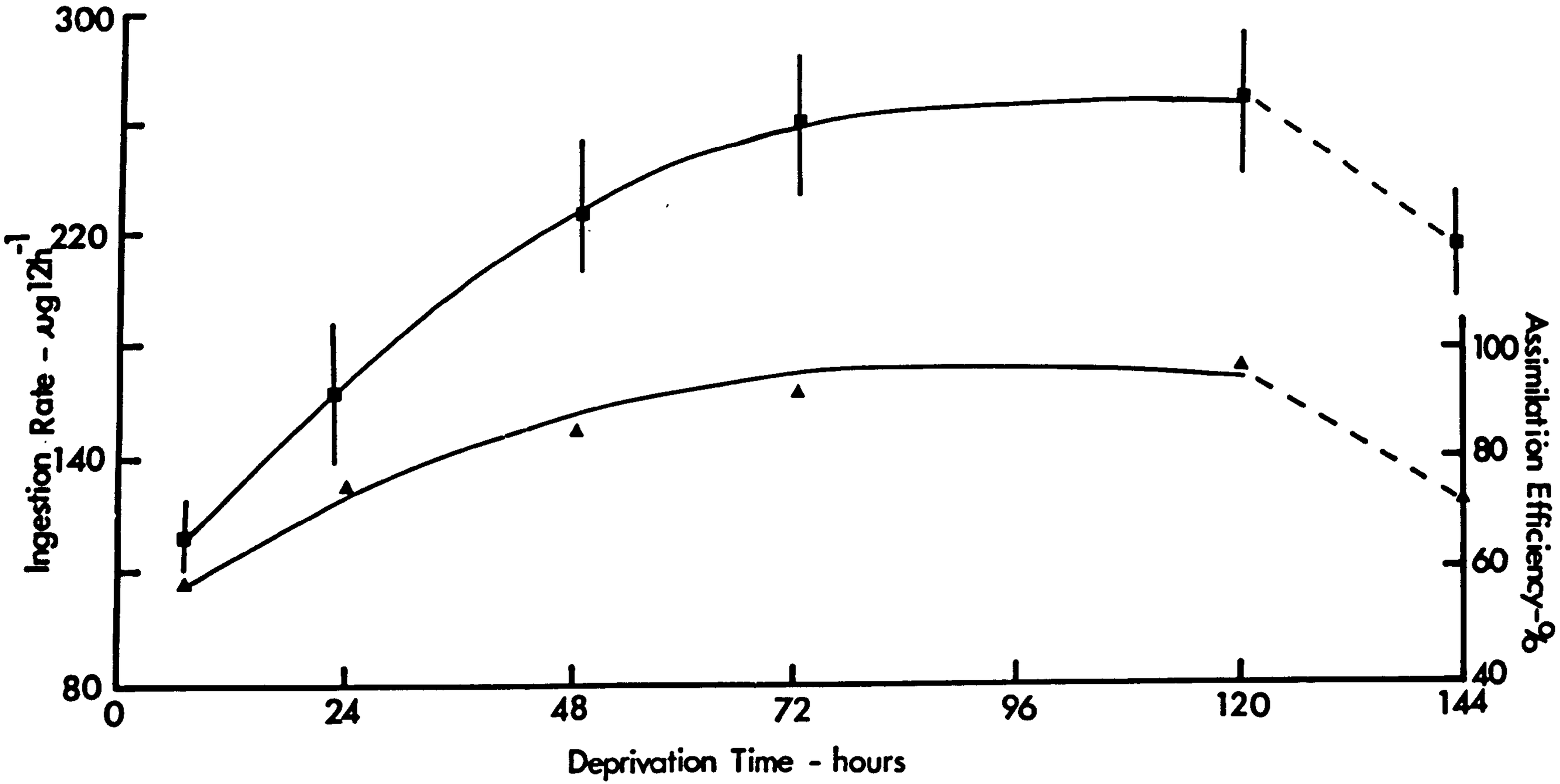

300
220
140
80
Ingestion Rate - µg 12h⁻¹
100
80
60
40
Assimilation Efficiency-%
0
24
48
72
96
120
144
Deprivation Time - hours

FIG. 85 : The effect of food deprivation on the ingestion rate (appetite) and assimilation efficiency of bacterium-D by P.contortus (for key see FIG. 84).

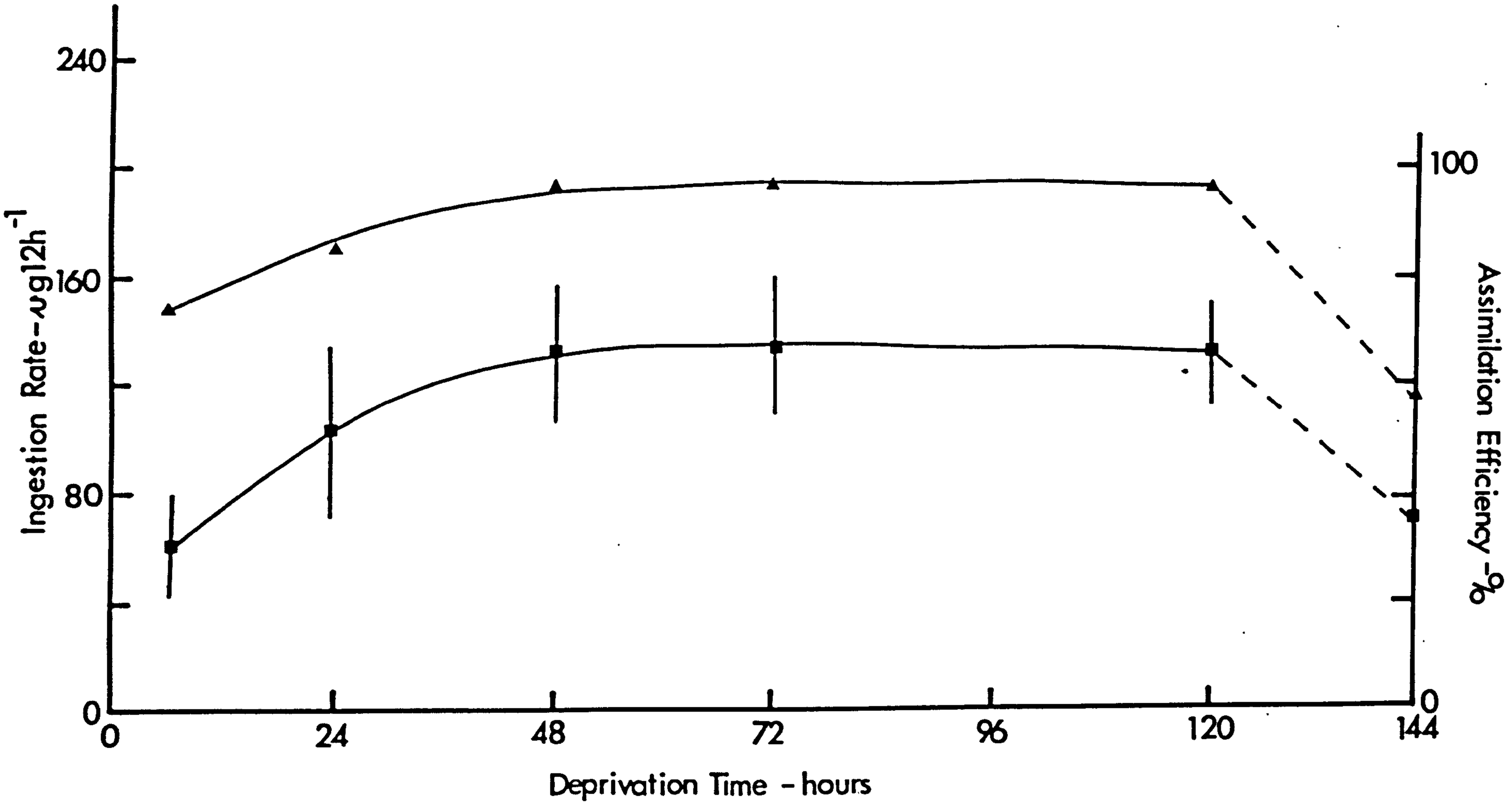

240
160
80
0
Ingestion Rate-µg12h⁻¹
100
0
Assimilation Efficiency-%
0
24
48
72
96
120
144
Deprivation Time - hours

FIG. 86 :

A : The pattern of gut-emptying, as indicated by the cumulative % loss of 51-Cr from the body of A.fluviatilis under various conditions of food deprivation (see text for further explanation).

B : The pattern of gizzard and liver string loss in the faecal pellets of A.fluviatilis (i.e. individuals under regimen a in FIG. 86A). Loss is expressed as a cumulative % of the total length of gizzard or liver string produced.

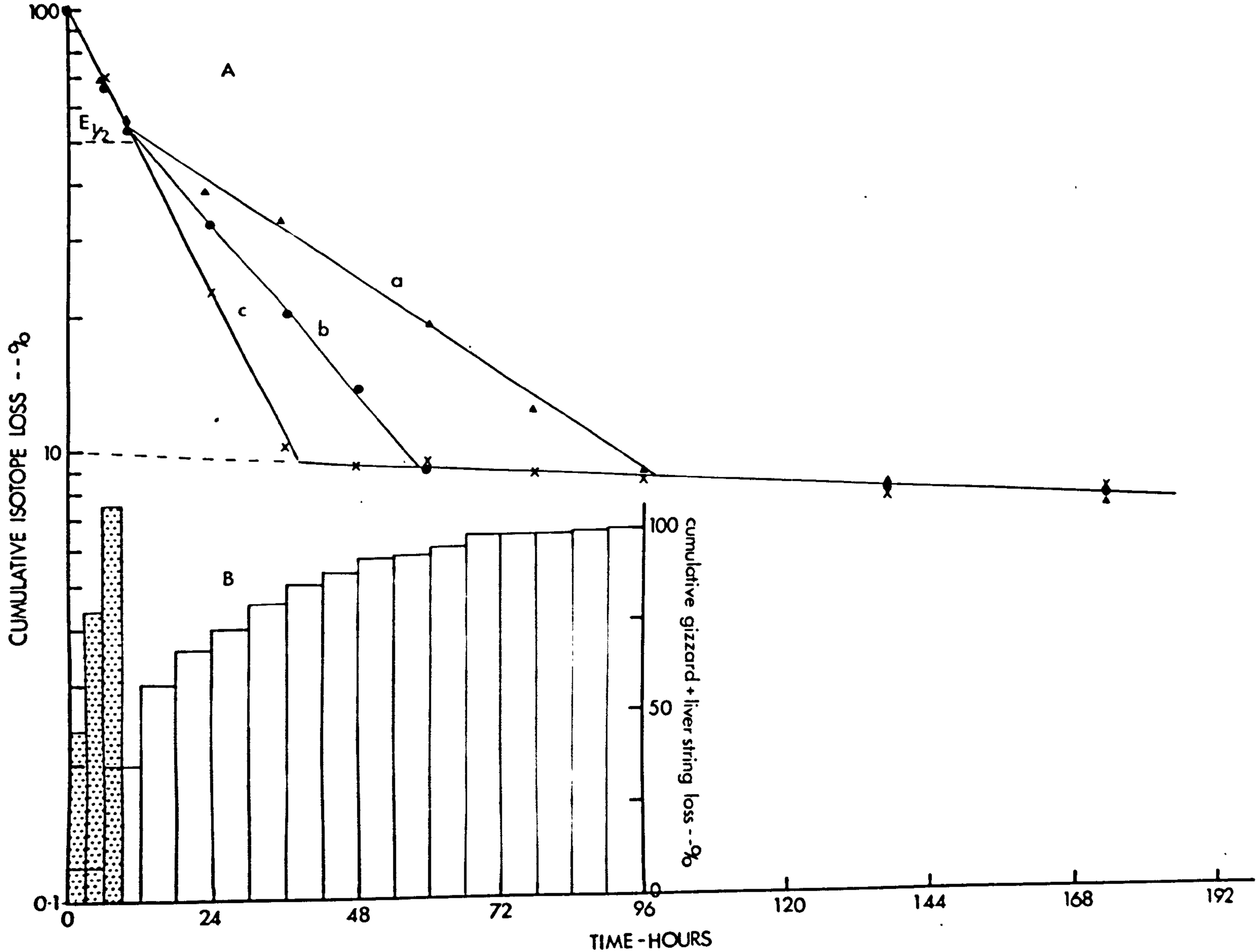

100
10
0·1
A
$E_{1/2}$
a
b
c
CUMULATIVE ISOTOPE LOSS - -%
B
100
50
0
cumulative gizzard + liver string loss - -%
0
24
48
72
96
120
144
168
192
TIME - HOURS

FIG. 87 :

A : The pattern of gut emptying, as indicated by the cumulative % loss of 51-Cr from the body of P.contortus under various conditions of food deprivation (see text for further explanation).

B : The pattern of gizzard and liver string loss in the faecal pellets of P.contortus (i.e. individuals under regimen a in FIG. 87A). Loss is expressed as a cumulative % of the total length of gizzard or liver string produced.

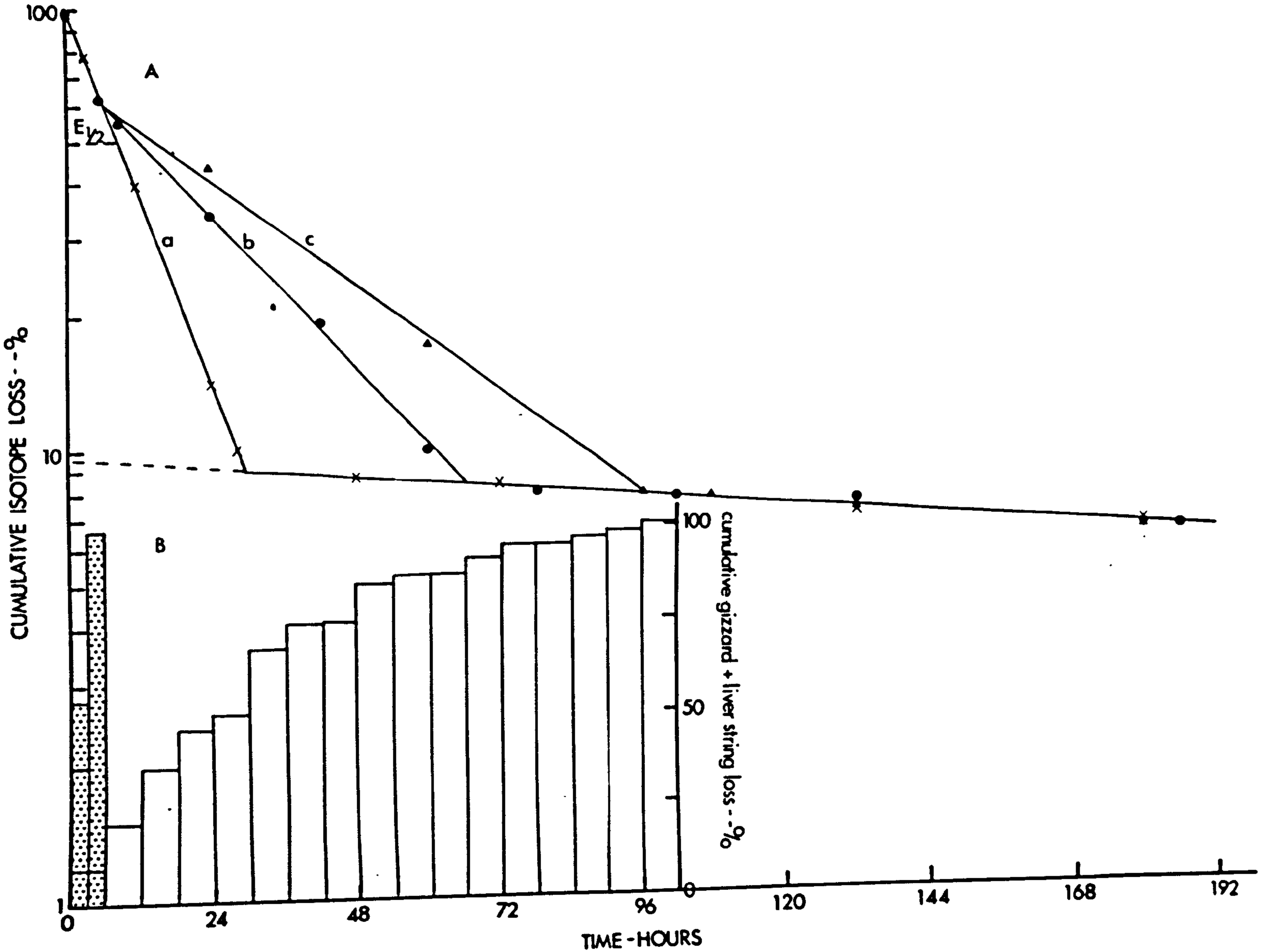

100
A
$E_{1/2}$
a
b
c
10
1
CUMULATIVE ISOTOPE LOSS - -%
B
100
50
0
cumulative gizzard + liver string loss - -%
0
24
48
72
96
120
144
168
192
TIME - HOURS

FIG. 88 : The effect of temperature on the exponentially reducing rate of gut emptying (K - defined in the text, see equation 1(7. 5)) in "large" individuals of P.contortus and A.fluviatilis.

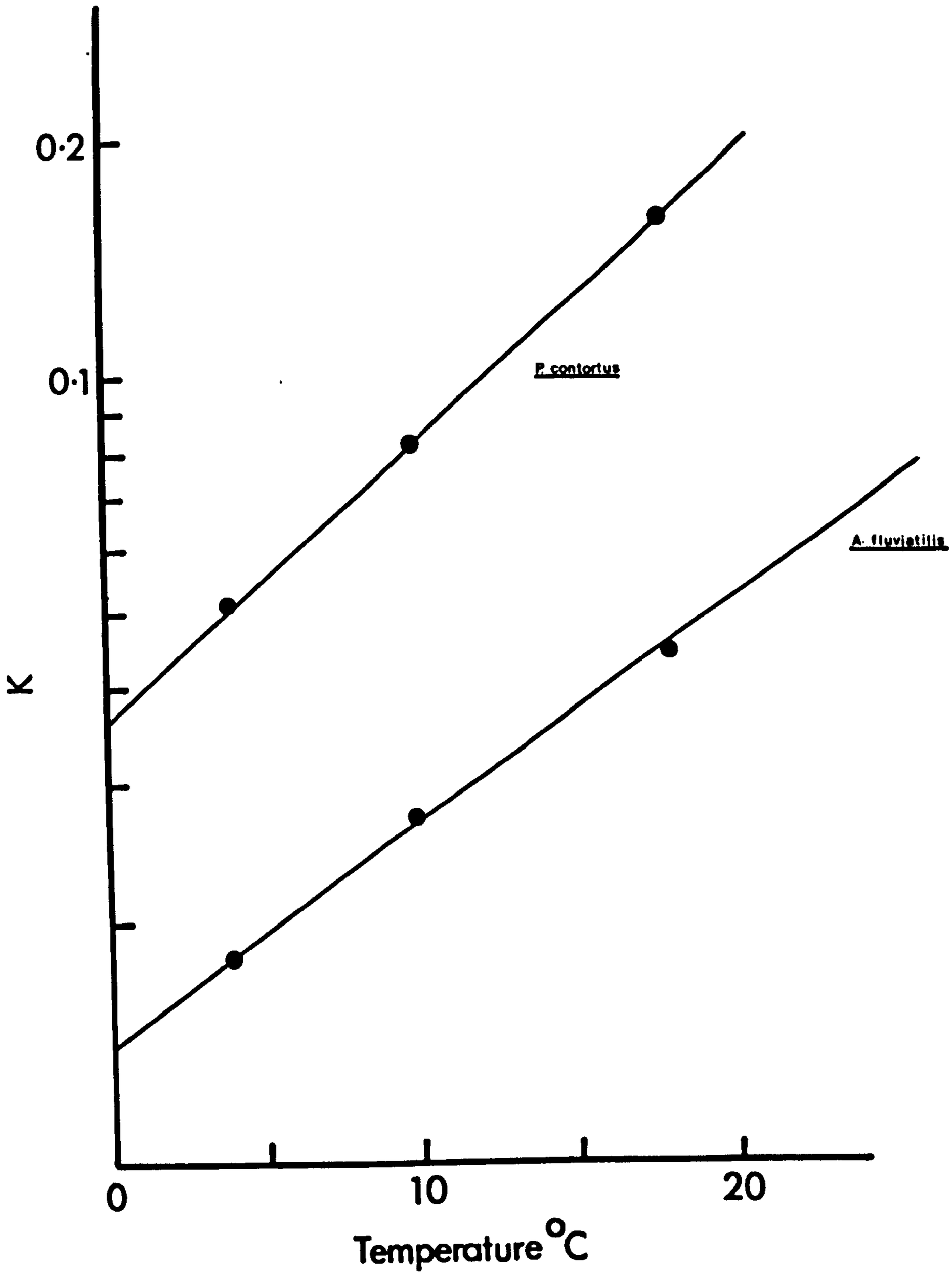

0·2
0·1
K
P. contortus
A. fluviatilis
0
10
20
Temperature °C

FIG. 89 : The effect of body size (MD or AL) on the exponentially reducing rate of gut emptying (K - see FIG. 88) in P.contortus and A.fluviatilis.

Key

▲ - P.contortus

■ - A.fluviatilis

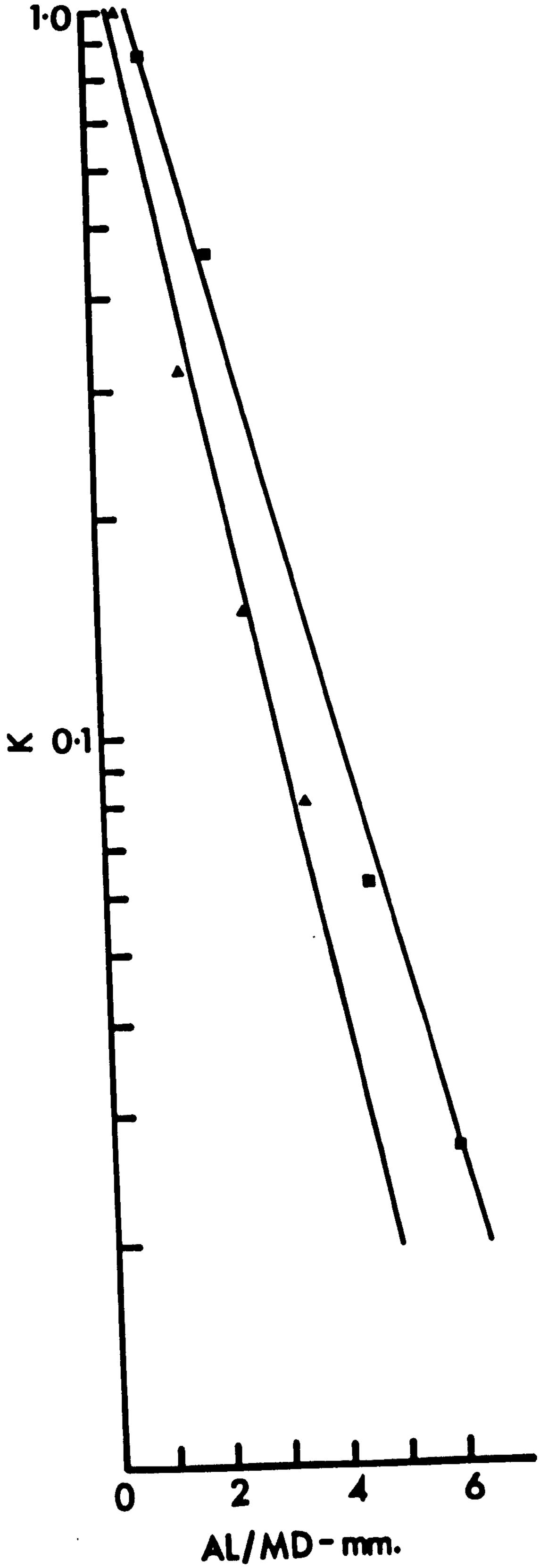

1·0
K 0·1
0
2
4
6
AL/MD - mm.

FIG. 90 : The relationship between ingestion rate and assimilation efficiency in P.contortus and A.fluviatilis.

Key

for A.fluviatilis

1. Rivularia
2. Cladophora
3. Scenedesmus
4. Navicula
5. Achnanthes
6. Gomphonema

for P.contortus

1. Lignin
2. Cellulose
3. Bacterium E
4. Bacterium D

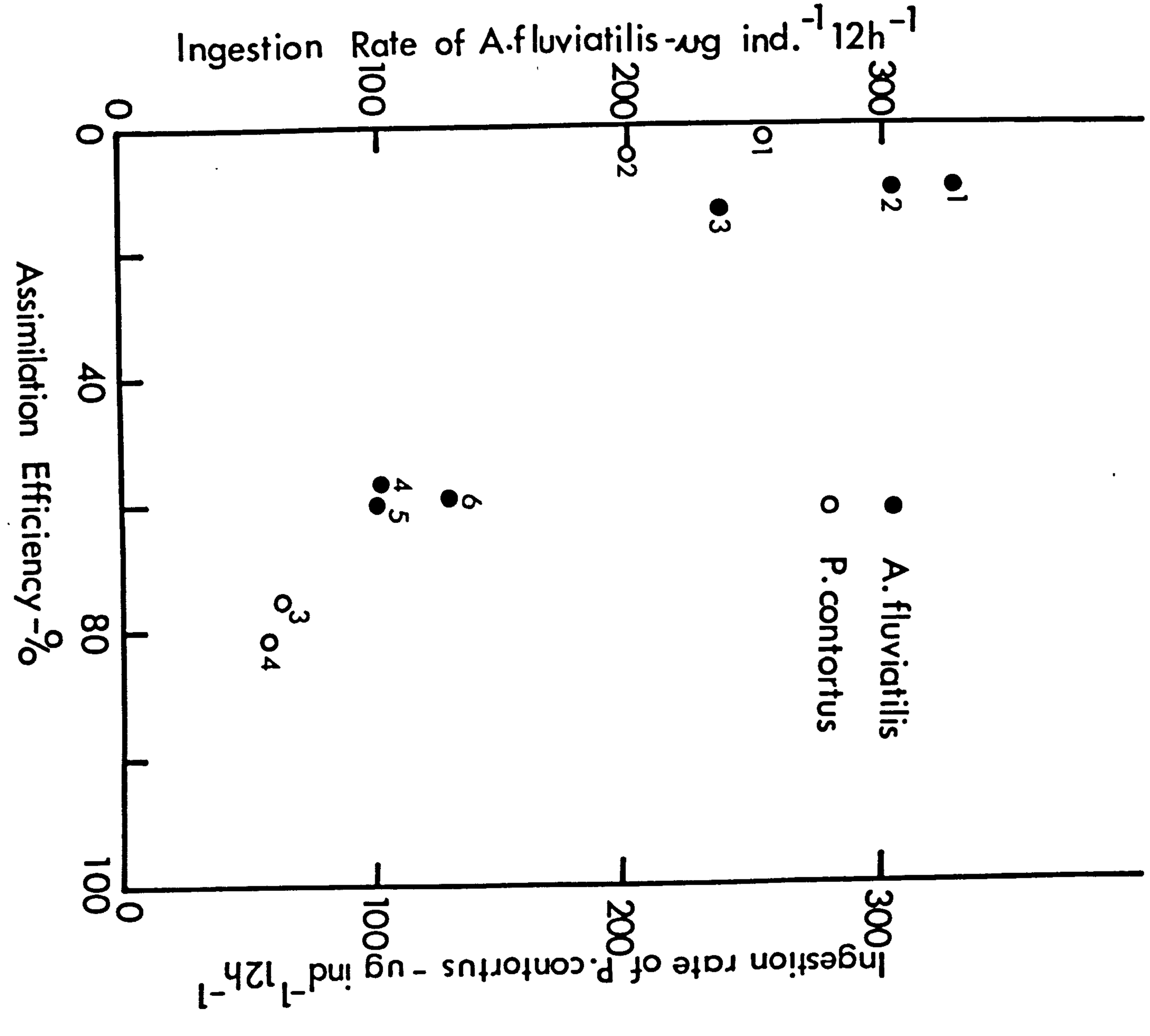

Ingestion Rate of A.fluviatilis-ug ind.$^{-1}$ 12h^{-1}
0
100
200
300
01
02
1
2
3
Assimilation Efficiency-%
0
40
80
100
4
5
6
03
04
A. fluviatilis
P. contortus
Ingestion rate of P. contortus - ug ind^{-1} 12h^{-1}
0
100
200
300

FIG. 91 : An estimation of the self-absorption effect of lignin during the G.M.-tube measurements of 14C disintigrations. The graph shows the disintigrations monitored from fixed quantities of bacteria, of the same specific activities, when mixed with different quantities of lignin.

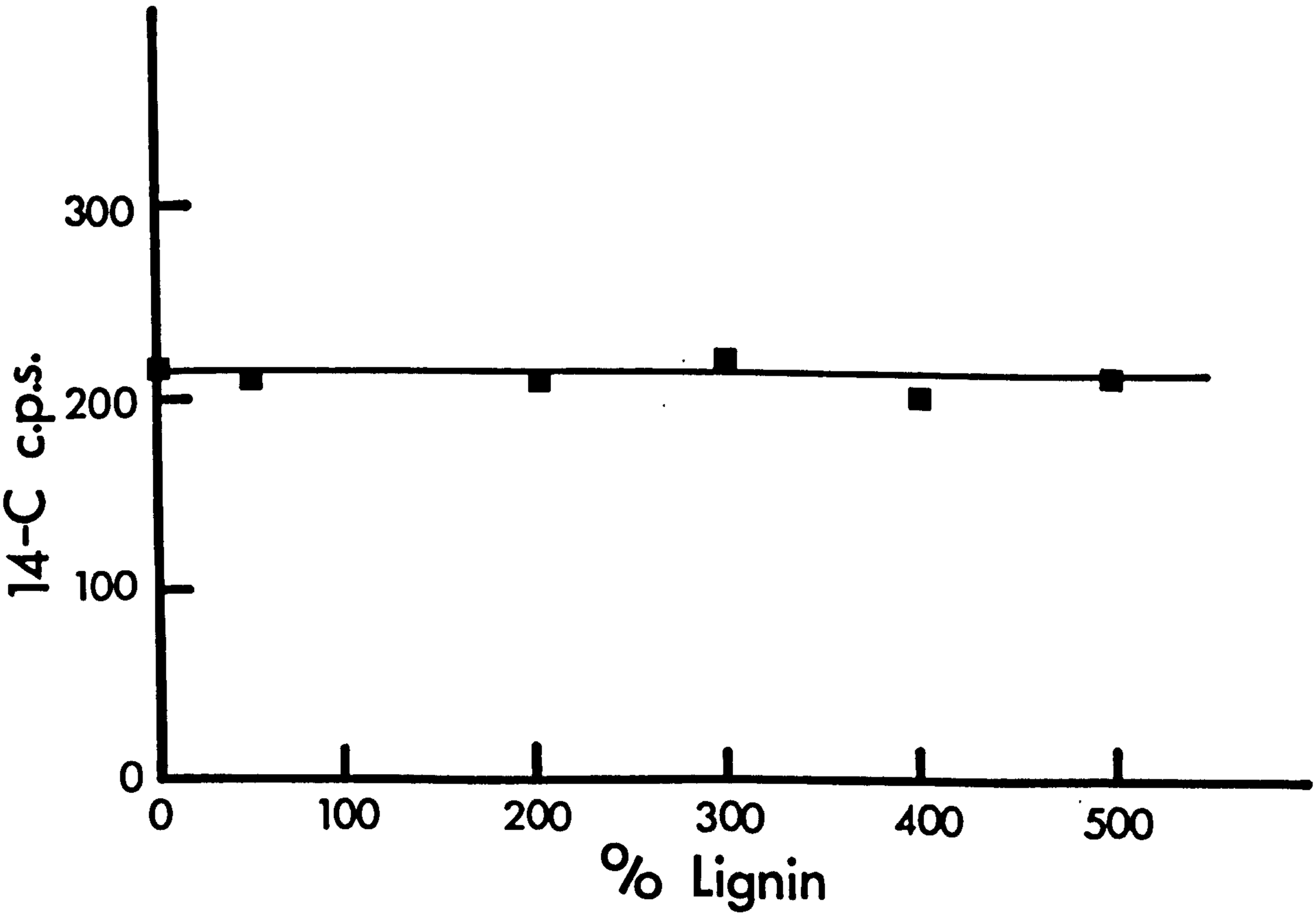

14-C c.p.s.
300
200
100
0
0
100
200
300
400
500
% Lignin

FIG. 92 : The relationship between assimilation rate and soft-body weight (ash-free) in P.contortus and A.fluviatilis at 10°C when each parameter is plotted on logarithmic co-ordinates.

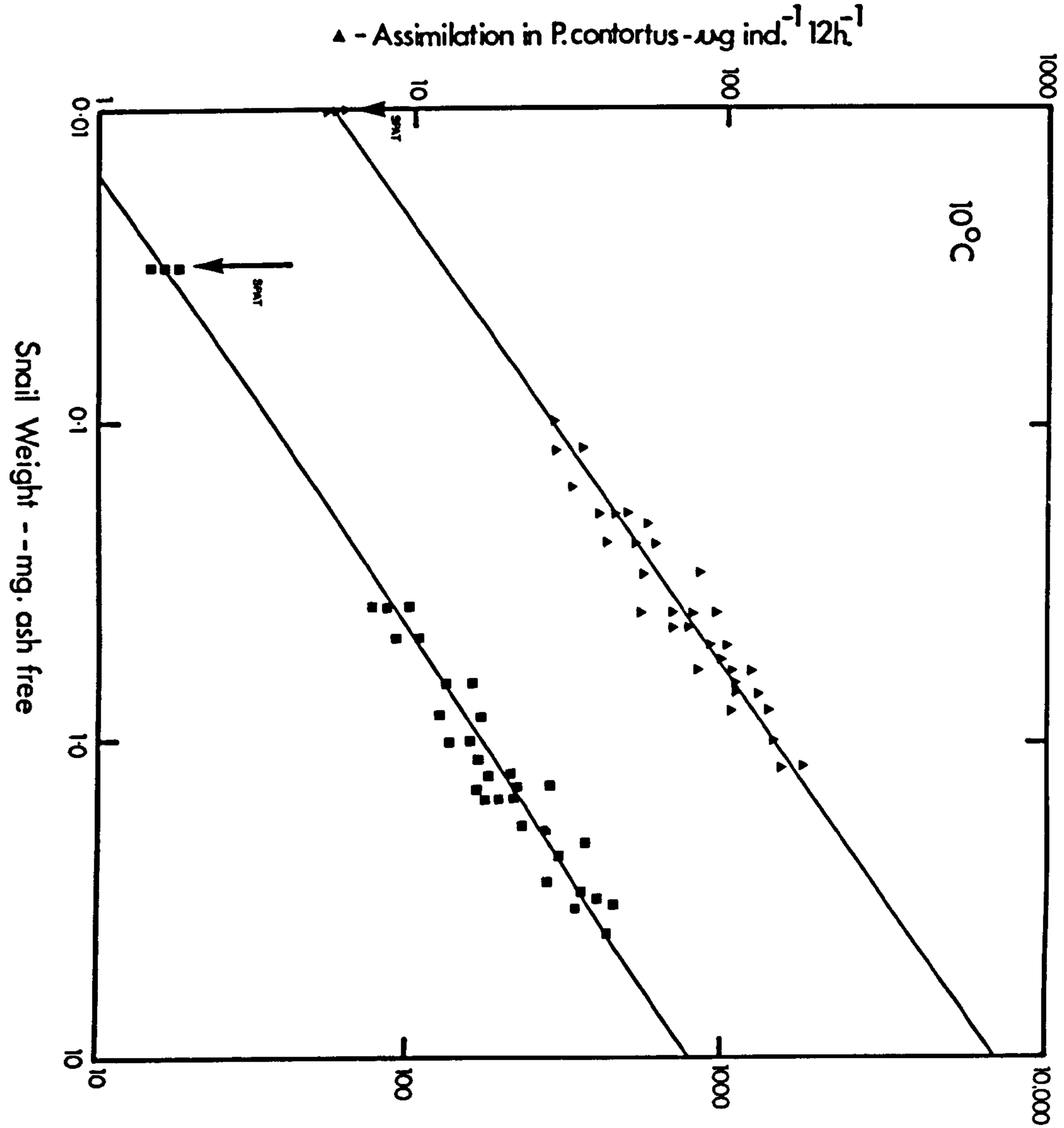

▲ - Assimilation in P.contortus - µg ind.$^{-1}$ 12h.$^{-1}$
1
0·01
10
100
1000
10°C
SMAT
SMAT
Snail Weight --mg. ash free
0·1
1·0
10
100
1000
10,000
■ - Assimilation in A.fluviatilis - µg ind.$^{-1}$ 12h.$^{-1}$

FIG. 93 : The relationship between the logarithm of coefficient 'a' (in the regression equation relating assimilation rate to snail weight) and temperature in A.fluviatilis (A) and P.contortus (B).

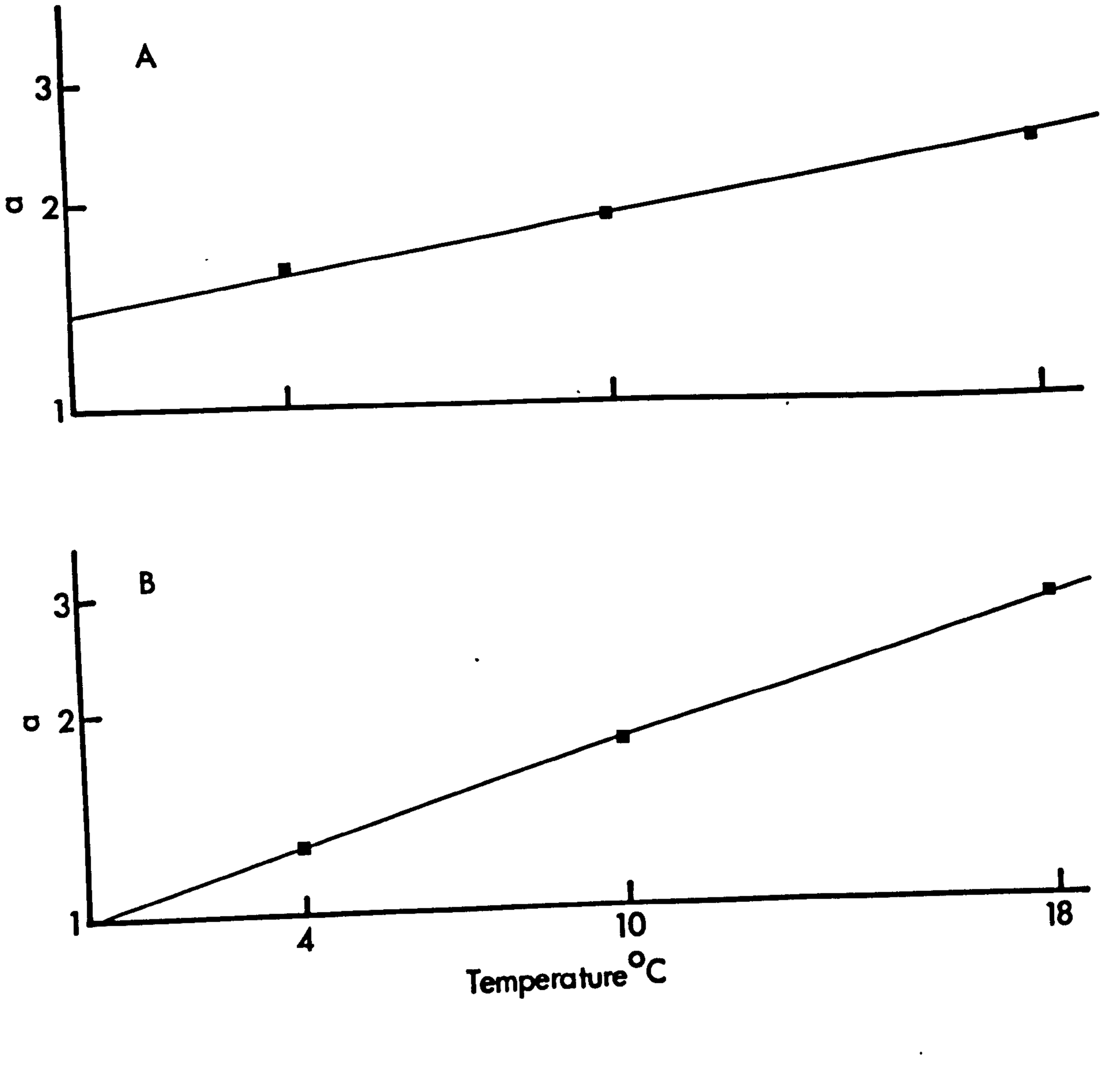

A
3
σ 2
1
B
3
σ 2
1
4
10
18
Temperature °C

FIG. 94 : Net, primary, algal production on Ha Mire shore and at station 2. The vertical bars indicate 95% confidence limits. The mass dimension of production is expressed in ash-free units.

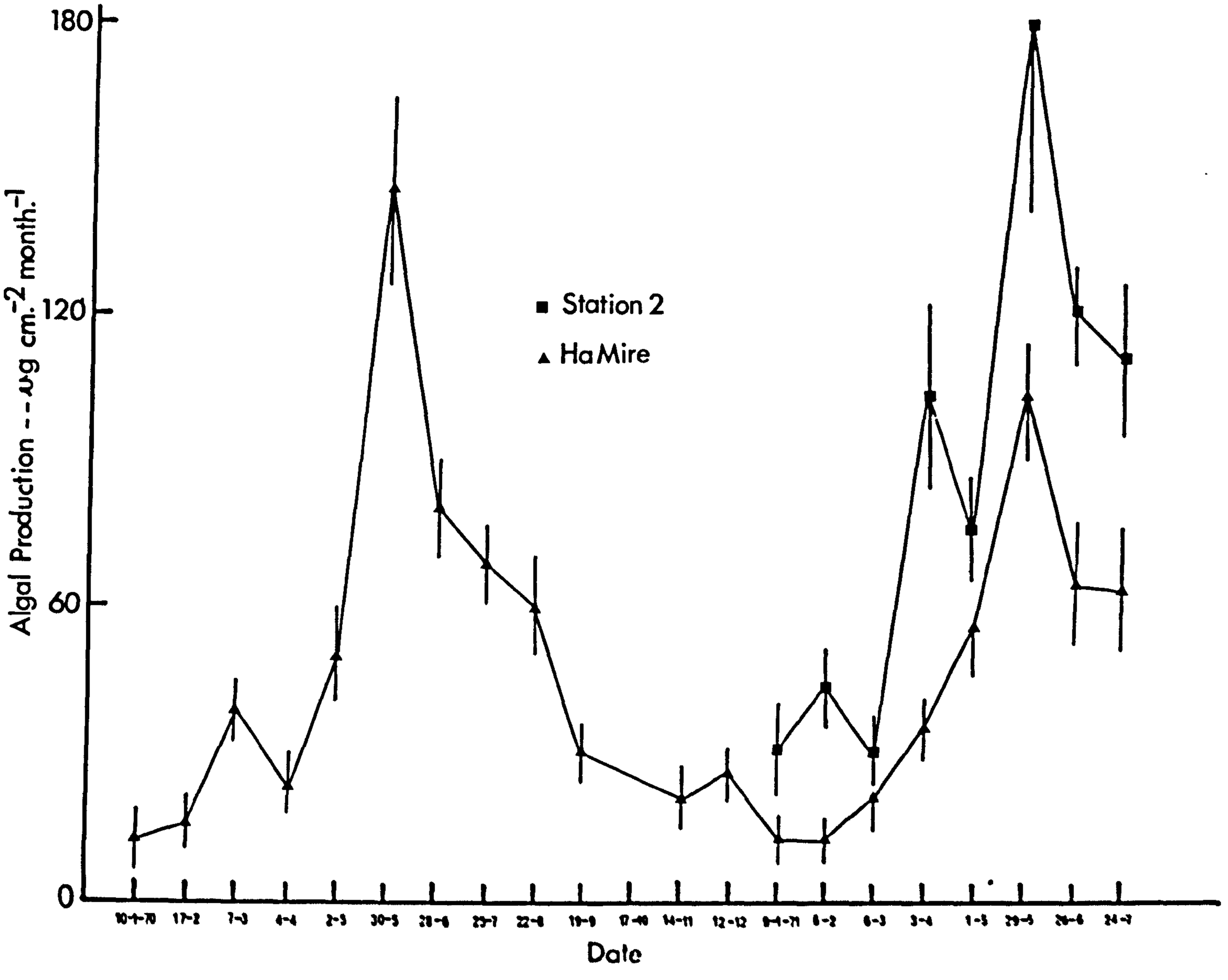

180
120
60
0
Algal Production -- Aug cm.$^{-2}$ month.$^{-1}$
■ Station 2
▲ Ha Mire
10-1-70
17-2
7-3
4-4
2-5
30-5
28-6
25-7
22-8
19-9
17-10
14-11
12-12
9-1-71
6-2
6-3
3-4
1-5
29-5
26-6
24-7
Date

FIG. 95 : Net, intermediary, bacterial production on Ha Mire shore, as monitored by protein accumulation on clean, sterile cover-slips suspended in the Tarn. The vertical bars indicate 95% confidence limits.

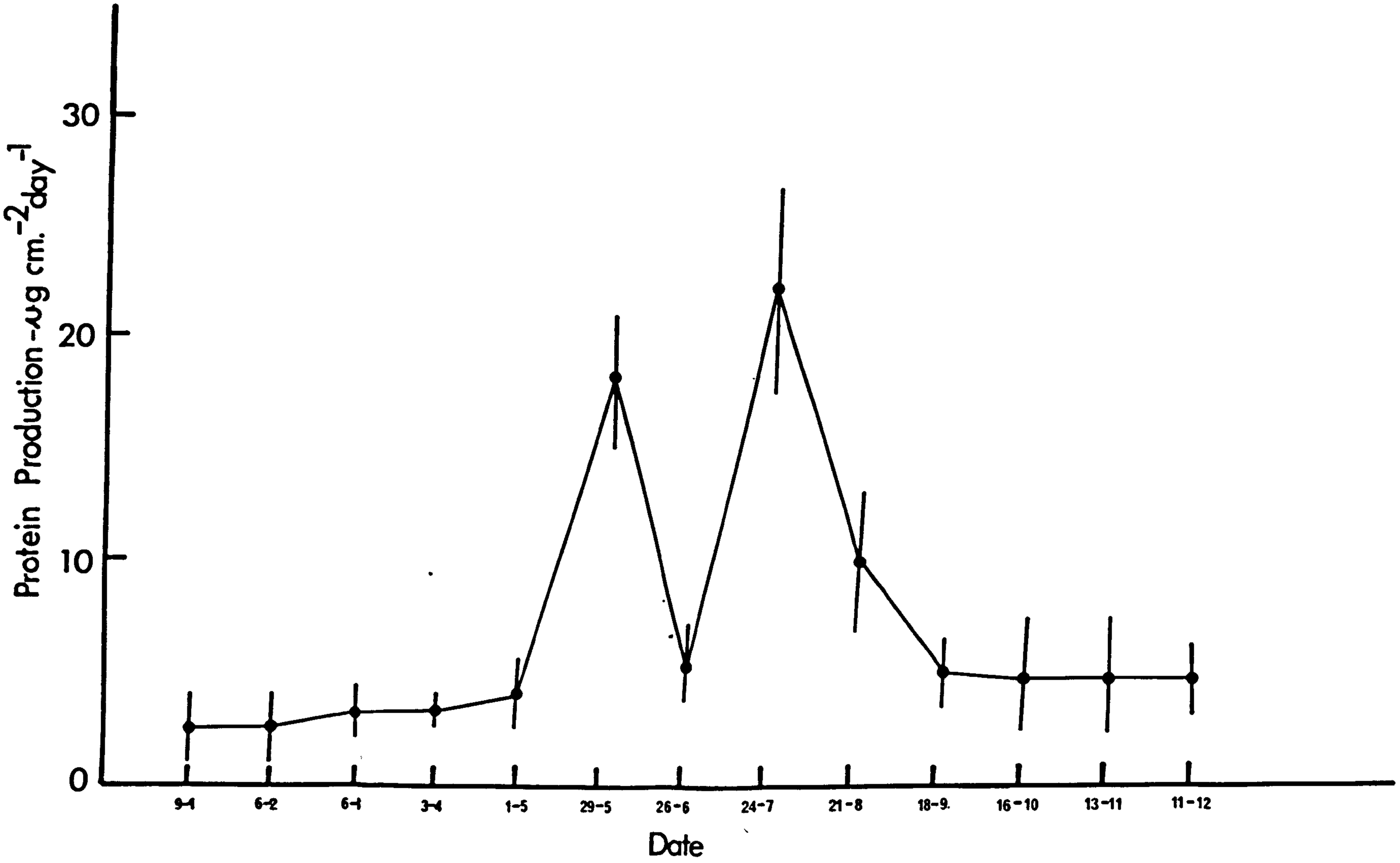

Protein Production - µg cm.$^{-2}$ day^{-1}
30
20
10
0
9-1
6-2
6-1
3-4
1-5
29-5
26-6
24-7
21-8
18-9
16-10
13-11
11-12
Date

FIG. 96 : Bacterial production at various parts of Malham Tarn in May, 1971. The vertical bars indicate 95% confidence limits.

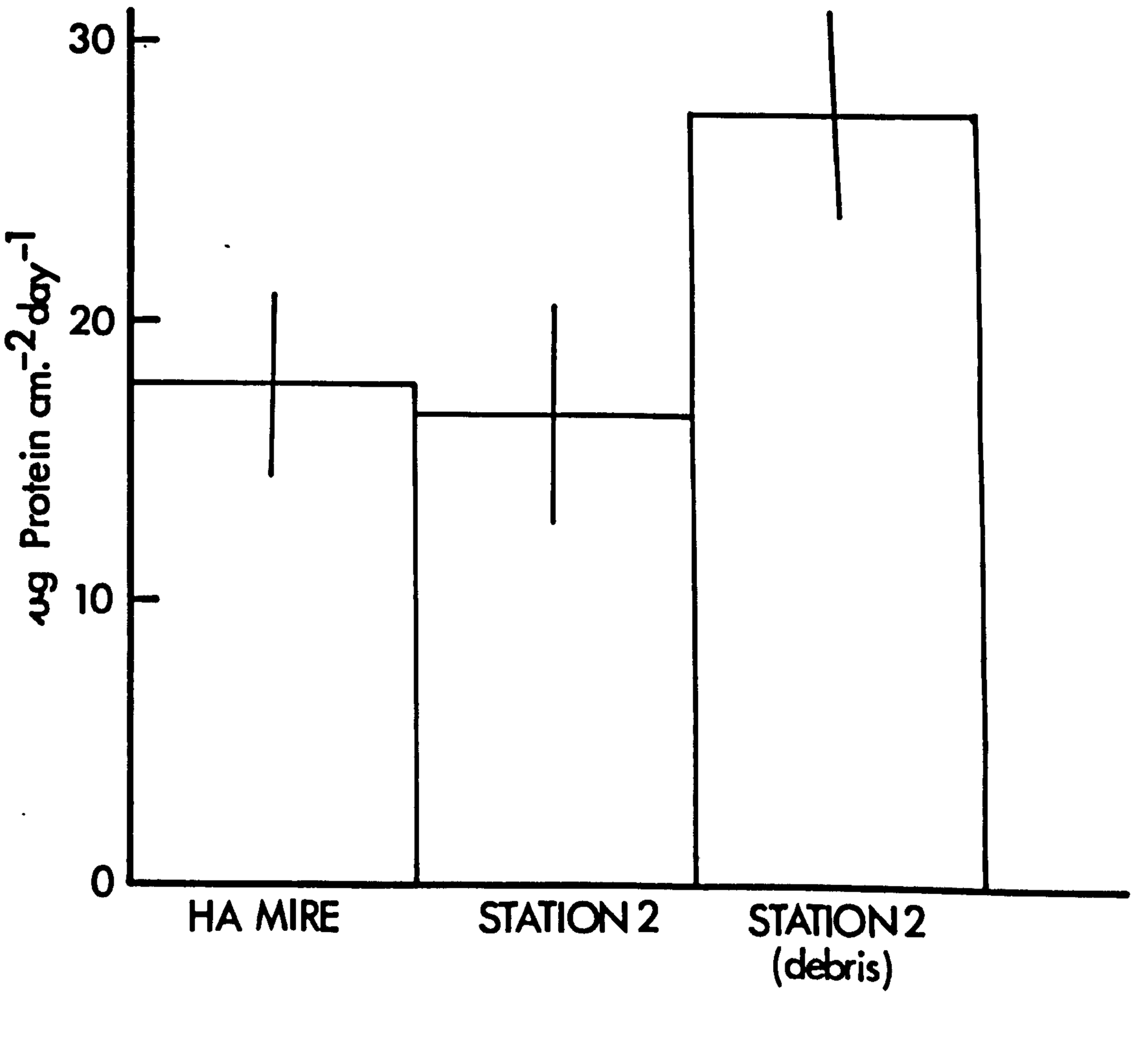

30
20
10
0
µg Protein cm.$^{-2}$ day^{-1}
HA MIRE
STATION 2
STATION 2
(debris)

FIG. 97 : The relationship between the assimilation efficiency of green algae (Scenedesmus), by various species of freshwater gastropods, and the cellulase activity of their gut extracts.

Key

*LS - L.stagnalis
*LP - L.pereger
*PF - P.fontinalis
AF - A.fluviatilis
PA - P.albus
PC - P.contortus
*PP - P.planorbis
*BT - B.tentaculata
PJ - P.jenkinsi
VC - V. cristata

* points represent mean of the cellulase activity of the crop-gizzard apparatus and the hepato-pancreas.

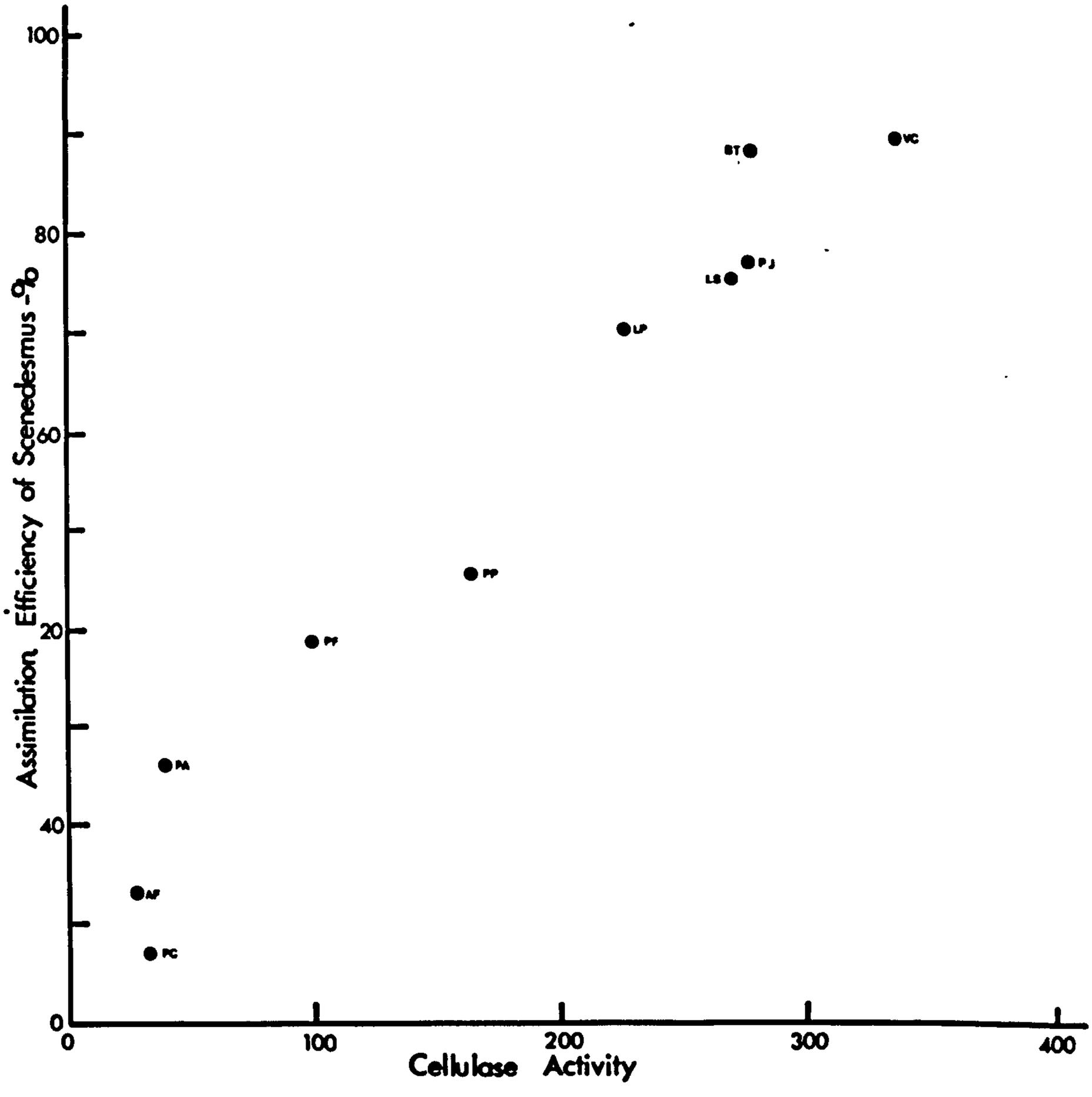

Assimilation Efficiency of Scenedesmus - %
100
80
60
40
20
0
0
100
200
300
400
Cellulase Activity

FIG. 98 : A hypothetical scheme of relationships between various members of the Gastropoda.

Key

C+ - Cellulase present (or high activity).

C- - Cellulase absent (or low activity).

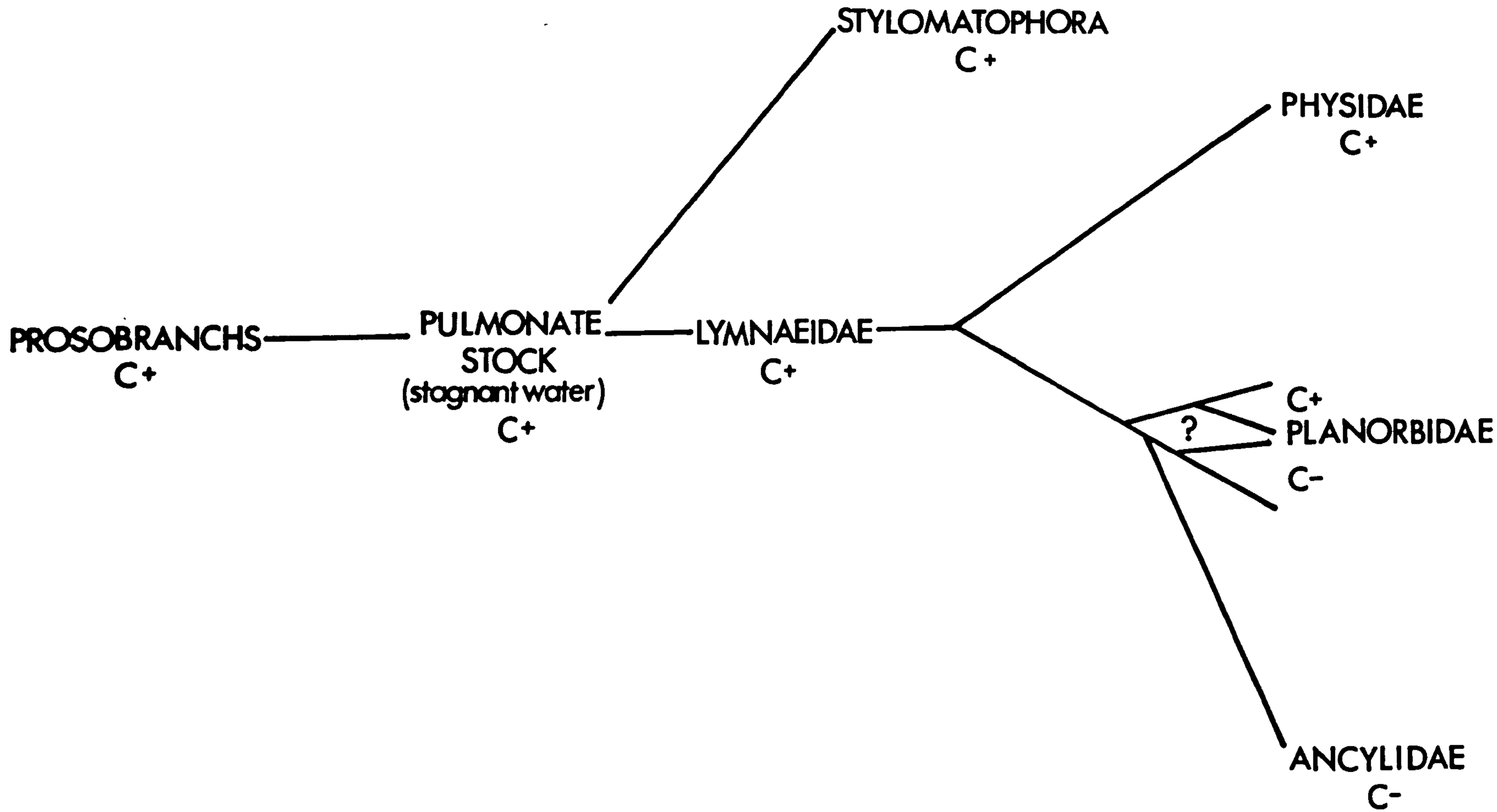

STYLOMATOPHORA
C+
PHYSIDAE
C+
PROSOBRANCHS
C+
PULMONATE
STOCK
(stagnant water)
C+
LYMNAEIDAE
C+
?
C+
PLANORBIDAE
C-
ANCYLIDAE
C-

FIG. 99 : Circuit diagram for the polarising unit used in the oxygen electrode apparatus. It provides a fixed polarising voltage of ca. 0.7v. (* - Beckman 10 inch recorder, 1 m.v. full scale deflection).

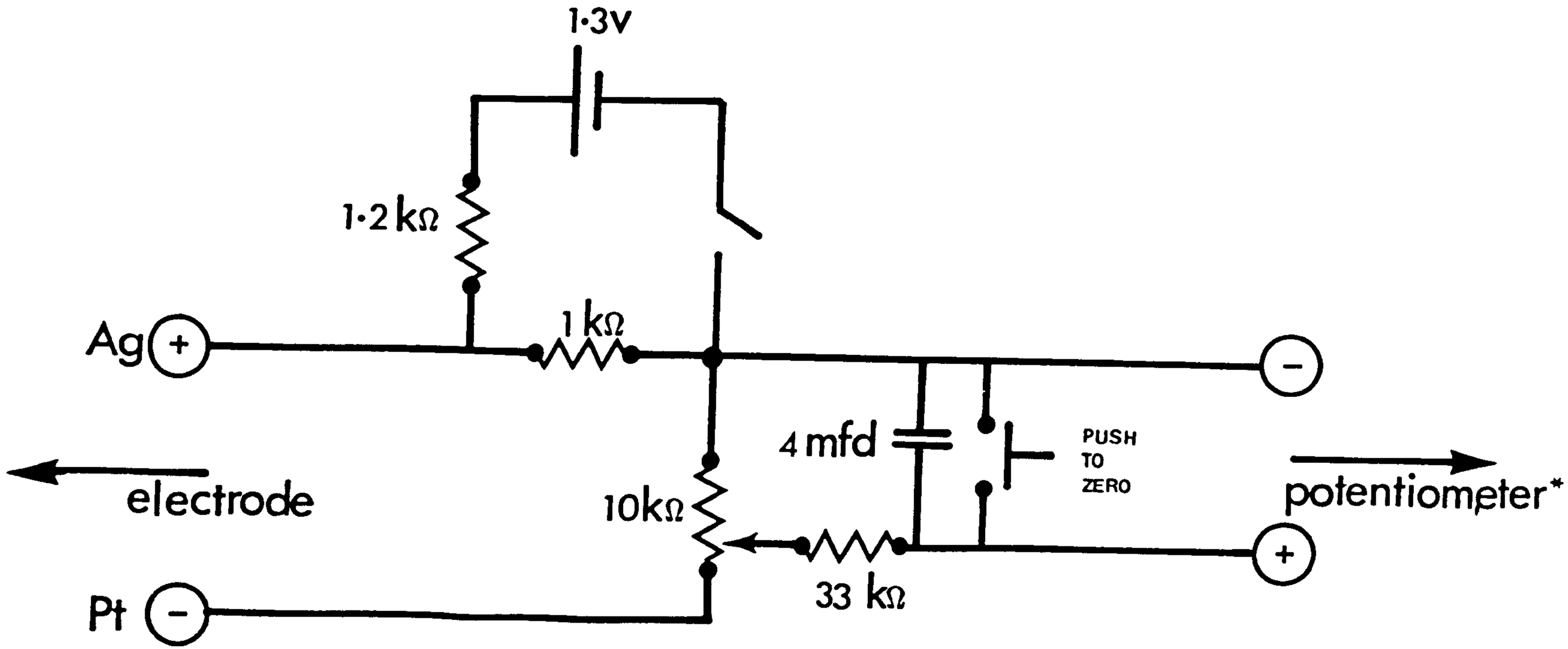

1·3v
1·2 kΩ
1 kΩ
Ag
+
electrode
10kΩ
Pt
−
4 mfd
PUSH
TO
ZERO
33 kΩ
potentiometer*
−
+

FIG. 100 : The oxygen electrode response, in terms of potentiometer deflection (%), to tapwater solutions containing different, known concentrations of oxygen at 10°C.

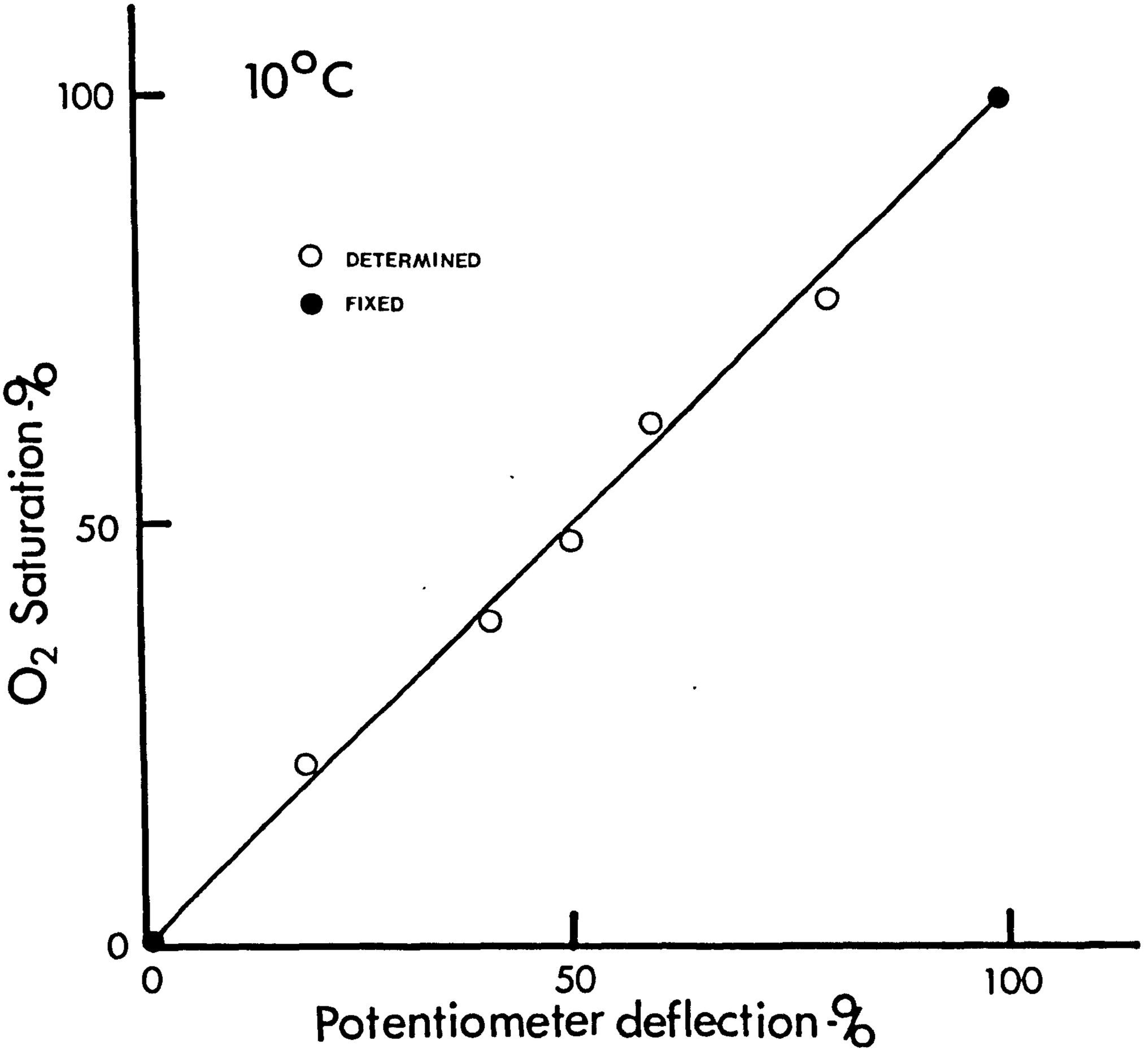

10°C
100
50
0
O DETERMINED
● FIXED
O2 Saturation-%
0
50
100
Potentiometer deflection-%

FIG. 101 : The acclimatory response of A.fluviatilis. Vertical bars indicate the 95% confidence limits. Horizontal lines show the respiratory rates of cohorts maintained at constant temperatures, whereas the curves show the response of cohorts which had suffered an abrupt temperature change from either 4 or 18°C to 10°C. Dotted lines indicate an effect possibly due to adverse laboratory conditions.

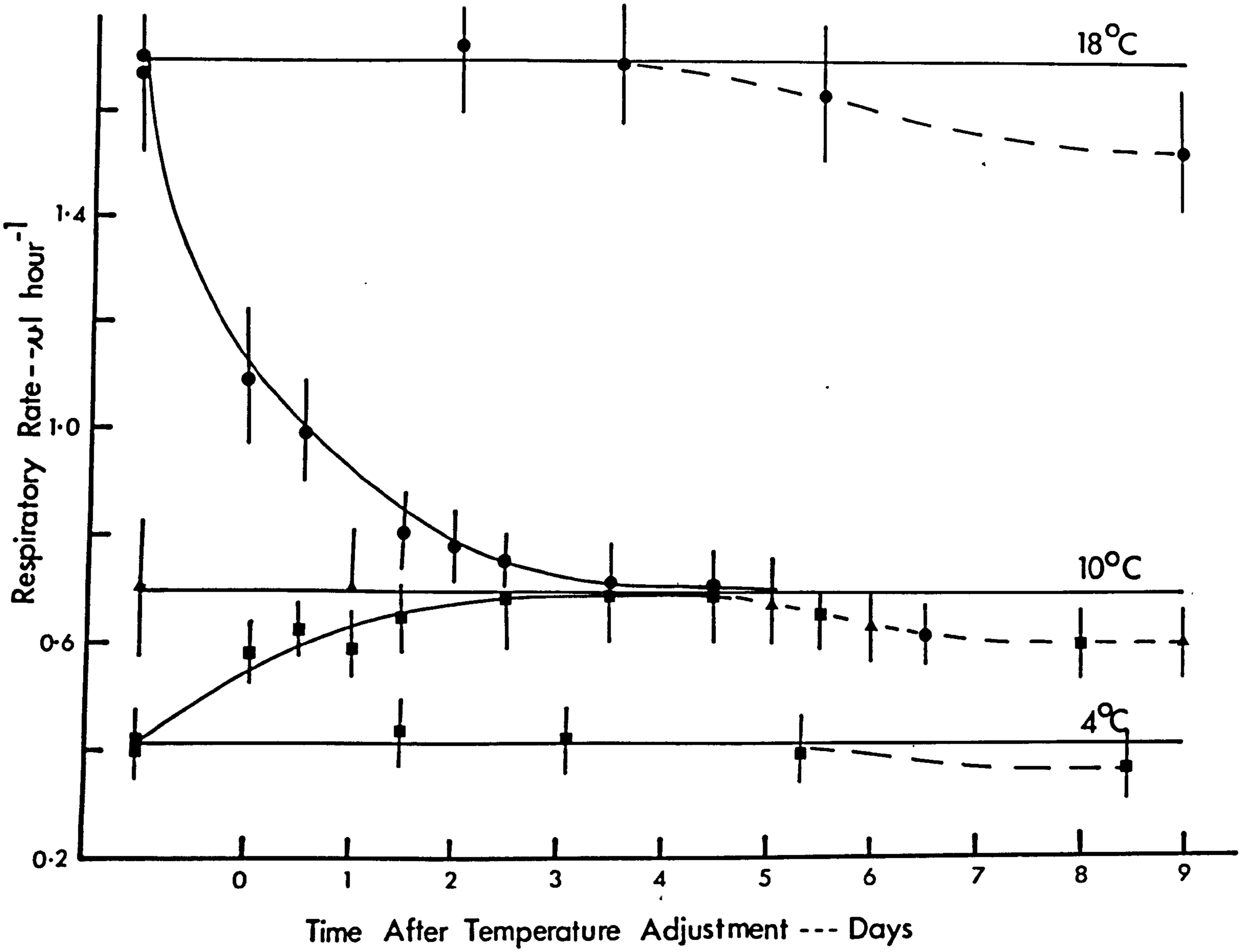

18°C
10°C
4°C
Respiratory Rate--µl hour⁻¹
1·4
1·0
0·6
0·2
0
1
2
3
4
5
6
7
8
9
Time After Temperature Adjustment --- Days

FIG. 102 : The acclimatory response of P.contortus. For further explanation see FIG. 101.

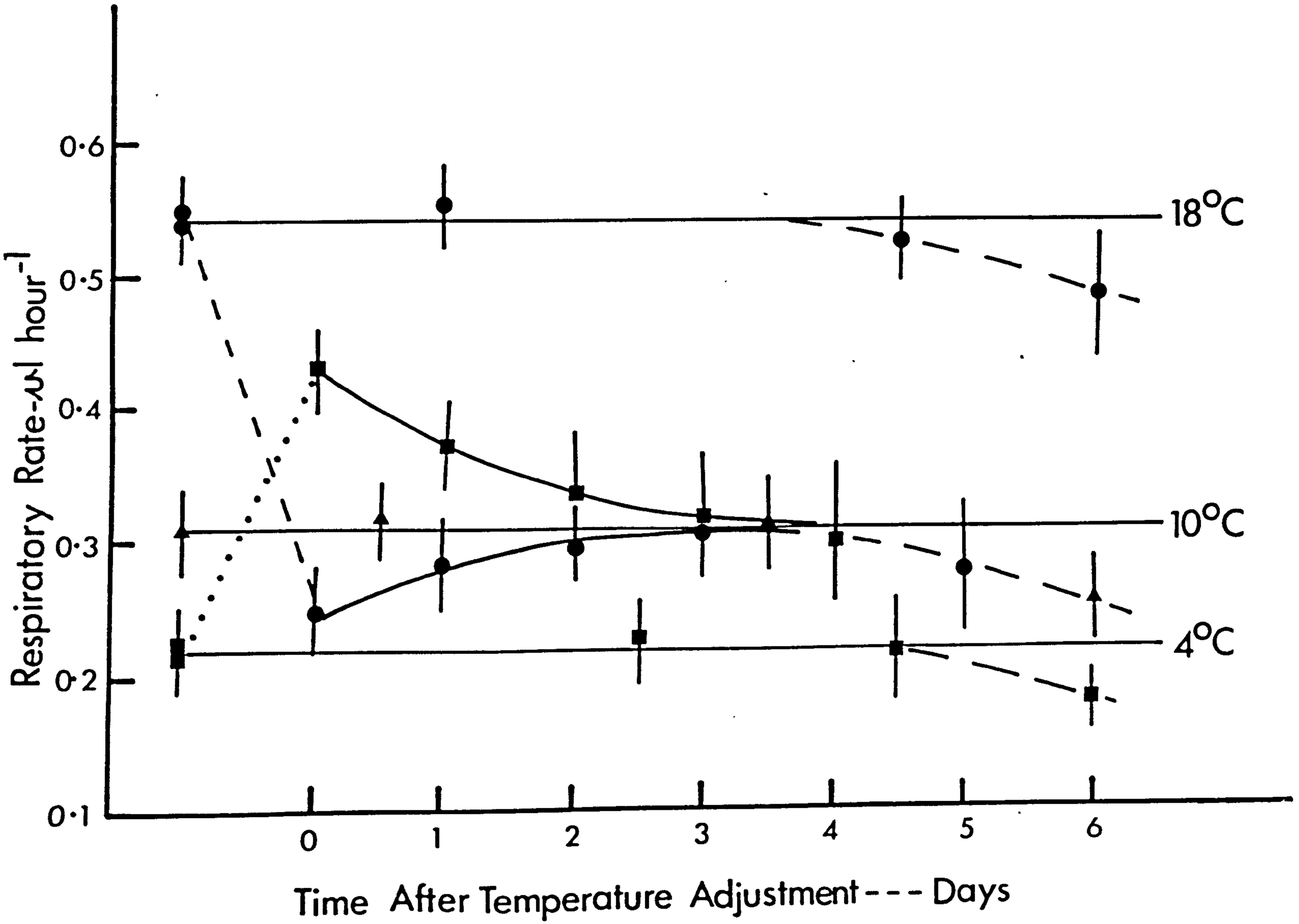

0·6
0·5
0·4
0·3
0·2
0·1
Respiratory Rate-µl hour⁻¹
18°C
10°C
4°C
0
1
2
3
4
5
6
Time After Temperature Adjustment - - - Days

FIG. 103 : R - T curves for 4°C and 18°C acclimated cohorts of A.fluviatilis. The broken lines link the respiratory rates of groups which were acclimated to each temperature of measurement. Vertical bars indicate 95% confidence limits.

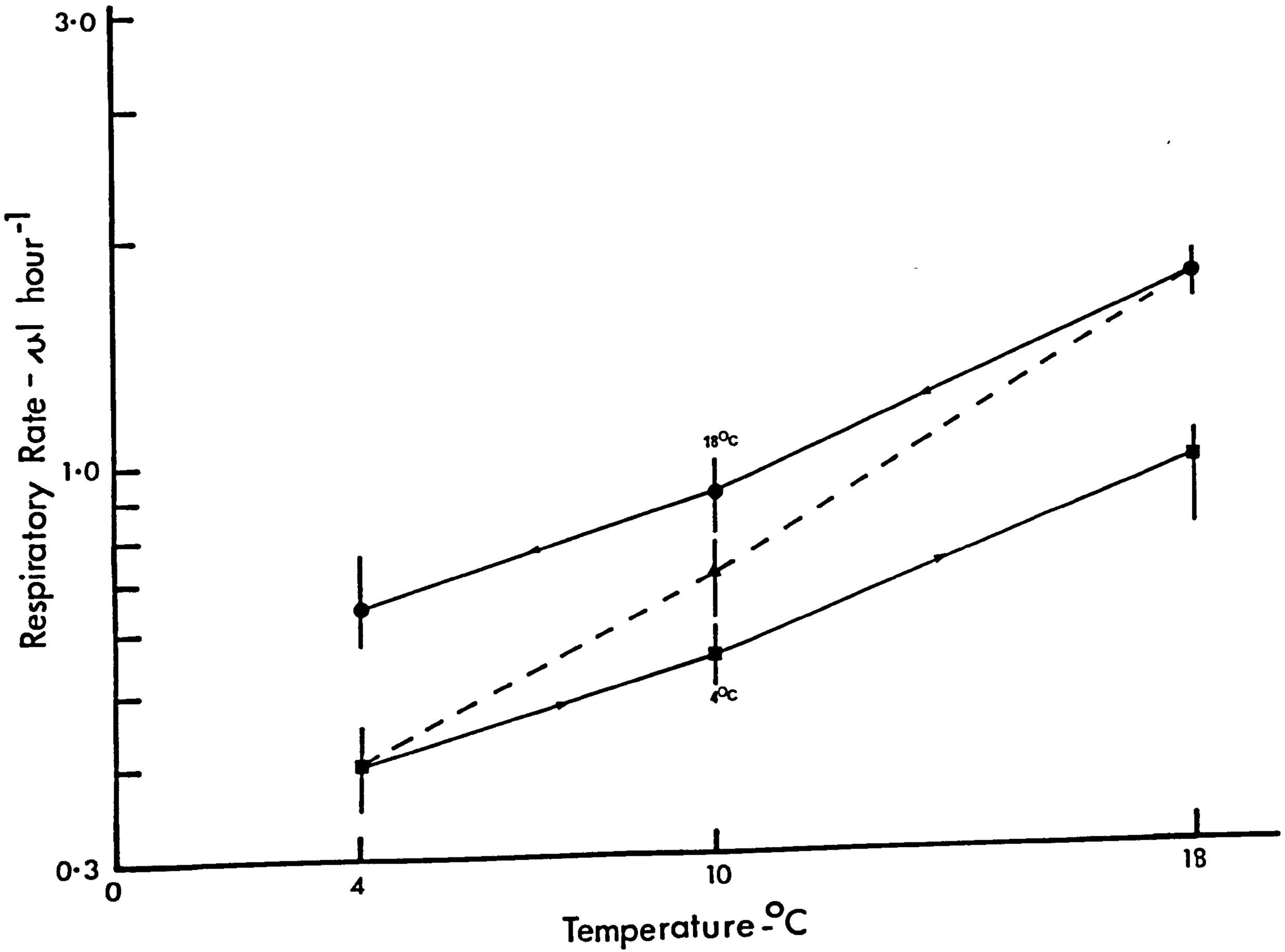

3·0
1·0
0·3
0
4
10
18
18°c
4°c
Respiratory Rate - µl hour⁻¹
Temperature - °C

FIG. 104 : R - T curves for 4 and 18°C acclimated cohorts of P.contortus. The broken lines link the respiratory rates of groups which were acclimated to each temperature of measurement. Vertical bars indicate 95% confidence limits.

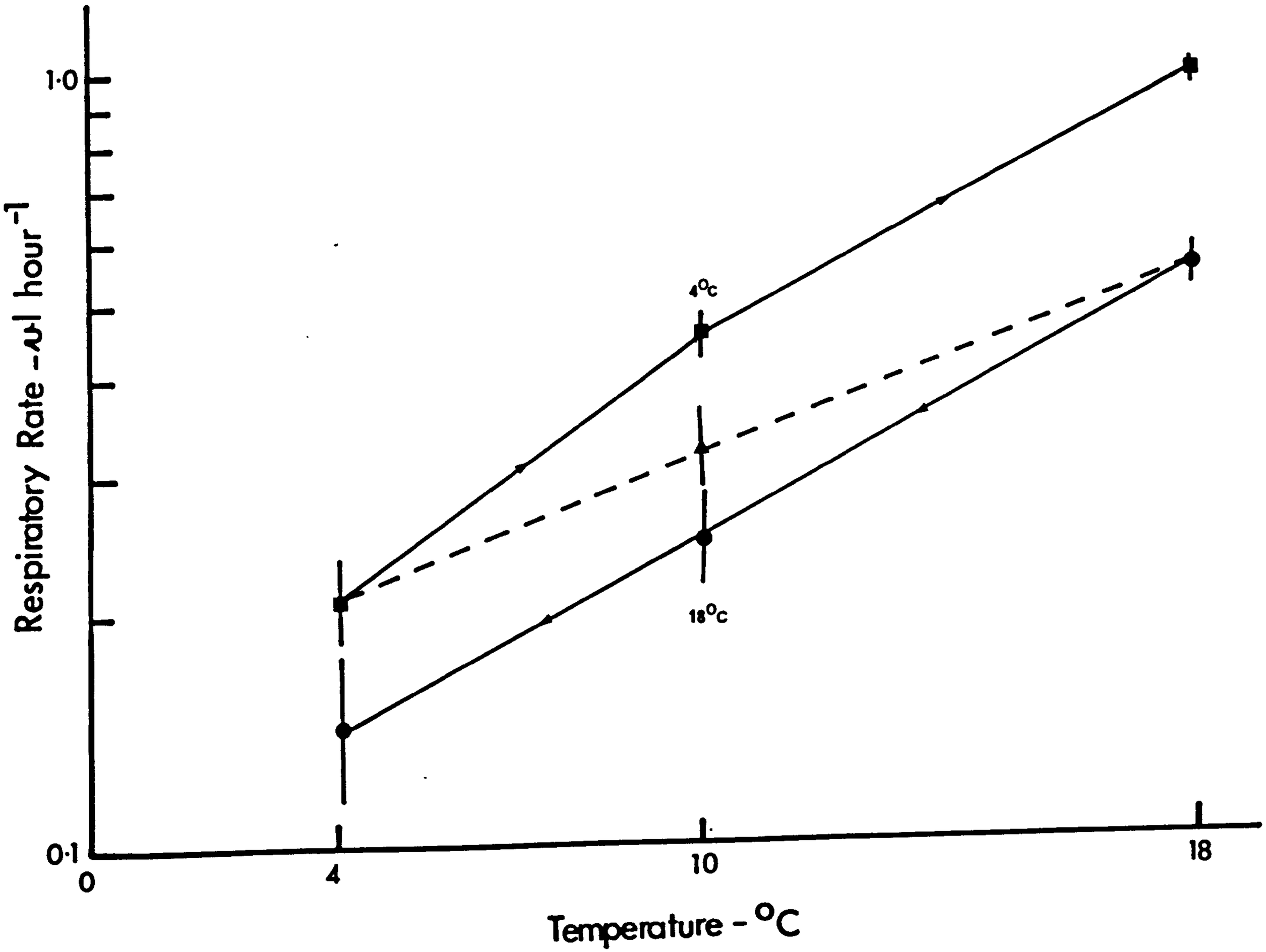

Respiratory Rate - µl hour⁻¹
1·0
0·1
0
4
10
18
4°c
18°c
Temperature - °C

FIG. 105 : The effect of environmental oxygen concentration on the respiratory rates of A.fluviatilis and P.contortus. Respiration is expressed as a % of the rate which was measured under conditions of complete saturation.

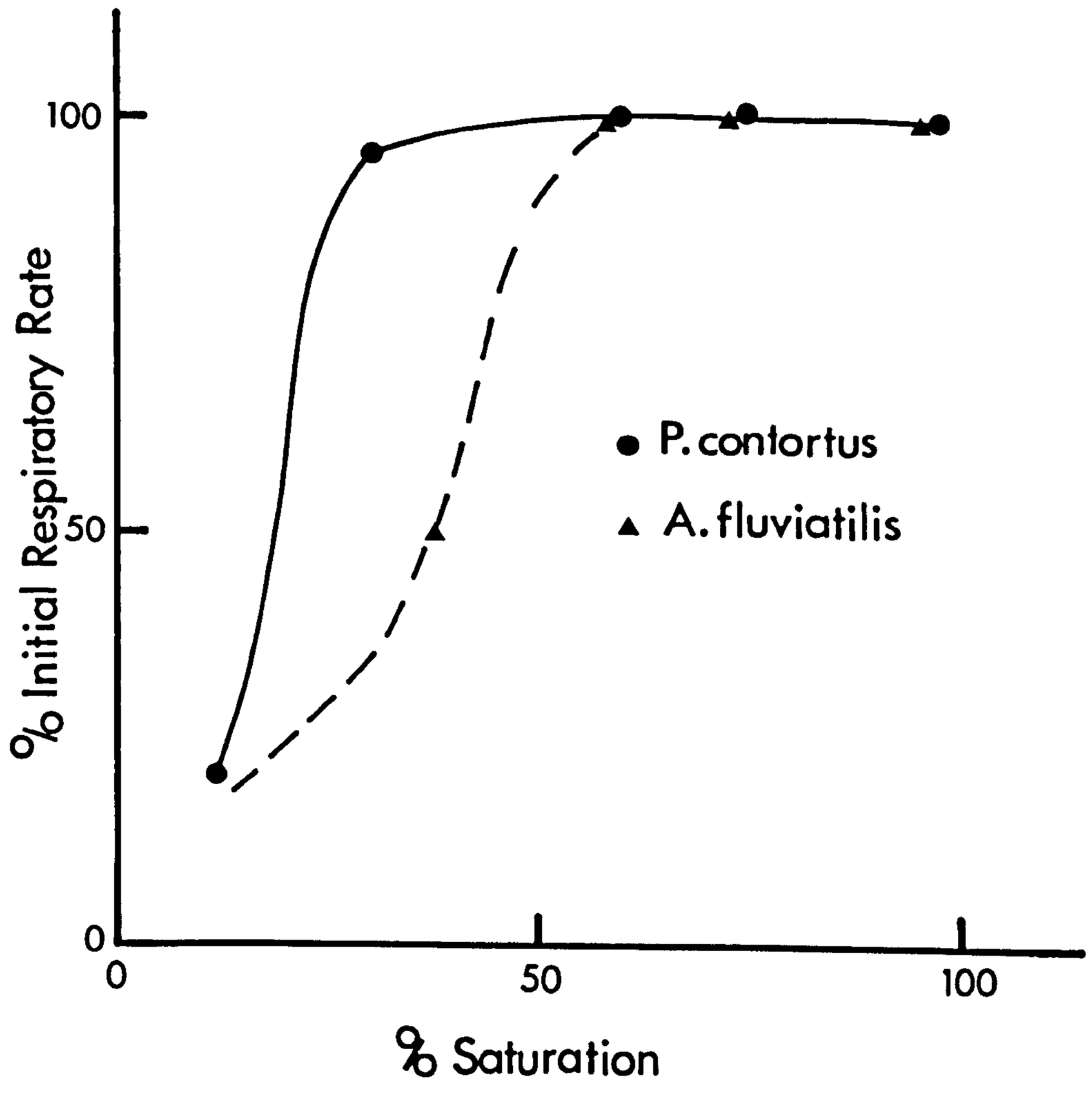

100
50
0
% Initial Respiratory Rate
0
50
100
% Saturation
P. contortus
A. fluviatilis

FIG. 106 : The survivorship curves of cohorts of A.fluviatilis and P.contortus in oxygen-free water. Berg's data for A.fluviatilis are also included (see text).

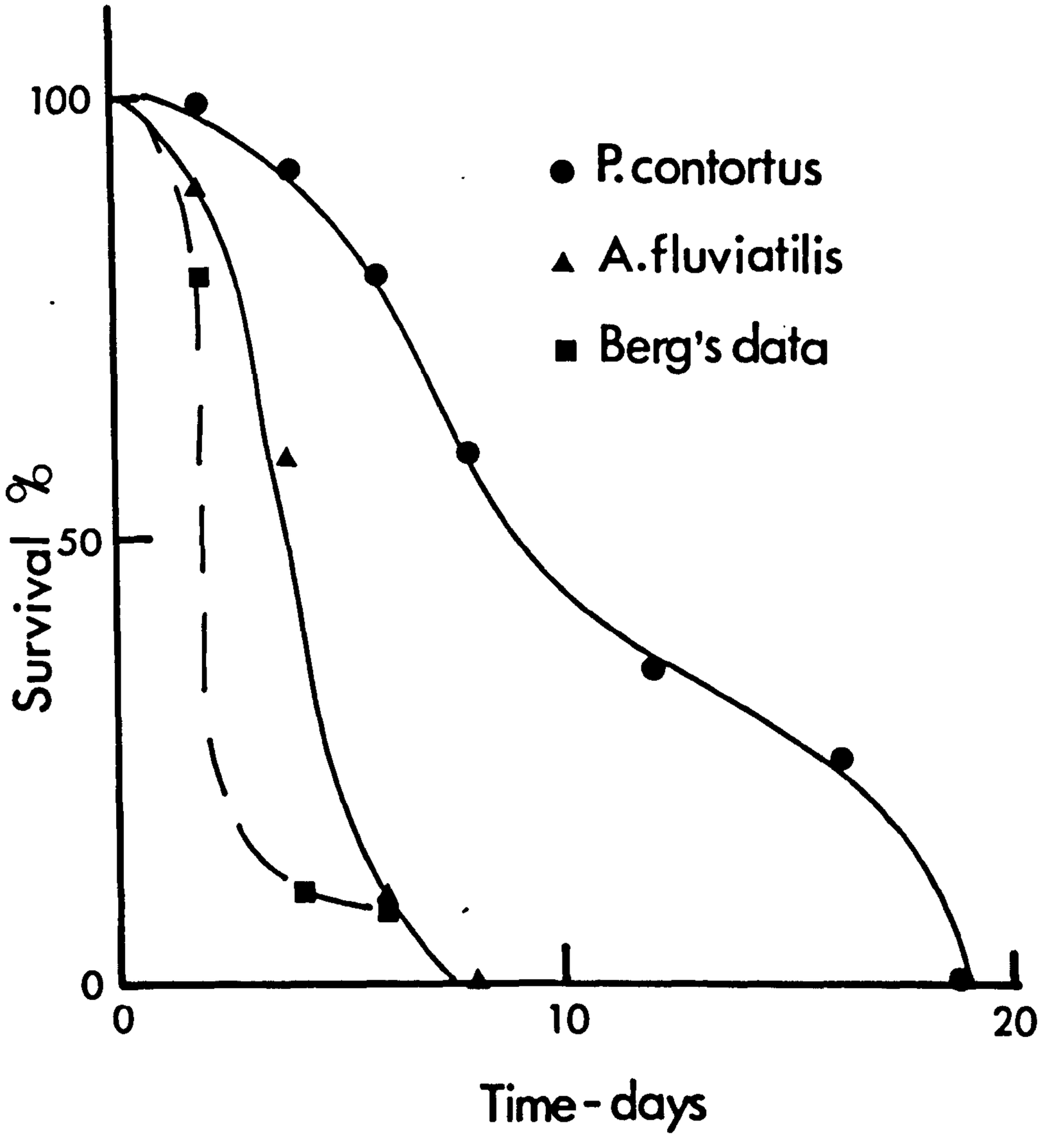

100
50
0
Survival %
0
10
20
Time - days
P. contortus
A. fluviatilis
Berg's data

FIG. 107 : The effect of starvation on respiration in constrained and mobile individuals of A.fluviatilis. Vertical bars indicate the 95% confidence limits and the broken line represents the time course of gut emptying as indicated by the loss of ingested 51-Cr from the body.

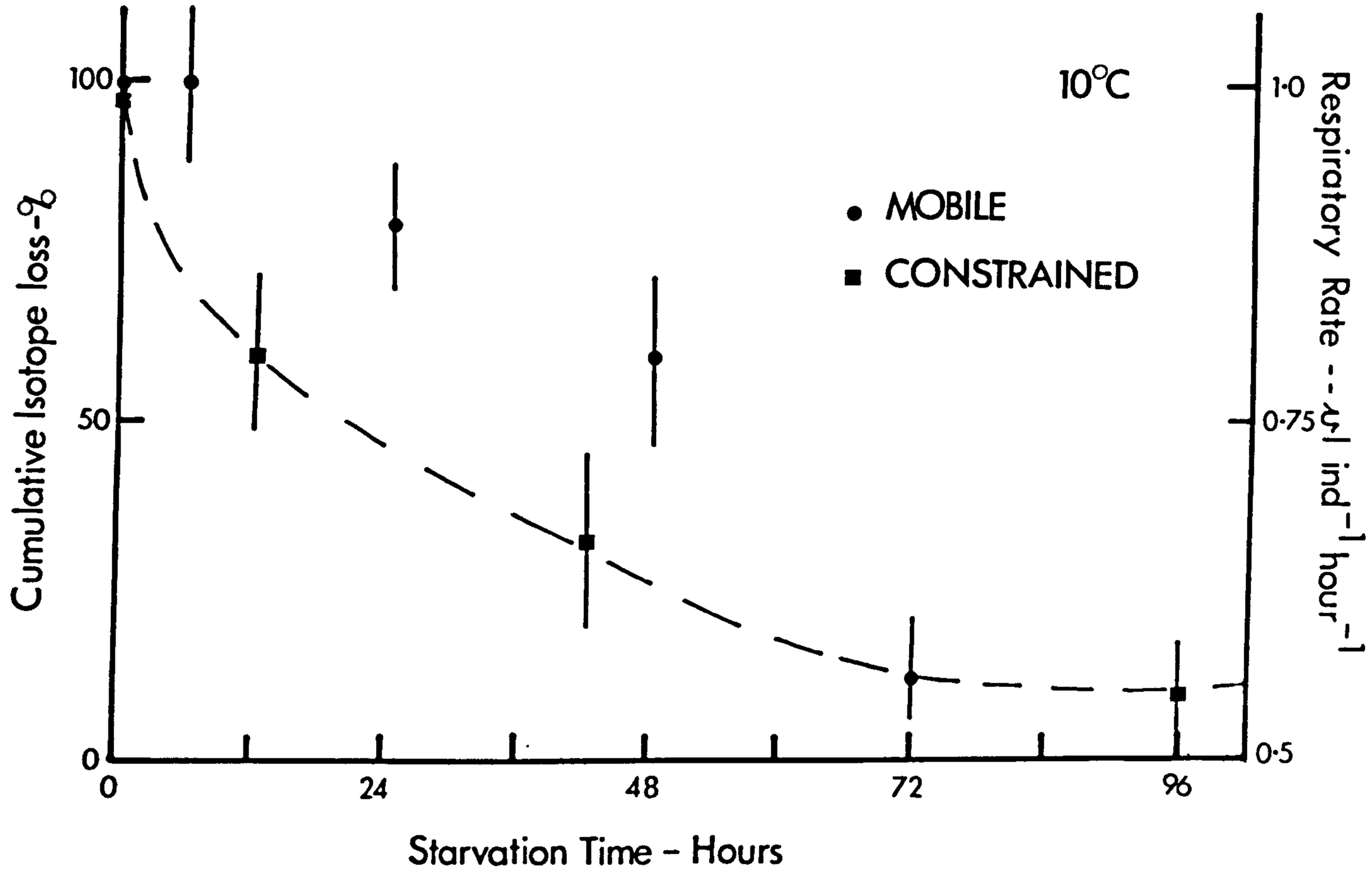

10°C
MOBILE
CONSTRAINED
Cumulative Isotope loss-%
100
50
0
0
24
48
72
96
Starvation Time – Hours
Respiratory Rate -- µl ind⁻¹ hour⁻¹
1·0
0·75
0·5

FIG. 108 : The effect of starvation on respiration in constrained and mobile individuals of P.contortus. For further explanation see FIG. 107.

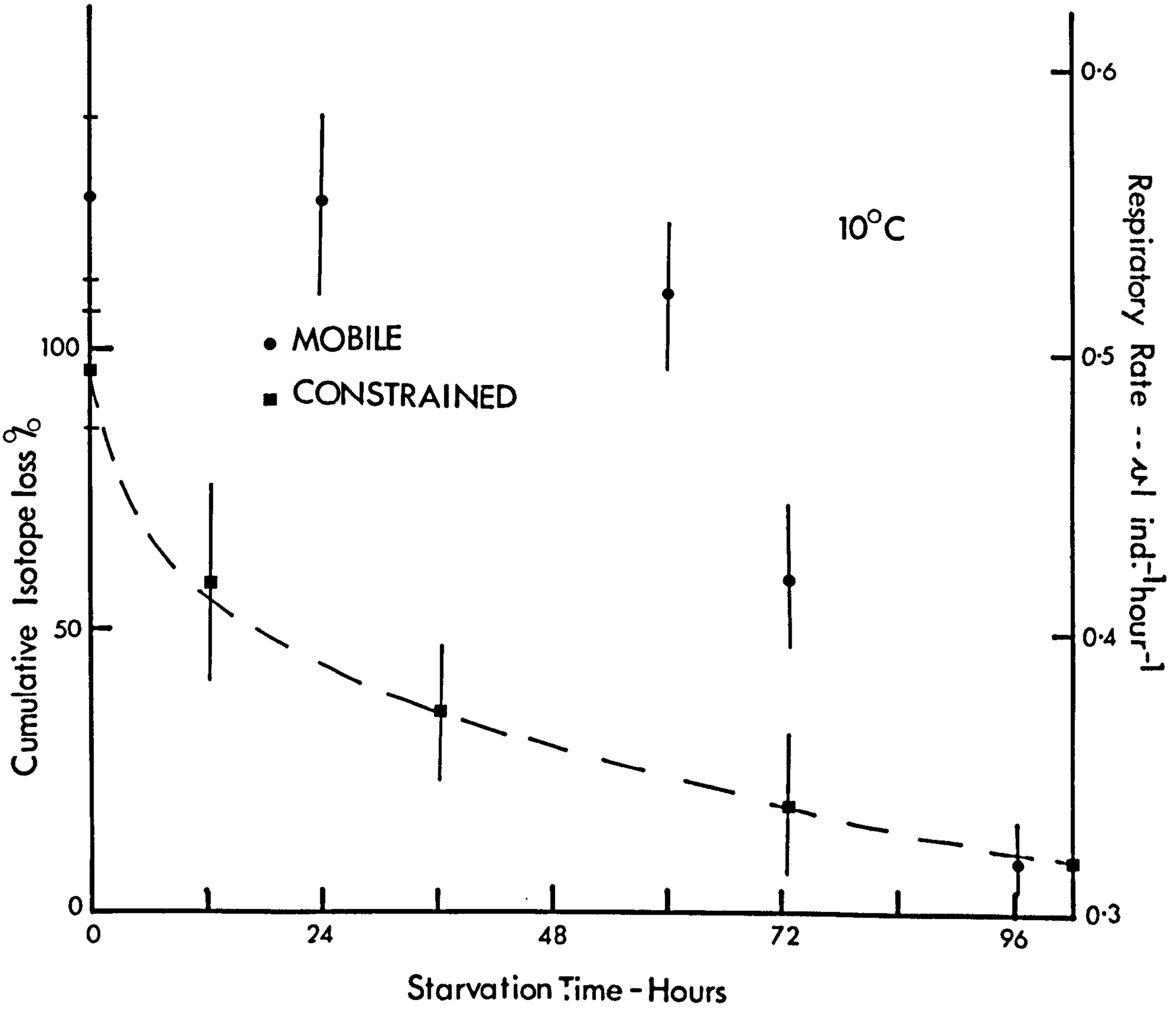

10°C
• MOBILE
■ CONSTRAINED
Cumulative Isotope loss %
100
50
0
0
24
48
72
96
Starvation Time - Hours
Respiratory Rate -- µl ind⁻¹hour⁻¹
0·6
0·5
0·4
0·3

FIG. 109 : The relationship between the respiratory rate and the shell-free tissue weight of A.fluviatilis and P.contortus, at 10°C, when the data are plotted on logarithmic co-ordinates.

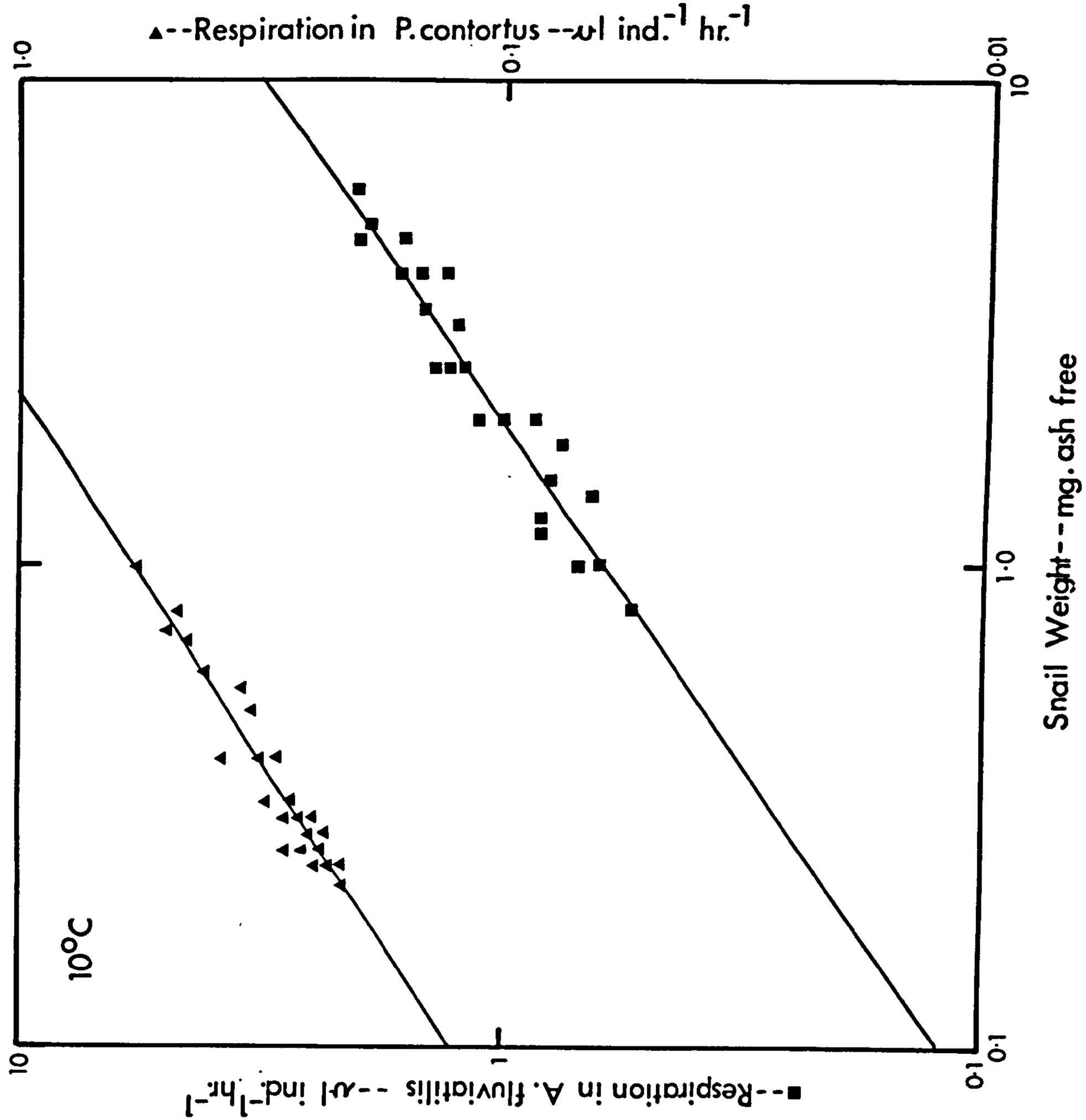

▲--Respiration in P. contortus --µl ind.$^{-1}$ hr.$^{-1}$
1·0
0·1
0·01
10
1·0
0·1
10°C
■--Respiration in A. fluviatilis --µl ind.$^{-1}$hr.$^{-1}$
10
1
0·1
Snail Weight--mg. ash free

FIG. 110 : The relationship between shell-free wet, and dry weight in L.stagnalis Individuals were taken from Malham Tarn. Wet weights were determined immediately after killing in boiled water. Dry weights were determined, on the same individuals, after drying to constant weight in an oven at 40°C.

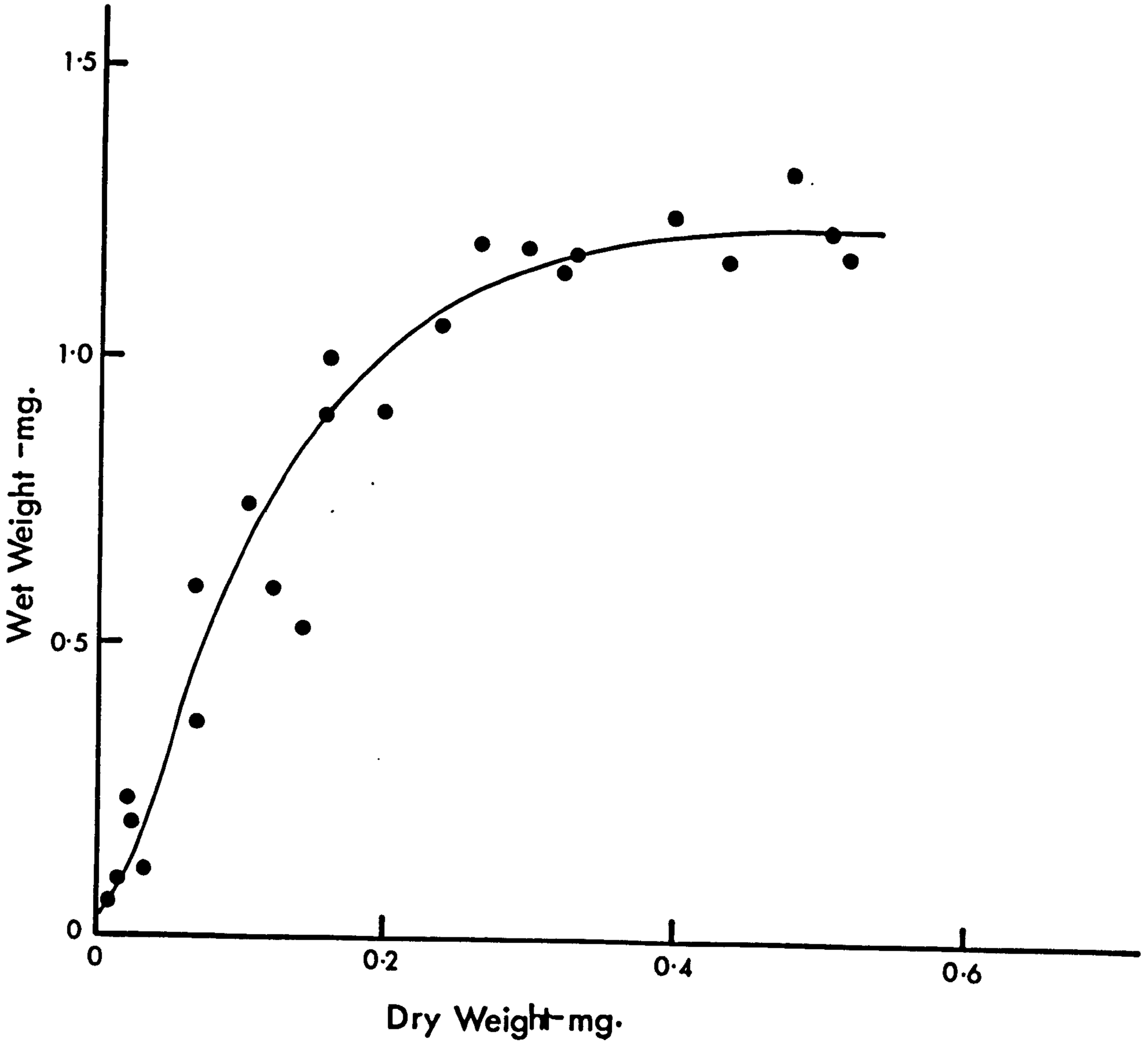

1·5
1·0
0·5
0
Wet Weight - mg.
0
0·2
0·4
0·6
Dry Weight - mg.

FIG. 111 : A comparison of the respiratory rates of A. fluviatilis, predicted from equation 9(8. 2), and based on observations made at one time of the year (March) and day (day-time), with observations made at other times of the year and day (night-time). The vertical bars and curved lines represent 95% confidence limits made on the point estimates and regression line respectively.

Key

1 - April
2 - May
3 - June
4 - July
5 - August
6 - November
7 - December
8 - February
9 - night-time estimation in March 1971.

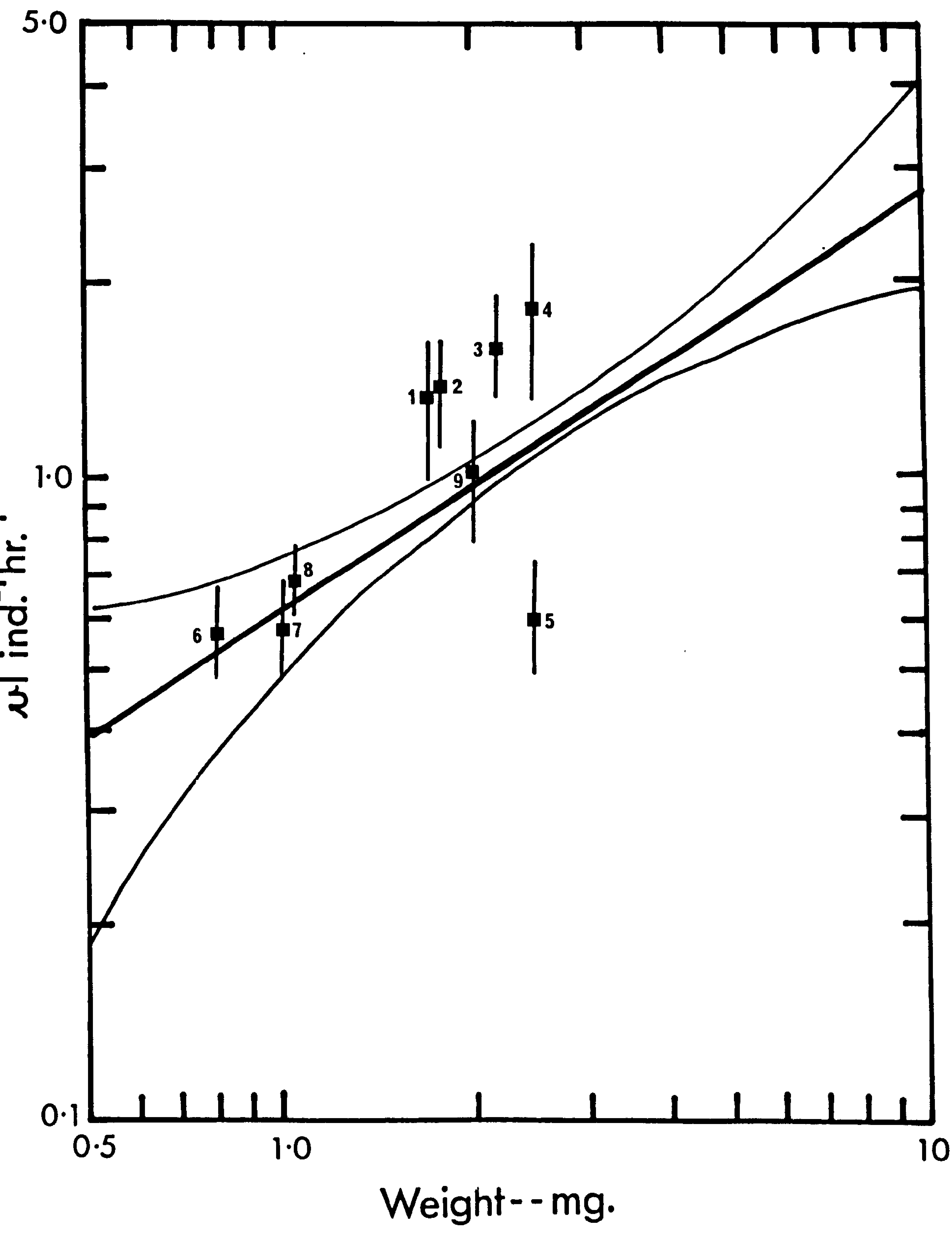

5·0
1·0
0·1
µl ind.⁻¹ hr.⁻¹
1
2
3
4
5
6
7
8
9
0·5
1·0
10
Weight--mg.

FIG. 112 : A comparison of the respiratory rates of P.contortus, predicted from equation 12(8. 2), and based on observations made at one time of the year (March) and day (day-time), with observations made at other times of year and day (night-time). The vertical bars and curved lines represent 95% confidence limits made on the point estimates and regression lines respectively. For key see FIG 111.

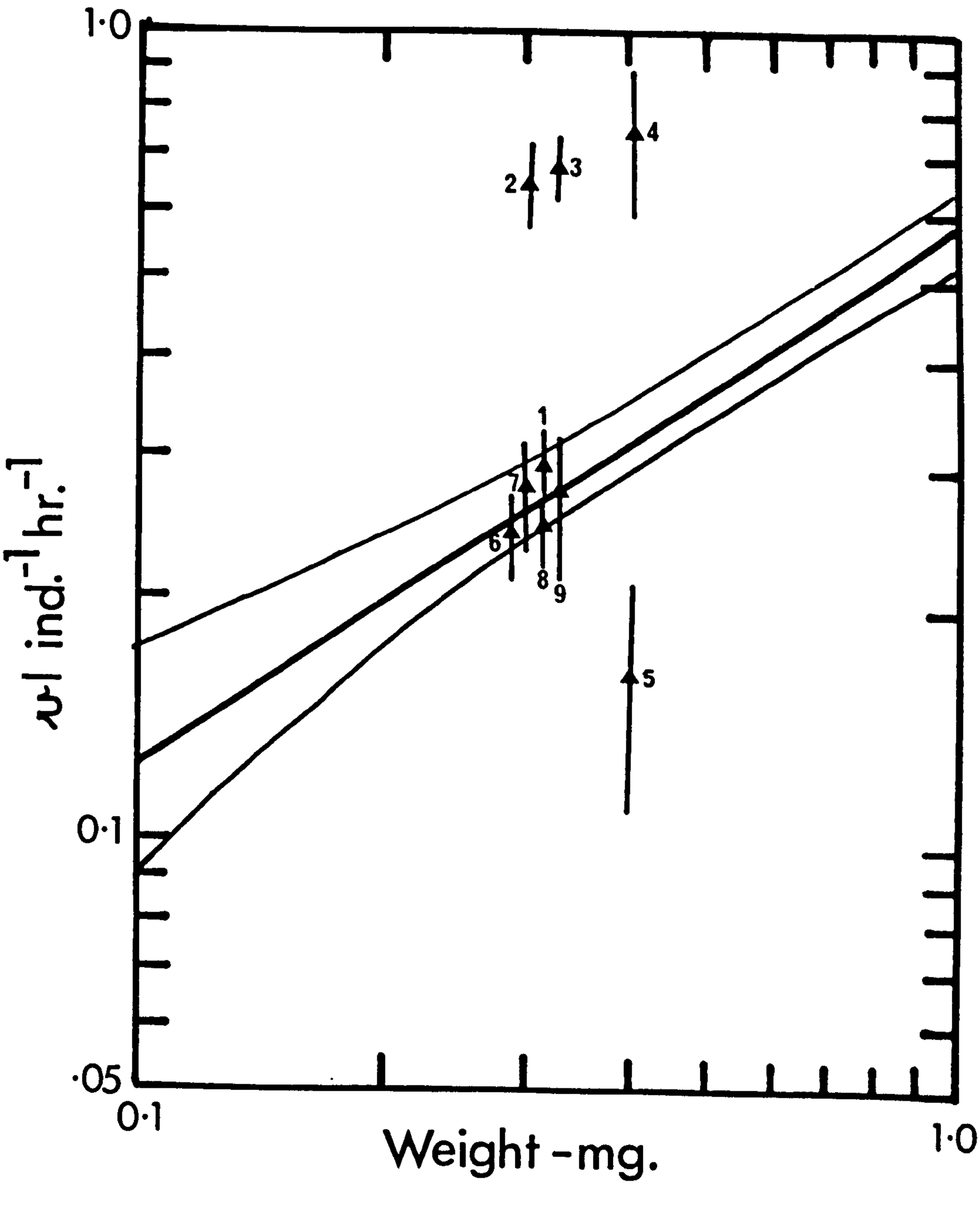

1·0
0·1
·05
0·1
1·0
Weight -mg.
ml. ind.⁻¹ hr.⁻¹
1
2
3
4
5
6
7
8
9

FIG. 113 : The effect of food availability, starvation and water movement, on the pattern and rate of movement in P.contortus. The vertical bars indicate the 95% confidence limits. Patterns within the squares, above the histograms, represent mucus trails traced from the movement chambers.

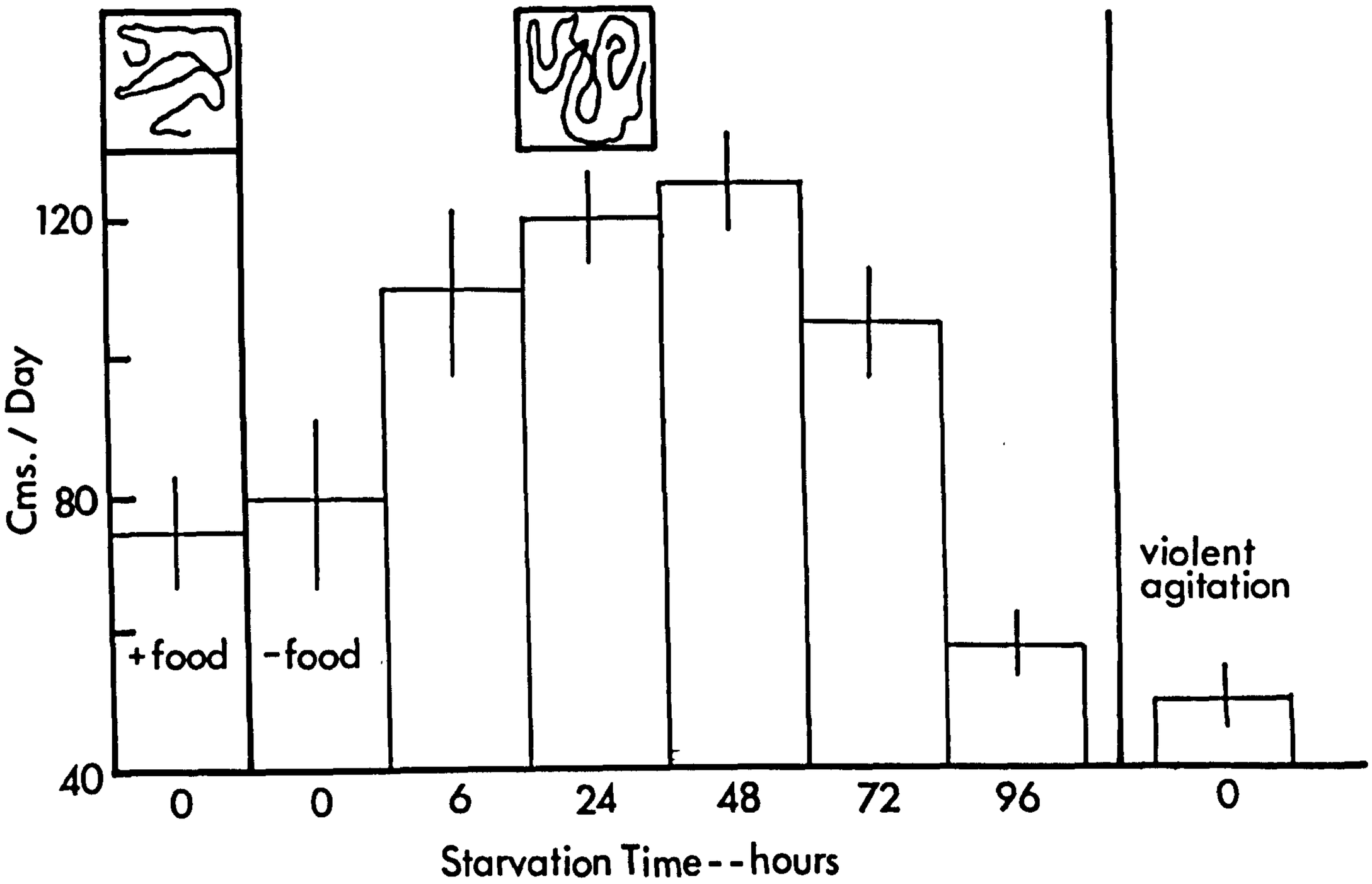

120
80
40
Cms. / Day
+food
-food
violent
agitation
0
0
6
24
48
72
96
0
Starvation Time--hours

FIG 114 : The effect of food availability, starvation and water movement, on the pattern and rate of movement of A. fluviatilis. The vertical bars and patterns illustrated in the squares are as defined in FIG. 113.

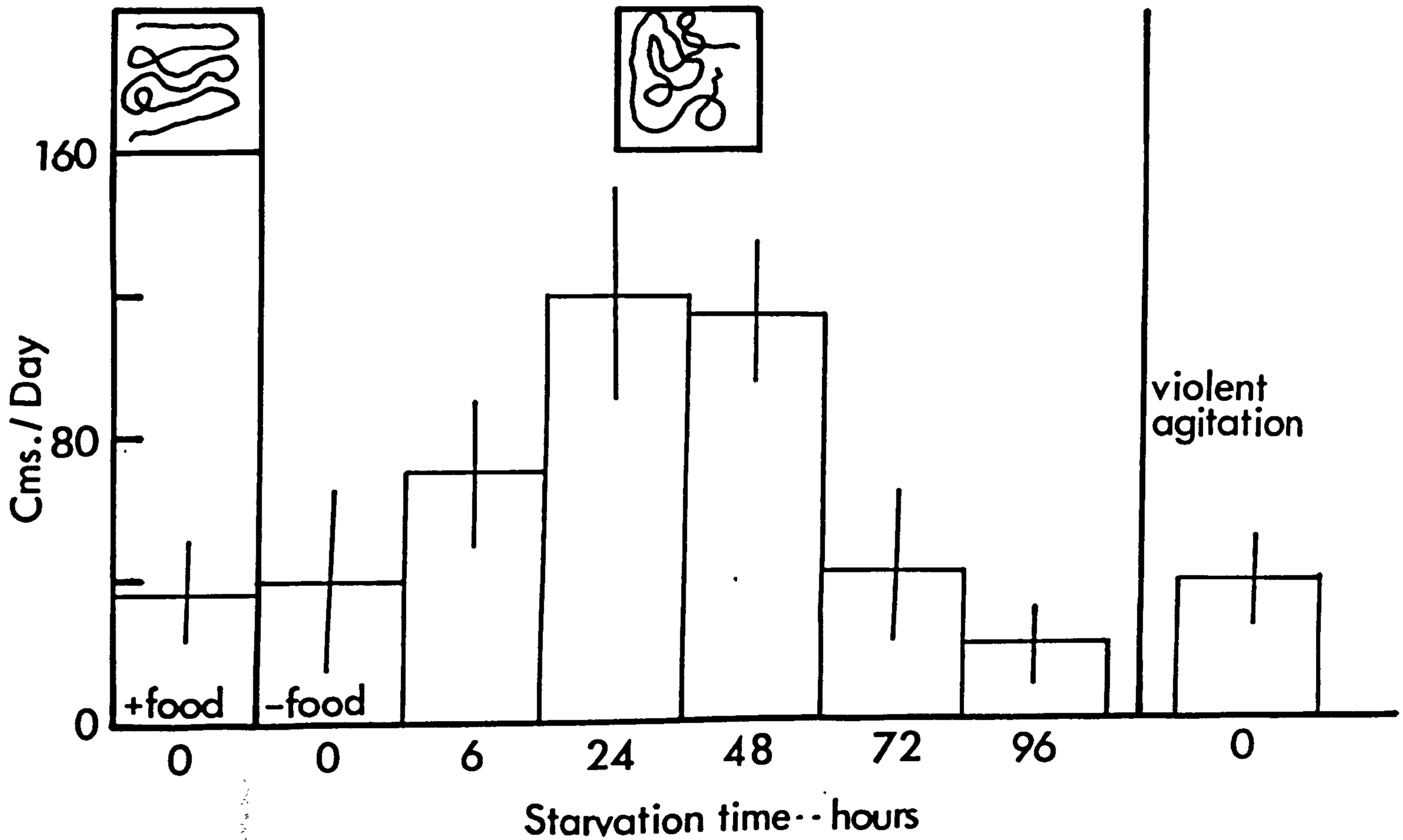

160
80
0
Cms./Day
+food
-food
violent
agitation
0
0
6
24
48
72
96
0
Starvation time--hours

FIG. 115 : Monthly variations in mean density (B), biomass (C), energy flow (D), and production (E), in A.fluviatilis. Monthly variations in mean temperature (A) are also depicted.

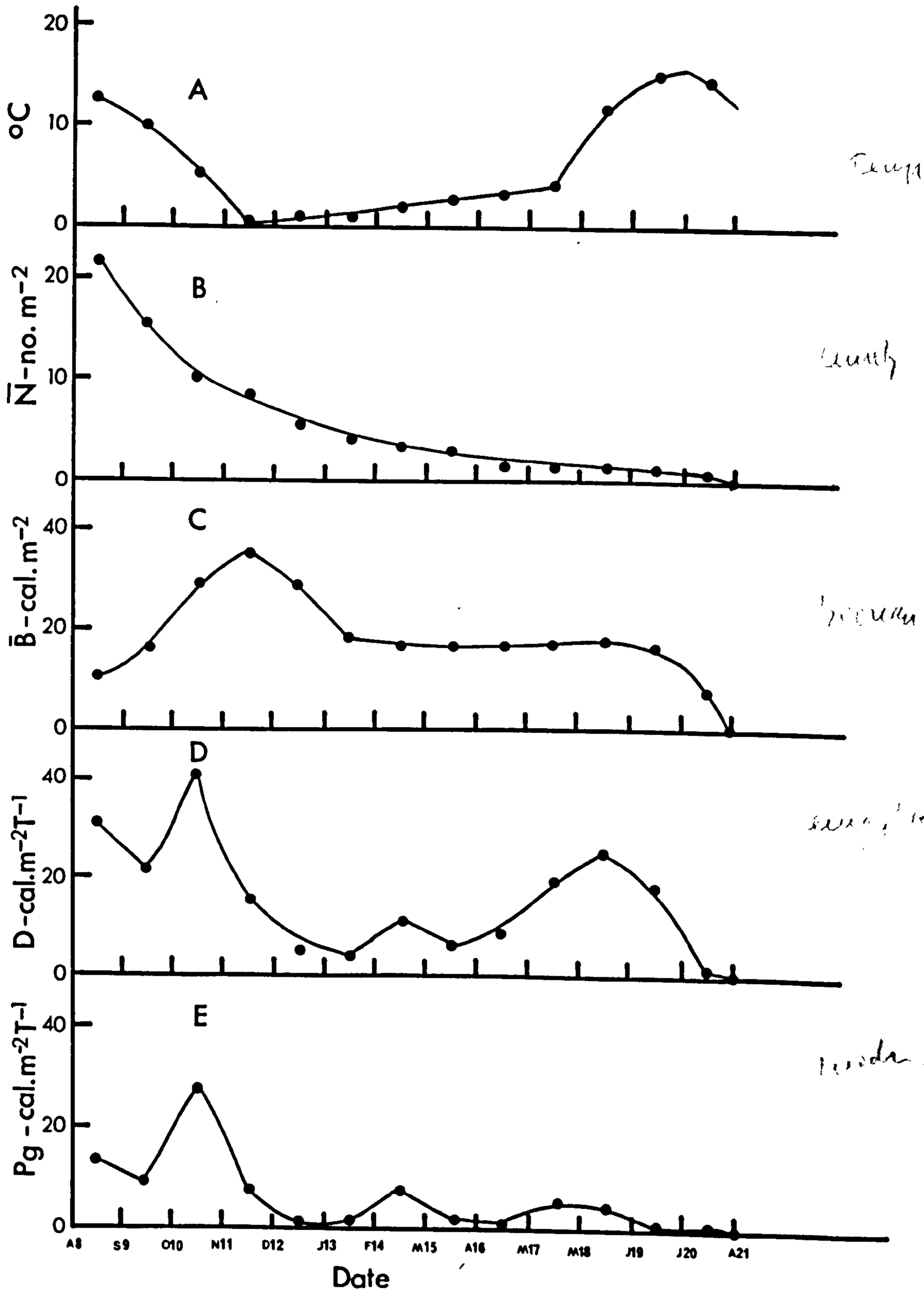
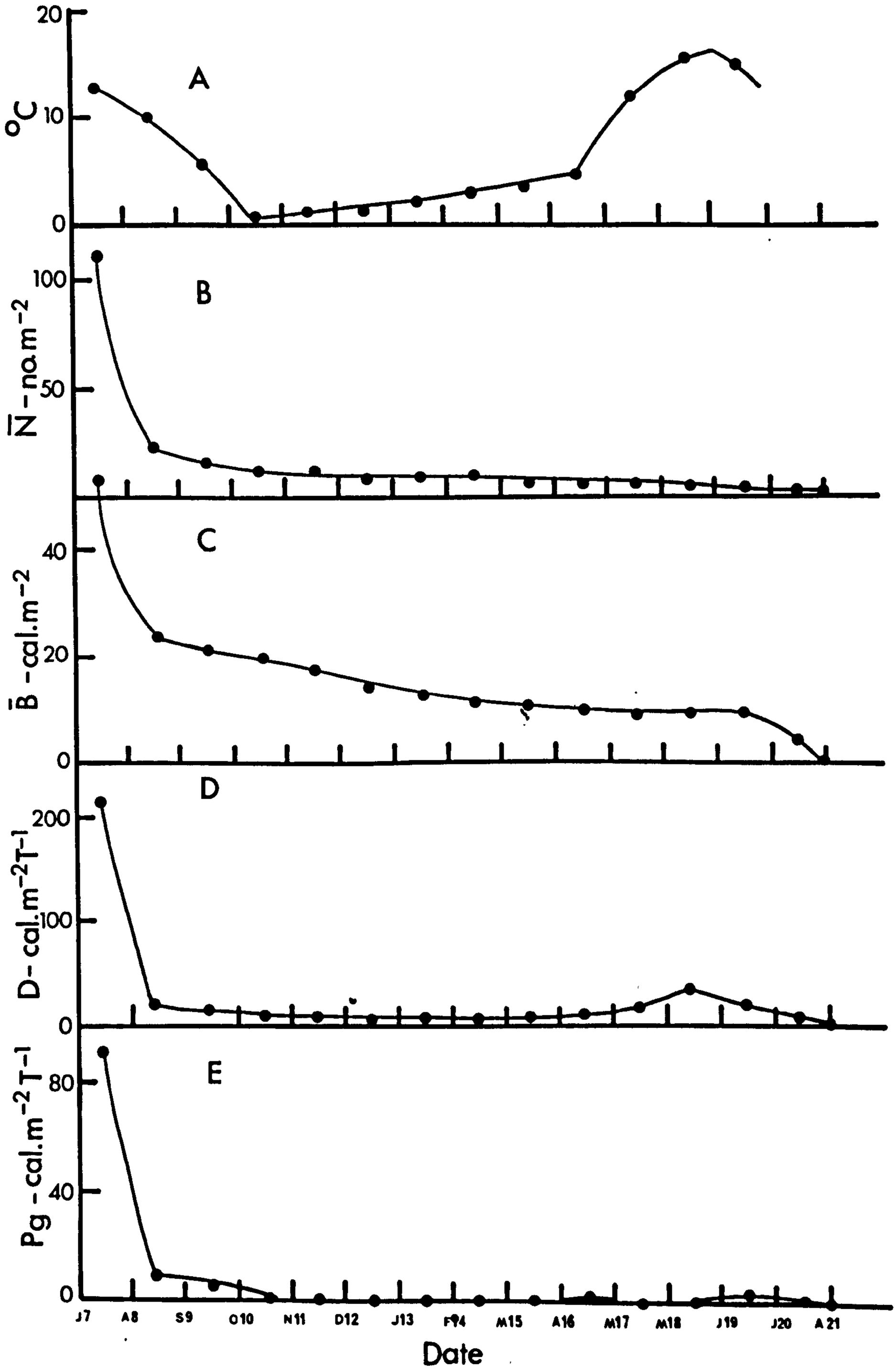

A
°C
20
10
0
B
N-no. m⁻²
20
10
0
C
B-cal. m⁻²
40
20
0
D
D-cal. m⁻² T⁻¹
40
20
0
E
Pg - cal. m⁻² T⁻¹
40
20
0
A8
S9
O10
N11
D12
J13
F14
M15
A16
M17
M18
J19
J20
A21
Date

FIG.116 : Monthly variations in mean density (B), biomass (C), energy flow (D), and production (E), in P.contortus. Monthly variations in mean temperature (A) are also depicted.


20
A
°C 10
0
100
B
$\bar{N}$ - no.m^{-2}
50
C
40
$\bar{B}$ - cal.m^{-2}
20
0
D
200
D - cal.m^{-2}T^{-1}
100
0
E
80
Pg - cal.m^{-2}T^{-1}
40
0
J7
A8
S9
O10
N11
D12
J13
F94
M15
A16
M17
M18
J19
J20
A 21
Date

DATA APPENDICES

DATA APPENDIX I. The dates on which population samples were removed from Ha Mire shore, together with the definitive code used in the text and an indication of the temporal, generation extent in the populations of P.contortus and A.fluviatilis on Ha Mire shore. GENERATION 2 has been considered in most detail.

Year	Date	Code Used in text	Generations of P.contortus	Generations of A.fluviatilis
1970	7/2	F1		
	7/3	M2		
	4/4	A3		
	2/5	M4	1	1
	30/5	M5	FE	FE
	28/6	J6	FY	FY
	25/7	J7	*	*
	22/8	A8		+
	19/9	S9		*
	17/10	O10		
	14/11	N11		
	12/12	D12		2
1971	9/1	J13		
	6/2	F14	2	
	6/3	M15		
	3/4	A16		
	1/5	M17	FE	FE
	29/5	M18	FY.	FY
	26/6	J19	*	*
	24/7	J20		+
	21/8	A21	3	* 3

Total no. of samples= 21

Sampling interval= 28 days

FE = first egg, FY = first young

* Start of new generation

+ Lag between Ancylus and Planorbis (due to differences in hatching time - Ancylus = 2X Planorbis).

DATA APPENDIX II. A species list of the Gasropoda present at Malham Tarn with some indication of the date on which they were first recorded.

Species		Date First Recorded	Authority
Subclass Euthyneura			
Order Pulmonata			
Suborder Basommatophora			
Ancylus fluviatilis Müll.	*	1888	Soppitt & Carter
Lymnaea stagnalis L.	**	1988	" "
Lymnaea pereger Müll.	***	1890	Roebuck
Lymnaea palustris Müll.		1910	Unknown see Stratton (1956)
Physa fontinalis L.		1891	Roebuck
Planorbis contortus L.		1888	Soppitt & Carter
Planorbis albus Müll.		1891	Roebuck
Planorbis crista L.		1888	Soppitt & Carter
Planorbis leucostoma (Millet)	****	1890	Roebuck
Subclass Streptoneura(Operculates)			
Order Pectinibranchia			
Bythinia tentaculata L.		1887	Soppitt & Carter
Valvata cristata Müll.		1947	Macan (see Stratton 1956)
Valvata piscinalis Müll.	*****	1883	Roebuck & Butterell (see Stratton,1956)
Potamopyrgus jenkinsi=Smith		1950	Unknown see Stratton, 1956.

* var. capuloides. Jan. ** var. fragilis-variegata. Taylor.

*** var. ovata. Drapernaud.

**** considered only a varietal form of P.spirobis L. by Ellis (1926). Germain (1931) and Ehrmann (1933) regard it as a good species. It is broader with more slowly increasing whorls than P.spirobis and there is a white thickening around the inside of the mouth.

***** var. acuminata. Jeffrays.

DATA APPENDIX IIIA. The relative abundance (%) of freshwater snails in the weed beds at Malham.

Station no.	9	10	11	12	13
A.fluviatilis	-	-	-	-	-
P.contortus	8.1	15.7	0.9	6.4	1.4
P.albus	3.3	6.5	19.3	29.7	-
P.crista	16.6	22.8	1.8	2.1	-
P.leucostoma	-	-	-	-	95.0
L.pereger	1.3	8.9	11.4	-	-
L.stagnalis	-	29.1	28.7	10.0	-
L.palustris	0.2	0.9	10.0	4.9	-
Ph.fontinalis	-	0.9	7.0	19.1	1.4
B.tentaculata	0.6	-	0.2	25.5	-
V.cristata	-	6.3	-	-	-
V.piscinalis	8.4	8.9	20.7	2.3	2.2
H.jenkinsi	61.5	-	-	-	-

DATA APPENDIX IIIB. The relative abundance (%) of freshwater snails in various littoral situations at Malham.

Station no.	1	2	3	4	5	6	7	8
A.fluviatilis	49.0	70.0	75.0	75.0	3.5	3.5	1.3	1.1
P.contortus	28.0	2.4	2.0	15.0	90.0	54.0	83.0	65.0
P.albus	4.0	3.6	-	-	-	3.5	-	7.0
P.crista	2.0	0.4	-	-	-	0.8	-	-
P.leucostoma	-	-	-	-	-	-	-	-
L.pereger	5.0	10.8	1.2	1.2	-	-	-	-
L.stagnalis	12.0	13.2	1.8	8.0	6.5	5.4	5.7	8.0
L.palustris	-	-	-	-	-	-	-	-
Ph.fontinalis	-	1.0	-	-	-	-	-	-
B.tantaculata	-	-	-	0.8	-	0.8	-	-
V.cristata	-	-	-	-	-	-	-	-
V.piscinalis	-	-	-	-	-	-	-	-
H.jenkinsi	-	-	-	-	-	-	-	-

DATA APPENDIX IV. The proportions of the total snails sampled, each month, which were collected from each sector on Ha Mire shore. All results are in arcsines.

Sample Date*	M2	A3	M4	M5	J6	J7	A8	S9	O10	N11
Sector										
P.contortus										
A	26.56	37.58	29.27	38.82	39.76	28.18	30.26	27.20	32.39	36.03
B	31.50	34.20	38.70	29.13	31.50	35.49	38.41	33.89	30.59	37.76
C	46.55	33.96	37.47	37.47	34.33	41.55	36.87	43.80	42.36	31.95
A.fluviatilis										
A	18.53	40.40	25.92	23.26	31.37	27.76	42.71	49.37	43.11	50.36
B	28.79	27.97	41.61	10.14	26.78	41.55	23.50	35.61	28.38	22.63
C	54.76	36.87	37.41	64.38	46.49	35.85	38.12	16.93	33.65	30.59

Sample Date*	D12	J13	F14	M15	A16	M17	M18	J19	J20	A20
Sector										
P.contortus										
A	34.20	26.49	24.43	25.84	28.32	29.60	26.56	22.87	30.72	32.52
B	45.23	48.50	41.09	45.11	37.23	43.05	47.35	39.11	20.70	24.14
C	25.10	29.33	39.00	33.71	39.76	32.58	30.59	42.19	51.59	39.00
A.fluviatilis										
A	40.98	52.71	12.11	42.19	61.82	36.99	34.27	22.71	44.14	47.70
B	16.22	20.70	18.44	39.41	5.74	44.03	23.11	6.29	24.35	18.63
C	44.54	29.47	67.70	22.46	27.42	23.19	46.66	66.34	35.97	36.33

* See DATA APPENDIX I.

DATA APPENDIX V. The proportion of snails, in each month's sample, found on the different stone aspects. All results are expressed in arcsines.

	N11	D12	J13	F14	M15
A.fluviatilis					
T	5.13	7.71	16.32	14.30	0.00
TS	30.13	40.57	49.54	42.42	40.92
BS	46.66	34.70	30.85	40.63	35.24
B	27.35	28.32	16.32	14.89	29.20
P.contortus					
T	7.71	11.39	10.31	6.55	0.00
TS	27.83	33.15	29.20	21.81	15.79
BS	44.48	35.55	43.62	35.55	34.76
B	31.50	34.76	30.26	45.75	51.47

	A16	M17	M18	J19	J20
A.fluviatilis					
T	10.47	0.00	9.28	0.00	0.00
TS	37.29	31.82	20.96	8.53	28.73
BS	33.21	38.59	30.40	34.82	35.91
B	33.21	35.24	50.13	53.85	40.63
P.contortus					
T	10.63	0.00	7.50	0.00	6.29
TS	16.43	20.70	12.70	21.89	18.34
BS	17.46	35.91	24.50	43.85	43.22
B	63.20	46.78	55.06	38.17	40.40

DATA APPENDIX VI. Partitioning the caloric density of egg capsules.

A.fluviatilis	Ave. Ash-free dry wt. mg.	Ave % Ash	Ave. Total Calories	Ave. k.cals/ g.
N				
200 Egg capsule	0.121	10.00	0.710	5.917
250 Egg membrane	0.045	5.73	0.206	4.571
Capsule contents by Difference	0.076	-	0.504	6.630
P.contortus				
N				
225 Egg capsule	0.060	10.37	0.304	5.067
350 Egg membrane	0.024	7.31	0.108	4.480
Capsule contents by Difference	0.036	-	0.196	5.455

where N = total number of capsules constituting a single sample.

DATA APPENDIX VII. Dimensions analysis on the relationship between shell length, and body and shell weight.

A. In snails with a patelloid shell

All notations are from text FIG. 58.

Assuming the limpet shell shape tends to a perfect cone :

$$\text{Volume} = \frac{\Pi}{3} r^2 h \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1A$$

$$\text{and } r = \frac{AL}{2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 2A$$

$$\text{let } \frac{6}{\Pi} = k_1$$

$$\text{then } k_1 \text{ (volume)} = (AL)^2 \, h.$$

$$\text{but } \frac{r}{h} = \frac{AL}{2h} = \tan\alpha$$

$$\therefore \quad AL = 2h \tan\alpha \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 3A$$

$$\text{let } 2\tan\alpha = k_2$$

$$\text{and } k_1 . k_2 = K_1$$

$$\text{then } K_1 \text{ (volume)} = (AL)^3 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 4A$$

since volume and weight are directly related then coefficient b in text equation 7(6. 2) should be 3.0.

Assuming the shell is of uniform thickness throughout :

$$\text{shell weight} \propto \text{curved shell surface} = \Pi r \sqrt{\left(r^2 + h^2\right)} \ldots 5A$$

from equations 2A ($AL \propto r$) and 3A ($AL \propto h$) :

$$\text{shell weight} = K_2 \, AL^2$$

and b in text equation 7(6. 2) should be 2.0

B. In snails with a turbinate or discoidal shell

All notations are from text FIG. 58.

Volume of the coiled cone can be defined in terms of r and h (see equation 1A). d is related to r ($2r = d$) and h is related to r (equation 3A) so that d and h are related, and :

$$d^3 = k_3 \text{ volume} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 6A$$

a, b, c, and d are the diameters of successive whorls on the same radius of the coiled cone. MD or SL represent the sum of these

parameters.

From Thompson (1917) the lengths of successive diameters are related by :

$$\frac{a}{b} \text{ or } \frac{b}{c} \text{ or } \frac{c}{d} = e^{2\pi \cot \beta}$$

where e is the base of natural logarithms, and β is the angle between the radius vector and the tangent to the curve. In an equiangular spire, β should remain constant irrespective of the position of the radius vector.

$$\therefore \quad b = ae^{2\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 7A$$

$$c = be^{2\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 8A$$

$$d = ce^{2\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 9A$$

and by equations 7A - 8A :

$$d = ce^{2\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 10A$$

$$d = be^{4\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 11A$$

$$d = ae^{6\pi \cot \beta} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 12A$$

so that by equations 10A - 12A ;

$$\text{MD or SL} = d\left(\frac{1}{e^{3x}} + \frac{1}{e^{2x}} + \frac{1}{e^{x}} + 1\right) \quad \ldots\ldots\ldots 13A$$

where $x = 2\,\Pi \cot.\beta$

Let $(1/e^{3x} + 1/e^{2x}$ etc.) $= k_4$

then MD or SL $= k_4 d$

assuming volume and weight are related and using equation 6A, MD^3 or SL^3 should be related linearly to animal weight. Coefficient b in text equation 7(6. 2) should, therefore, be 3.0. Similarly, using equation 5A, and because r, d, and AL are related, shell weight will be linearly related to MD^2 so that b in text equation 7(6. 2) should be 2.0. The latter only holds if the shell has uniform thickness throughout.

C. The case of the "Archimedes" Spire

An alternative family of spires is the "Archimedes" group. These are obtained when a cylinder (not a cone) is coiled. Here angle β is not constant but progressively increases and tends to 90° as the whorls increase in number. Defined formally, members of this

family are described by a point moving at uniform speed along a uniformly rotating radius vector.

Since the diameter of the whorls remains constant, then spire volume is linearly related to the plan area and this in turn to the square of the plan radius. If shell shape approximated to an "Archimedes" spire MD^2 or SH^2 would thus be related linearly to body weight and coefficient b in text equation 7(6. 2) would tend to 2.0. Volume and weight are assumed proportional.

Making the same assumptions about shell thickness as in A and B above :

$$\text{Shell weight} \propto \text{Shell area} = 2\,\Pi\, r'\, H \quad \ldots\ldots\ldots\ldots\ldots 14A$$

where r' is the radius of the coiled cylinder and is constant. H is the length of the cylinder and is linearly related to the length of the spire generating vector and thus to MD :

$$\frac{MD}{2} = H = k_5 \gamma \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 15A$$

where γ is the angle through which the radius vector has revolved.

Combining equations 14A and 15A indicates that MD in this instance would be linearly related to shell weight so that b in text equation 7(6. 2) would be 1.0.

D. The case of the truncated 'ellipsoidal', cone

All notation is from FIG. 60.

(N.B. constancy of a is demanded by arithmetic progression of r, and the gradual exponential rise in b by the logarithmic progression of Σw)

Volume of truncated ellipsoidal cone

$$= \frac{\Pi}{3}\, a.\, h\, (b_1 + \sqrt{[b_1 + b_2]} + b_2) \quad \ldots\ldots\ldots\ldots\ldots\ldots 16A$$

MD represents the sum of successive widths (a) of whorls on the same radius passing from shell centre to aperture. Viewing the shell in cross-section, the cumulative horizontal dimensions of these parameters from whorl to whorl (Σw), will be in arithmetic progression (see above), whereas their vertical dimensions (b_1' , b_2' , b_3' etc) will be in geometric progression. Furthermore, by equations 7A - 12A b_i (where $i = 1, 2, 3$, etc. and $b_1' = b_1$) will be related, and by equation 3A b_2 is related to $h + h''$.

Since h'' is virtual and constant :

$$h \propto b_2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{17A}$$

and since distance

$$MD = \Sigma w \propto h \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{18A}$$

letting $K_6 = \frac{\Pi\ a}{3}$ in equation 16A gives :

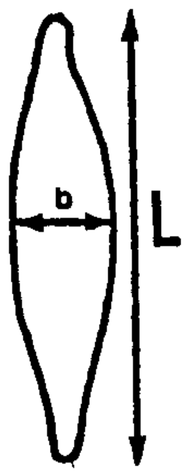
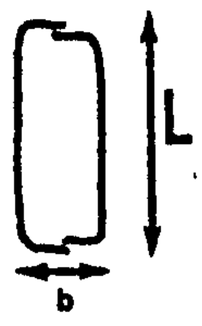
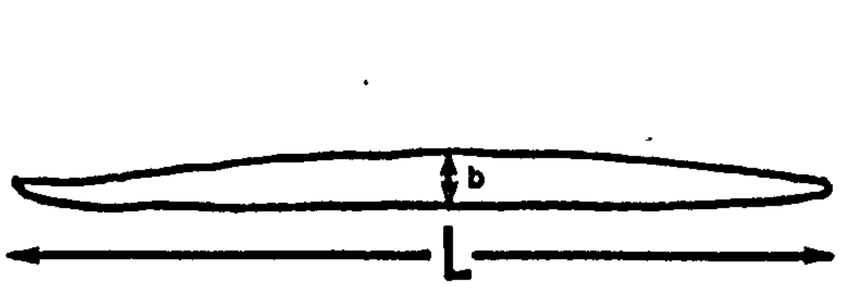
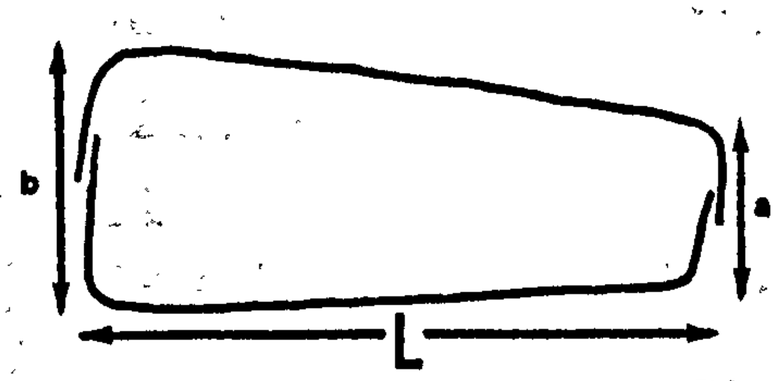
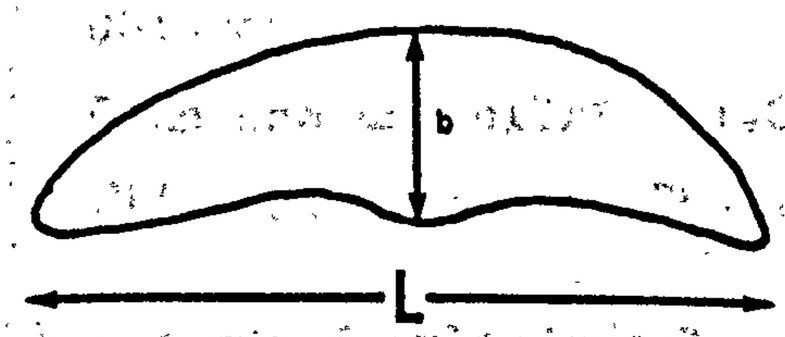
shell volume (and hence body weight) = $K_6\ (MD)^2$ 19A
so that coefficient b in text equation 7(6. 2) should be 2.0.

Assuming the shell is of uniform thickness :

$$\begin{aligned} \text{shell weight} &\propto \text{shell surface area} \\ &= \Pi\left(\sqrt{ab_1} + \sqrt{ab_2}\right)\sqrt{\left[h^2 + \left\{(ab_2)^2 - (ab_1)^2\right\}\right]} \\ &= \Pi\sqrt{a}\,(b_1 + b_2)\,(h + \sqrt{a}\,\{b_1 - b_2\}) \end{aligned}$$

but Π and $\sqrt{a}$ are constants h, b_1, b_2 and MD are related (see above) so that shell weight will be related linearly to MD^2 and coefficient b in text equation 7(6. 2) will be 2.0 provided the assumption of uniform thickness holds.

DATA APPENDIX VIII : A summary of the approximate shapes and conversion equations used for the volume estimation of algal cells. The parameters used in the equations given in column 3 are defined in column 1 of the table.

1	2	3
Aspect and Dimensions	Approximate Shape	Volume V
1. Navicula  Valvar View	Sphoroid	$V = \frac{4}{3}.\pi.\frac{L}{2}.\left(\frac{b}{2}\right)^2$
2. Achnanthes  Girdle View	Cylinder	$V = \pi.\left(\frac{a}{2}\right)^2.L$
3. Synedra  Valvar View	Cylinder	$V = \pi.\left(\frac{a}{2}\right)^2.L$
4. Gomphonema  Girdle View	Truncated Cone	$V = \left\{\left(\frac{a}{2}\right)^2 + \left(\frac{b}{2}\right)^2 + 2\left(\frac{a}{2}.\frac{b}{2}\right)\right\}\frac{\pi}{3}.L$
5. Cymbella  Valvar View	Homisphoroid	$V = \left\{\frac{4}{3}.\pi.\frac{L}{2}\left(b\right)^2\right\}\frac{1}{2}$

DATA APPENDIX IX. The mean size of algae taken by adult snails in June, 1971.

1 Algal Type	2 Mean Volume. μm^3	3 $\pm 2\sqrt{(S^2/N)}$	4 N	5 Limits L.(μm)	6 Limits b.(μm)
Bacillarophyceae					
Navicula	95.3	15.58	115	7 - 30	6 - 1
Achnanthes	91.9	14.18	102	5 - 22	6 - 1
Synedra	254.9	57.60	60	80 - 24	5 - 1
Gomphonema	90.2	12.40	99	10 - 4	4 - 1
Cymbella	97.9	20.22	82	6 - 13	2 - 6
Cyanophyta					
Rivularia +	110.1	28.0	60	100 - 12	3 - 1
Chlorophyceae					
Crustose unicells*	41.04	7.0	175	9 - 1	
Filamentous +	259.17	55.50	72	69 - 30	10 - 4

+ assumed cylindrical * assumed spherical

DATA APPENDIX X. The mean size of algae present on the sides of snail-bearing stones in June, 1971.

1 Algal Type	2 Mean Vol. μm^3	3 $\pm 2\sqrt{(S^2/N)}$	4 N	5 Limits L (μm)	6 Limits b (μm)
Bacillarophyceae					
Navicula	233.3	60.80	85	6 - 70	12 - 2
Achnanthes	188.5	22.20	88	8 - 20	5 - 2
Synedra	546.16	115.88	86	175 - 30	5 - 1
Gomphonema	253.28	50.40	50	37- 16	12 - 3
Cymbella	156.1	25.35	88	8 - 15	2 - 5
Cyanophyta					
Rivularia	181.42	19.10	77	137 - 24	5 - 1
Chlorophyceae					
Crustose unicells*	41.04	7.00	175	9 - 1	
Filamentous +	259.17	55.50	72	69 - 30	10 - 4

+ assumed cylindrical * assumed spherical

DATA APPENDIX XI. The assimilation efficiencies of some aquatic micro-herbivores.

Animal Species	Marine or Freshwater	Assimilation Efficiency % Diatoms	Greens	Blue-greens	Method and units of measurement	Literature Source
Daphnia pulex	F	-	7-24	-	Gravimetric - calories	Richman (1958)
Daphnia longispina D.gracilis Acanthocyclops viridis Asplanchna priodonta Fish larvae (Blicca)	F	-	0.13-16.4	-	Radiotracer (using 14C) -carbon	Sorokin (1966)
Palaeomonetes pugio	M	47-49	-	-	Gravimetric - carbon	Johannes & Satomi (1967)
Hyalella azteca	F	75.0	45-55	5.5-15.0	Radiotracer (using 14C) -dry weight	Hargrave (1970)
Daphnia longispina	F	38.4	100-10.5	17.9-50.8	Gravimetric - dry wt.	Schindler(1971)
Diamptomous gracilis	F	-	39.7-78.0	-	Gravimetric - dry wt.	Schindler(1971)
Cyclops strenuus	F	38.0	8.0-19.0	3.7-25.9	"	"
D.gracilis	F	-	39-78	-	Gravimetric -calories	Kibby (1971)
Range		38.4-75.0	0.13-100	5.5-50.8		

DATA APPENDIX XII. The assimilation efficiencies of some terrestrial (poikilotherm) herbivores.

Animal Species	Food	Assimilation Efficiency	Method and Units of Measurement	Literature Source
Philaenus spumarius	Xylem sap (vascular plants)	39-58	Gravimetric-Energy	Wiegert (1964)
Leptoterna dolobrata	Grass leaf cell contents	28-36	By difference (C-(P+R))-Energy	McNeill (1971)
Hylaphora cercopia	Acer negundo	36.6	Gravimetric-Energy	Schroeder (1971)
Pteronemobius	grass	44	Gravimetric-Energy	Van Hook (1971)
Conocephalus	grass	38	"	"
Range		28-58		

DATA APPENDIX XIII. The assimilation efficiencies of some terrestrial (homeotherm) herbivores.

Animal species	Food	Assimilation Efficiency %	Method and Units of Measure-ment	Literature Source
<u>Cleithrionomys glareolus</u>	Beechmast	88.98		
	mixed oat-meal	84.79		
		85.28	Gravimetric - Energy	Drożoż (1967)
<u>Apodemus flavicollis</u>	Hazelnuts	91.35		
	Mixed	89.26		
	Acorns	77.60		
Savanah Sparrow Sparrow	?	90.0 91.8	By diff. (C-(P+R)) - Energy	Johnson & Groepper (1970)
Variety of Rodents	Synthetic diets	78.9-97.7	Gravimetric - energy	Johnson & Groepper (1970)
Pigs	mixed synthetic diets mainly wheat or oats	65.9-84.6	Gravimetric - energy	Skitso & Boland (1970)
Range		65.9-97.7		

DATA APPENDIX XIV. A review of the values obtained for the b- coefficient in the allometric equation ($R = aW^b$) relating respiratory rate to body weight in the freshwater Gastropoda. Whether body weight is expressed in dry or wet forms is indicated in column 3 of the table.

Species	b	Wet (W) or Dry (D) wt.	Literature Source
Pulmonata			
A.glabratus Physa spp. P.gyrina L.palustris L.stagnalis	0.67		Von Brand et.al. (1948)
P.corneus	0.73 +	W	Bertalanffy (1951)
P.corneus L.stagnalis	>0.67 <1.00	W	Füsser & Krüger (1951)
P.fontinalis	1.00		
M.glutinosa	0.75		
L.auricularia	0.72		
L.pereger	0.94-0.59	W	Berg & Ockelman (1959)
L.palustris	0.76-0.45		
A.lacustris	0.67-0.70		
A.fluviatilis	0.70-0.80		
L.auricularia	1.00	W	Krywiencyk (1959)
L.palustris	0.91-0.96 1.00*-0.31**	W	Duerr (1965) Duer (1967)
M.comuarietis	0.45-0.75	D	Åkerlund (1969)
P.hawnii	0	W	Daniels & Armitage (1969)
L.palustris	0.91-0.95	W	Wright (1971)

DATA APPENDIX XIV. - Continued.

Species	b	Wet (W) or Dry (D) wt.	Literature Source
Prosobranchia			
B.tantaculata	0.81	W	Berg & Ockelman (1959)
B.leachii	0.80		
V.piscinalis	0.74		
T.fluviatilis	0.94-0.95		
P.jenkinsi	0.73		
P.jenkinsi	0.74	W	Heywood & Edwards (1962)
	0.77	D	
P.jenkinsi	0.824-0.795	W	Lawton & Richards (1970)
Composite slopes based on data from a number of species of Gastropod			
	> 0.75	W	Berg & Ockelman (1959)
	0.75	W	Hemmingsen (1960)
Pulmonates	0.70	W	Wesemeier (1960)
Prosobranchs	0.65	W	

* Non-parasitised ** Parasitised

\+ Based on CO_2 output.

DATA APPENDIX XV. A list of the rates of movement previously recorded for various species of gastropod.

Species	Speed (cm./day)	Literature Source
A.fluviatilis	1872	
P.fontinalis	8640	
P.corneus	10080	Pelseneer (1935)
L.stagnalis	12240	
L.pereger	25200	
Various terrestrial species	28.8-187.2	Verdcourt (1948)
A.fluviatilis	144-288	Hunter (1953a)
P.jenkinsi	4320	Lumbye and Lumbye (1965)
L.pereger	144-2592	Storey (1971)

DATA APPENDIX XVI. Details of the monthly variations in pg, pr, sh, and r in a typical individual of P.contortus throughout GENERATION 2. The units are in calories/ 28 days except for the last interval which is expressed over a 14-day interval.

	pg	pr	sh	r	pg+pr+sh+r = (d calc.)-u
J7-A8	0.782		0.330	0.400	1.512
A8-S9	0.374		0.070	0.740	1.184
S9-O10	0.373		0.110	0.777	1.260
O10-N11	0.162		0.040	0.555	0.757
N11-D12	-		-	0.419	0.419
D12-J13	-		-	0.480	0.480
J13-F14	-		-	0.457	0.457
F14-M15	-		-	0.509	0.509
M15-A16	-		-	0.619	0.619
A16-M17	0.075		-	0.739	0.814
M17-M18	-	0.891	-	2.858	3.749
M18-J19	0.170	2.034	0.288	2.995	5.497
J19-J20	0.301	0.030	0.293	3.348	3.972
J20 + 14 days	-		-	0.550	0.550
$\sum$	2.237	2.955	1.131	15.446	21.769

DATA APPENDIX XVII. Details of the monthly variations in pg, pr, sh, and r in a typical individual of A.fluviatilis throughout GENERATION 2. The units are in calories/ 28 days except for the last interval which is expressed over a 14-day interval.

	pg	pr	sh	r	pg+pr+sh+r = d(calc.)-u
A8-S9	0.659		0.195	0.563	1.417
S9-O10	0.692		0.115	0.731	1.538
O10-N11	2.876		0.350	0.702	3.928
N11-D12	1.251		0.130	0.686	2.067
D12-J13	-		-	0.993	0.993
J13-F14	-		-	0.974	0.974
F14-M15	3.093		0.270	1.103	4.466
M15-A16	0.977		0.080	1.646	2.703
A16-M17	0.185		0.015	4.120	4.320
M17-M18	3.458	0.405	0.145	7.278	11.286
M18-J19	2.745	4.679	0.175	9.815	17.414
J19-J20	1.686	3.550	0.010	9.260	14.506
J20 + 14 days	-		-	0.977	0.977
$\sum$	17.622	8.634	1.485	38.848	66.589

DATA APPENDIX XVIII. The extent of agreement between d(obs.) and d(calc.) -u throughout GENERATION 2 in P.contortus

Sampling occasion	d(obs.) cals	d(calc.) - u cals	$\frac{d(calc.)-u}{d(obs.)} \times \frac{100}{1}$ %
J7-A8	1.341	1.512	112.8
A8-S9	2.753	1.184	43.0
S9-O10	1.782	1.260	70.7
O10-N11	0.633	0.757	119.6
N11-D12	0.297	0.419	141.0
D12-J13	0.398	0.480	120.6
J13-F14	0.387	0.457	118.2
F14-M15	0.507	0.509	100.4
M15-A16	0.749	0.619	82.6
A16-M17	1.188	0.814	68.5
M17-M18	5.304	3.749	70.6
M18-J19	6.106	5.487	89.9
J19-J20	6.834	3.972	58.1
J20 + 14 days	0.595	0.550	92.4
$\sum$	28.874	21.769	75.4

DATA APPENDIX XIX. The extent of agreement between d(obs.) and d(calc.)-u throughout GENERATION 2 in A.fluviatilis

Sampling occasion	d(obs.)cals.	d(calc.) - u cals.	$\frac{d(calc.)-u}{d(obs.)} \times \frac{100}{1}$
A8-S9	1.510	1.417	93.8
S9-O10	1.725	1.538	89.2
O10-N11	1.636	3.928	240.1
N11-D12	1.651	2.067	125.2
D12-J13	2.007	0.993	49.5
J13-F14	1.955	0.974	49.8
F14-M15	2.641	4.466	169.1
M15-A16	3.580	2.703	75.5
A16-M17	6.018	4.320	71.1
M17-M18	13.899	11.286	81.2
M18-J19	17.218	17.414	101.1
J19-J20	17.099	14.506	84.8
J20 + 14 days	1.152	0.977	84.8
$\sum$	72.091	66.589	92.4

DATA APPENDIX XX. Monthly variations in, and methods of calculating C(b), f(b), C(L), C(b+L) and f(b+L) in typical individuals of P.contortus during GENERATION 2. The data are expressed in cals./28 days except for the last interval when only 14 days are considered.

Sampling Occasion	d(obs.)	AE %	$C(b)=\frac{d(obs)}{AE}$	$f(b)=c(b)-\frac{C(L)}{d(obs.)}$	C(L)	C(b+L)= C(b)+C(L)	f(b+L)* f(b)+C(L)
J7-A8	1.341	85.2	1.574	0.233	1.197	2.771	1.430
A8-S9	2.753		3.608	0.855	2.741	6.349	3.596
S9-O10	1.782		2.336	0.554	1.776	4.112	2.336
O10-N11	0.633		0.830	0.197	0.631	1.461	0.829
N11-D12	0.297		0.390	0.093	0.297	0.687	0.390
D12-J13	0.398		0.520	0.124	0.397	0.919	0.521
J13-F14	0.387		0.507	0.120	0.386	0.893	0.506
F14-M15	0.507	76.3	0.665	0.158	0.506	1.171	0.664
M15-A16	0.749		0.982	0.233	0.747	1.729	0.980
A16-M17	1.188		1.557	0.369	1.185	2.742	1.556
M17-M18	5.304		6.952	1.648	5.289	12.241	6.937
M18-J19	6.106		8.003	1.897	6.089	14.092	7.986
J19-J20	6.834		8.957	2.123	6.814	15.771	8.937
J20 + 14 days	0.595		0.780	0.185	0.593	1.373	0.778
Σ	28.874	76.70	37.663	8.789	28.649	66.312	37.437

* assumes that non of the inert food-carrier ingested is absorbed.

DATA APPENDIX XXI. Monthly variations in and methods of calculating C and f in a typical individual of A.fluviatilis during GENERATION 2. The date are expressed in cals./28 days except for the last interval when only 14 days were considered.

	d(obs.)	AE	$C = \frac{d(obs.)}{AE}$	f = C - d(obs.)
A8-S9	1.510	62.5	2.416	0.906
S9-O10	1.725		2.875	1.150
O10-N11	1.636		2.727	1.091
N11-D12	1.651		2.752	1.101
D12-J13	2.007		3.345	1.338
J13-F14	1.955		3.258	1.303
F14-M15	2.641	60.0	4.402	1.761
M15-A16	3.580		5.967	2.387
A16-M17	6.018		10.030	4.012
M17-M18	13.899		23.165	9.266
M18-J19	17.218		28.697	11.479
J19-J20	17.099		28.498	11.399
J20 + 14 days	1.152		1.920	0.768
Σ	72.091		120.052	47.961

PUBLICATION APPENDICES

PUBLICATIONS APPENDIX

I

Studies on the Natural Diet of Lymnaea pereger obtusa (Kobelt) and its Possible Ecological Implications.

Journal : Proceedings of the Malacological Society.

Submitted : December 1969.

Accepted : February 1970

Published : vol. 39, 1970. P. 203-215.

Proc. malac. Soc. Lond. (1970) 39, 203.

STUDIES ON THE NATURAL DIET OF *LYMNAEA PEREGER OBTUSA* (KOBELT) AND ITS POSSIBLE ECOLOGICAL IMPLICATIONS

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INTRODUCTION

Surprisingly little is known about the natural diets of many of the more common species of British freshwater gastropods. Boycott (1936) suggested that freshwater snails in general feed on detritus and algal periphyton rather than on higher plants, but he offered no experimental evidence in support. The whole subject of molluscan diets has been reviewed by Graham (1955), but few of the works cited by him provide any specific information on the natural diets of freshwater gastropods, in terms of which food materials are preferred, selected, and most easily assimilated by them. Such information is becoming increasingly important from an ecological point of view. Eisenberg (1966), for example, suggested that natural populations of *Lymnaea elodes* are limited solely by food quality rather than quantity. Furthermore, productivity assessments on bodies of freshwater require an intimate knowledge of the feeding habits of the organisms involved.

L. pereger is the commonest and most abundant species of British freshwater snail, and with the possible exception of *Pisidium cinereum,* is the commonest British mollusc. There is little reference in the literature, however, as to the exact nature of the diet of this species. Boycott (1936), for example, mentions the work of Turner, carried out shortly before his death and therefore unfortunately unpublished, which offered some evidence that *Lymnaea pereger* shows a selective preference for different types of algae.

In view of this lack of specific information regarding the diet of *L. pereger*, the present work was undertaken to determine the food taken by this species in nature, and to develop and suggest techniques which may be used for similar studies on other species. The investigation involved, therefore, the use of field studies, in which the food available in nature was determined and compared with that ingested, and laboratory studies, in which the extent of assimilation of the different food types ingested was assessed.

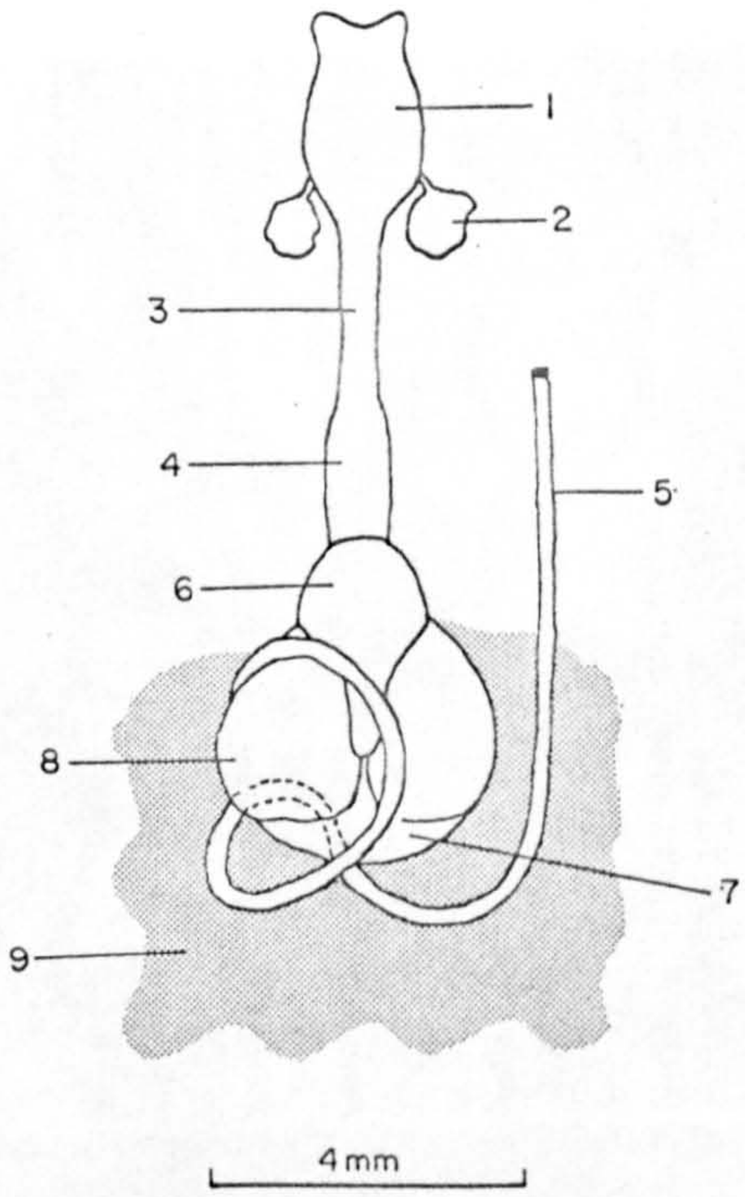


FIG. 1. General morphology of the alimentary system of *Lymnaea pereger*. 1, Buccal bulb; 2, salivary gland; 3, pro-oesophagus; 4, post-oesophagus; 5, intestine; 6, crop; 7, pylorus; 8, gizzard; 9, digestive gland.

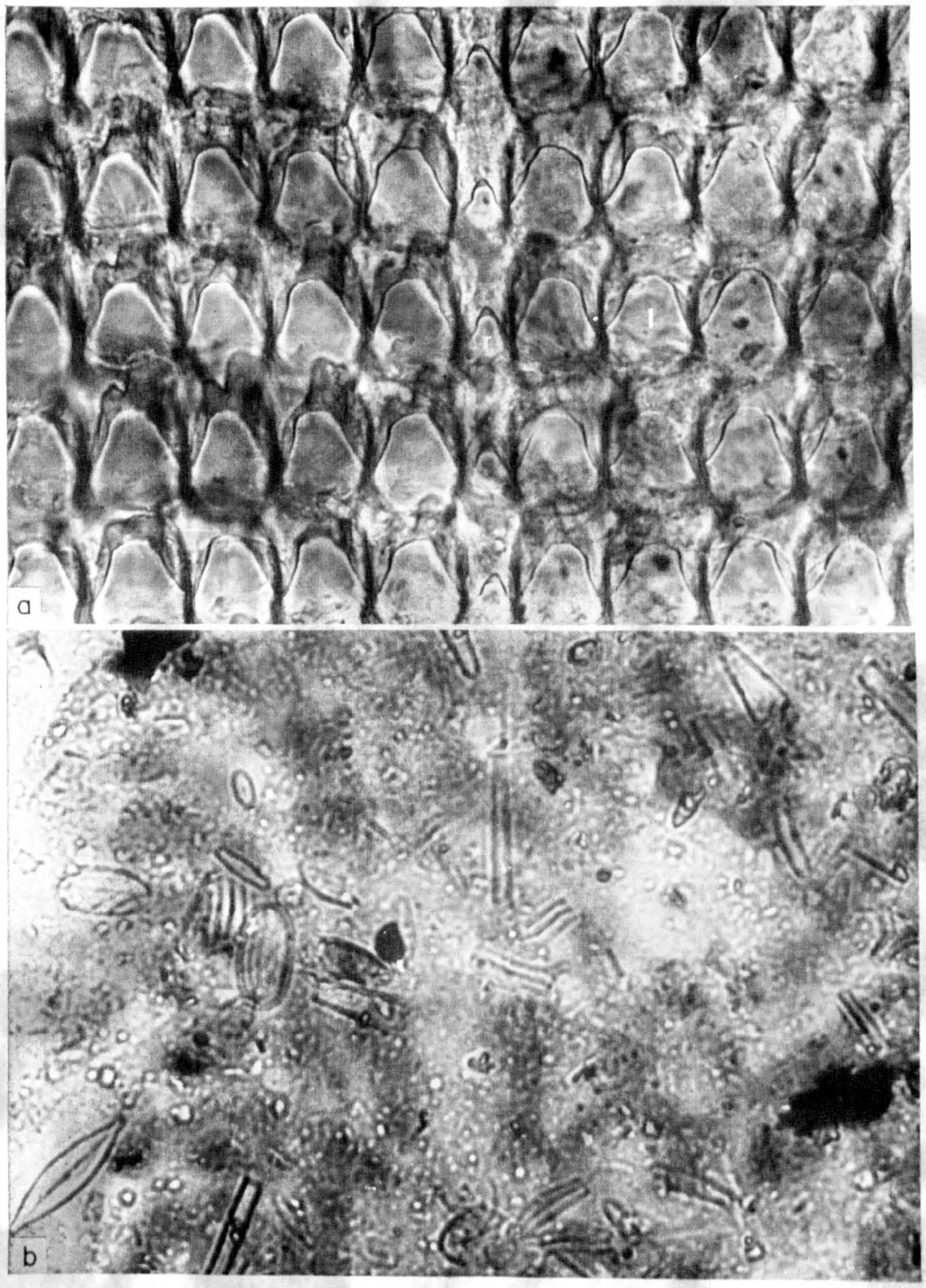
GENERAL ECOLOGY AND DESCRIPTION OF COLLECTING SITE

Lymnaea pereger is widely distributed throughout the whole of the British Isles, and is found in all types of freshwater in which molluscs are able to live (Boycott, 1936). Individuals for this study were obtained from a disused mill-pond at Baildon, Yorkshire (Grid ref. SE165403). The only other gastropod present was *Potamopyrgus jenkinsi* (Smith).

The dominant weed present in the pond was *Elodea canadensis* (Michx.), and the majority of the population of *Lymnaea pereger* was limited to this situation. A few snails however, were taken from submerged logs and stones around the perimeter of the pond, though no individuals were found on the predominately muddy bottom.

As Ellis (1926) has noted, *L. pereger* is exceedingly variable in form, and a large number of varieties have been described for this species. Individuals collected from the above site showed characteristics of variety *obtusa* (Kobelt, 1881) and further mention of *L. pereger* in this paper refers solely to this variety.

Unless otherwise stated, all snails used in the following experiments were obtained from the above collecting site.



(a) Middle portion of the radula of *Lymnaea pereger* showing a small rachidian tooth and a few lateral denticles, with their basal struts, and the outline of their tricuspid working parts. r, Rachidian denticle; l, lateral denticle. (b) Typical crop smear of *L. pereger* showing diatomaceous food (mainly *Navicula* spp.) and numerous refractile particles, the grit.

(*Facing p.* 206)

GENERAL MORPHOLOGY OF THE ALIMENTARY CANAL

Gut form and function in the Mollusca, as with other members of the animal kingdom, are intimately interrelated. Thus one would expect the gut form of a particular species to provide valuable indicators as to the general nature of the food taken.

The morphology of the alimentary system of *Lymnaea pereger* (Fig. 1) is virtually identical with that described by Carriker (1945, 1946) for *L. stagnalis appressa.* Of general note is the presence of a gizzard containing small stones, and a long, coiled intestine.

Stone-filled gizzards have been repeatedly described in numerous species of freshwater pulmonates, and this subject has been reviewed by Carriker (1945, 1946). The major role of this organ is the comminution of food material in the absence of an efficient buccal system for this purpose. The long, coiled intestine of *L. pereger* is characteristic of herbivorous species (Hyman, 1967).

A cursory consideration was made of the radula. This was carefully dissected from the buccal bulb, and mounted flat in glycerine jelly. As with *L. stagnalis appressa* (Carriker, 1945, 1946), the radula and its denticles were found to be little specialized. There are twelve lateral denticles which resemble those of the Physidae, in that they possess in the resting position an anterior, basal, supporting strut and a larger, but seemingly thinner, posterior tricuspid working part. The lateral denticles of *L. stagnalis appressa* are also tricuspid (Carriker, 1945, 1946). The marginal denticles in *L. pereger*, however, possess no basal strut and are not tricuspid, but are very numerous. There is a single rachidian tooth, but no dominant (Plate 1a).

Thus the general form of the gut, i.e. the presence of a stonefilled gizzard, and a long coiled intestine, together with the lack of specialization in the radula and its associated denticles tend to point to a basically herbivorous habit in *L. pereger.*

FOOD TAKEN IN NATURE

This phase of the study was mainly concerned with identifying, and quantitively assessing, the various types of food available to *Lymnaea pereger*, and comparing this with the amount and type of food actually ingested by this species in the field. It has already been noted that the majority of *L. pereger* were confined to *Elodea canadensis*, and consequently observations on food ingested in the field, were largely limited to this section of the population.

From the point of view of investigating food ingested by snails, it is essential to remember that the major sites of digestion in the molluscan alimentary system are the digestive diverticula (Enriques, 1902), and that the gizzard is concerned with the comminution of food material. The crop, however, which represents a posterior expansion of the oesophagus (Taylor, 1896) merely acts as a storage reservoir for food, prior to its entry into the gizzard and stomach. It was therefore felt that the crop contents, occurring anterior to the site of true digestion, and thus having been subject to least hydrolysis and trituration but being present in large amounts, would provide the best indication of food intake.

An initial survey was therefore instituted with one hundred snails taken from *Elodea*. Collection was by means of a standard pond net, and snails were fixed in 75% alcohol immediately on removal from the *Elodea*. Immediate fixation was essential to halt the processes of digestion and preserve the crop contents intact. Penetration of fixative was facilitated by cracking open the shells of the snails before they were dropped into the fixative.

Later examination of crop contents revealed complete absence of any portion of higher plant, but the presence of large quantities of unicellular and filamentous algae together with some grit (Plate 1b). It was therefore concluded that *Lymnaea pereger* was probably a microphagous herbivore taking the epiphytic algae present on the surface of the *Elodea* rather than the *Elodea* itself.

To test this hypothesis further, 250 snails were taken from the *Elodea* at the collecting site and fixed in the same way as described above. At the same time an extract of algal epiphytes was obtained from the *Elodea*, over which snails had actually been grazing, using the method described by West and Fritsch (1927). The *Elodea* was shaken to remove excess water, and then squeezed over a wide-mouthed container. The resultant thick, green exudate, containing the algal epiphytes, was transported back to the laboratory, where the proportions of its various algal constituents were immediately estimated.

This estimation was carried out by transferring a portion of the extract to a known area of microscope slide, and counting the numbers of the various algal types within this area. This process was repeated for twenty aliquots of extract and the counts of each algal type, in all samples, were summed and expressed as a percentage proportion of the total algal components present.

Crop contents were treated in a similar way, and the percentage proportion of the algal types found within the crops of the 250 snails was computed as above. Again no portion of *Elodea* or other macrophyte was found in any of the crops observed. A comparison between the percentage proportions of algal types found on the *Elodea*, and those found within the crops of snails feeding on the *Elodea* is summarized in Fig. 2.

This comparison indicates that the percentage proportion of algal types found within the crop reflects almost exactly, the percentage proportion of algal types found as epiphytes on the *Elodea*, and suggests that *Lymnaea* browses indiscriminately on the algal epiphytes which cover the surface of the *Elodea*. Furthermore, crop contents of snails taken from other submerged substrata, e.g. submerged logs and stones, were also found to contain algae exclusively. It can be concluded from these results, therefore, that *Lymnaea pereger* is a general, microphagous herbivore.

FEEDING EXPERIMENTS

The above data suggest that *Lymnaea pereger* is an indiscriminate browser. Indiscriminate browsing, however, does not preclude either the possibility that some of the food material ingested may be assimilated more readily than others, or that snails may be exerting selection for that portion of the substratum carrying the prefer-

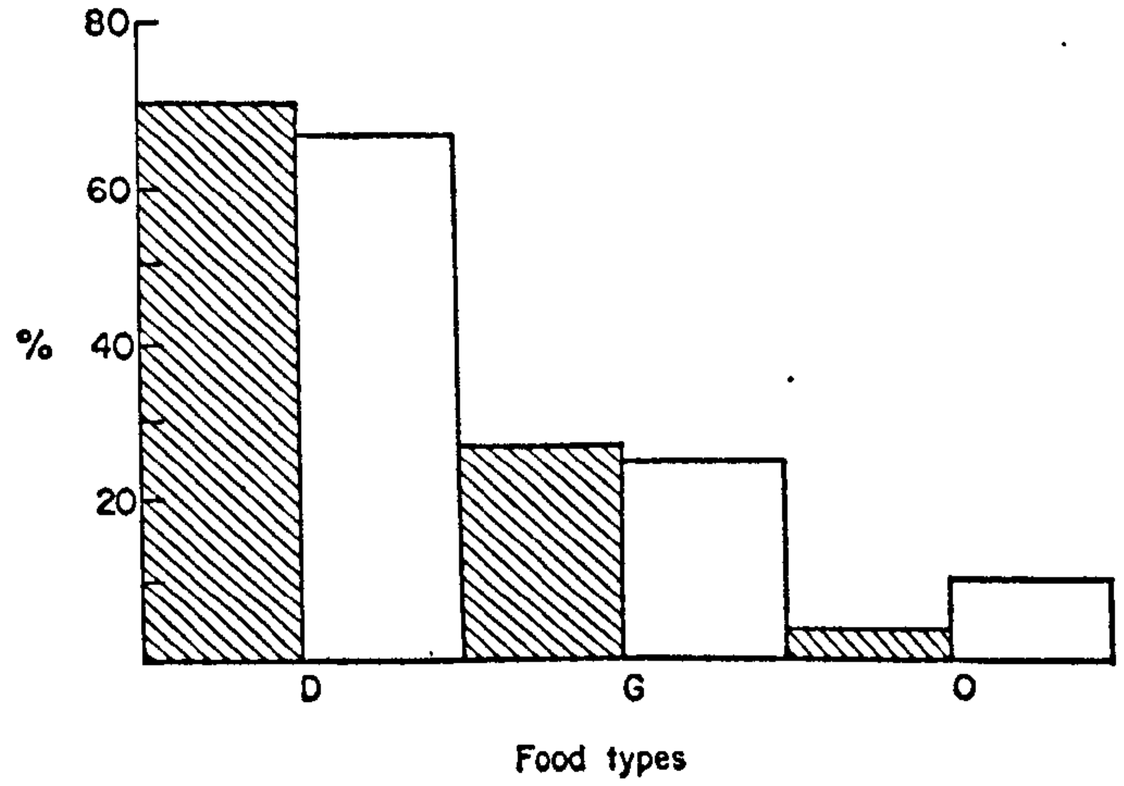


FIG. 2. Histogram comparing the percentage proportion of food types found in the crop of *Lymnaea pereger* (open columns), with those found on substratum (hatched columns) from which snails were taken. D, Diatomaceous algae; G, green filamentous algae; O, other species of algae.

red food type(s). Laboratory feeding experiments were consequently designed to test these two possibilities.

A good indication of the degree of assimilation of a particular food material may be obtained from a consideration of the faecal pellets. The faecal pellets of *L. pereger* are especially useful for this purpose, being divided into three distinct components, namely, the gizzard string, containing indigestible material derived directly from the gizzard, the caecal string, a mucoid cementing string derived from the caecum, and the liver string, containing material derived directly from the liver.

It has already been pointed out that the bulk of the digestion and assimilation in *L. pereger* is carried out in the liver. This requires that potentially utilizable food is diverted from the direct gizzard-intestinal pathway into the digestive diverticula where it is engulfed and digested intracellularly, whilst the indigestible residues of this process are ultimately cast out from the digestive cells. It is this material which constitutes the bulk of the liver string (Carriker, 1946). On the other hand, materials incapable of digestion are not diverted to the liver but are transported by separate ciliary tracts directly to the intestine, where they are compacted into the gizzard string.

Thus it was felt that whilst measurement of total faecal production of snails fed on a particular food material would provide a direct indication of the degree to which that food material was being ingested, a consideration of liver string production would provide further information as to the extent to which it was being diverted to the liver for digestion and assimilation.

In this experiment thirty snails (of 10–12 mm height) initially starved over a 5-day period, were each enclosed in plastic vials, 6·5 × 5·5 cm, the bottoms of which were

perforated to allow free escape of faeces but not snails. This prevented the snails consuming their own faeces, a trait recorded by Carriker (1946) in starved snails. The vials were suspended in a tank, each over a petri dish in which the faeces from the individual snails collected. The tank was filled with fresh water which had been previously filtered through sintered glass (porosity 3), and whose temperature was maintained at 12 ± 3° C.

Food was administered to the isolated snails on agar blocks. These blocks had two functions. Firstly to anchor the food materials concerned and thus prevent their free circulation in the tank and possible contamination of other vials, and secondly to provide a solid flat substratum over which the snails could graze. Four per cent sterilized agar was used for this purpose because it showed no dissociation in water and because it could be easily handled. Fine sterilized grit, 1 mm in diameter, was added to these blocks since snails require particles of stone to supplement the contents of the gizzard. Food was added to these blocks, just before they solidified and one block (3 × 3 × 1 cm), carrying a single food type was then placed inside each vial. The blocks were replaced every 2 days to ensure that snails had a continual superabundance of food. Each snail was provided with the same food type throughout the whole of the experiment.

The food types used were, normal *Elodea*, *Elodea* extract prepared as for the epiphytic samples made from *Elodea*, described in the previous section, cleaned *Elodea* from which epiphytes had been removed, a mixed culture of diatoms, and a mixed culture of green, filamentous algae. The most efficient means of cleaning the *Elodea*, i.e. removing all the epiphytes present, was found to be immersion in 10% copper sulphate solution for 48 hr. The *Elodea* was then thoroughly washed in fast flowing chlorinated tap water and subsequent examination showed that at least 95% of the epiphytic algae had been removed.

Of the thirty snails used, groups of five were each offered one particular food type, the remaining five being offered only the agar-grit medium as control. All the snails on each food type were placed in the apparatus at the same time, so that all were feeding under virtually the same conditions.

Faeces were collected from the petri dishes every 2 days when water in the apparatus was changed to prevent fouling and the agar blocks were changed. The total lengths of gizzard and liver string collected from each snail was then measured using a dial micrometer, and the blocks supporting both normal and cleaned *Elodea* were separated from the rest so that the *Elodea* could be examined for damage effected by the snails. The experiment was run over a 12-day period in February 1969.

The mean total length of gizzard and liver string production for each of the six groups of five snails fed separately on the different food types was computed, and results were expressed in lengths (millimetres) per unit height of snail, so that a comparison between the different groups was possible (Fig. 3).

To facilitate a comparison with the data compiled by Carriker (1946) for *Lymnaea stagnalis appressa* the gizzard and liver string production of one arbitrarily chosen snail, fed on normal *Elodea*, has been presented separately (Fig. 4), as the lengths

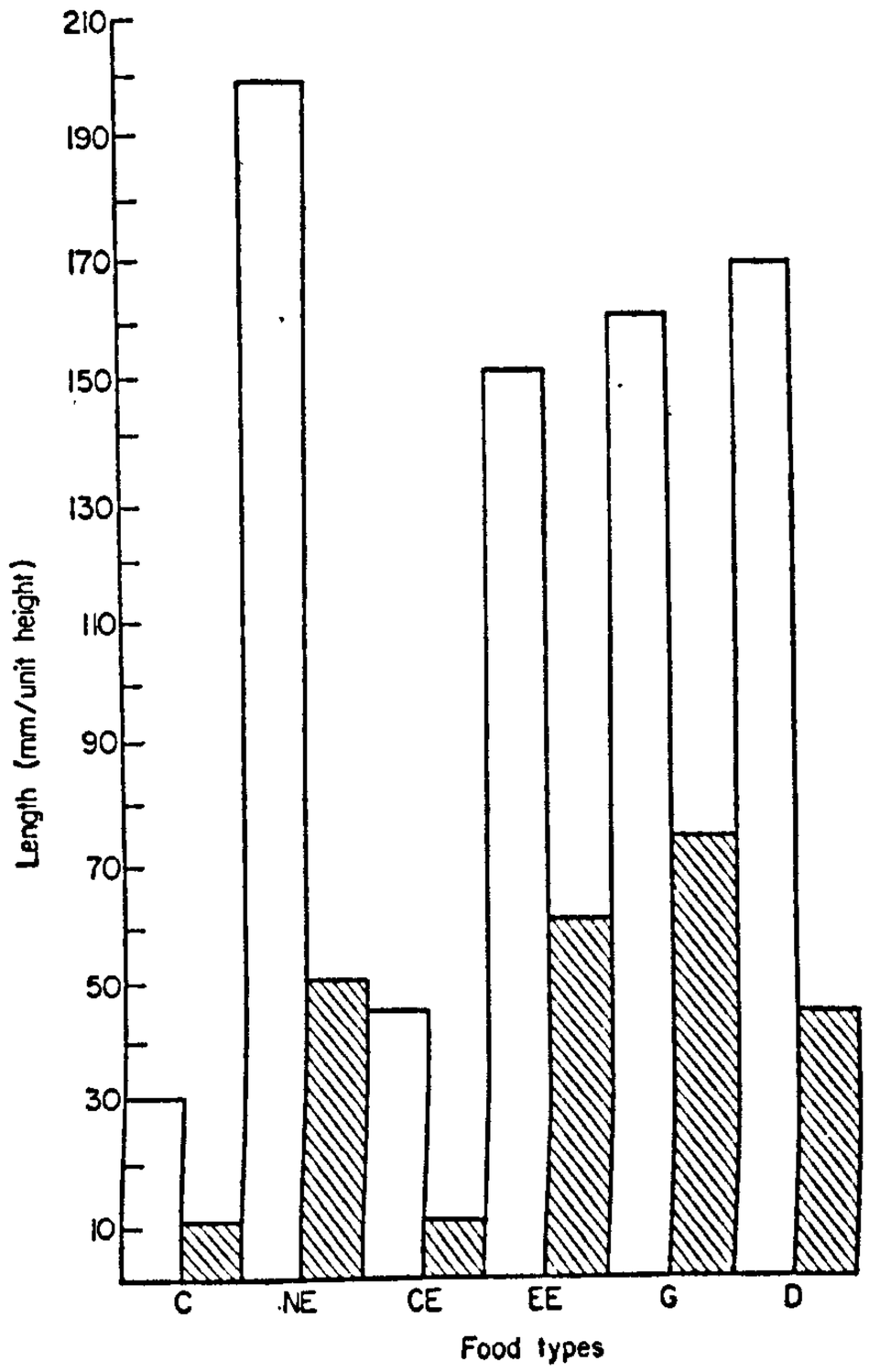


FIG. 3. Histogram showing the total length of gizzard (open columns) and liver strings (hatched columns) produced by different snails offered various food types, over a 12-day period. C, Control; NE, normal *Elodea*; CE, cleaned *Elodea*; EE, *Elodea* extract; G, filamentous green algae; D, diatoms.

(mm/unit height) of the total faecal pellets and liver strings produced for each 2-day interval in this snail.

Fig. 3 shows, as anticipated, that in the control snails kept on agar-grit medium only, faecal output, compared with that of snails kept on normal *Elodea,* was considerably reduced. It was not, however, reduced to zero, indicating that snails may ingest and assimilate some agar, though no evidence was found of this in the crops of these snails at the end of the experiment. A similar reduction in gizzard and liver string production was found on 'clean' *Elodea* though snails fed on *Elodea* extract showed essentially the same faecal output as snails fed on normal *Elodea,* again emphasizing the fact that *Lymnaea pereger* is a microphagous herbivore feeding on the epiphytes on the surface of *Elodea,* but not on the *Elodea* tissue itself.

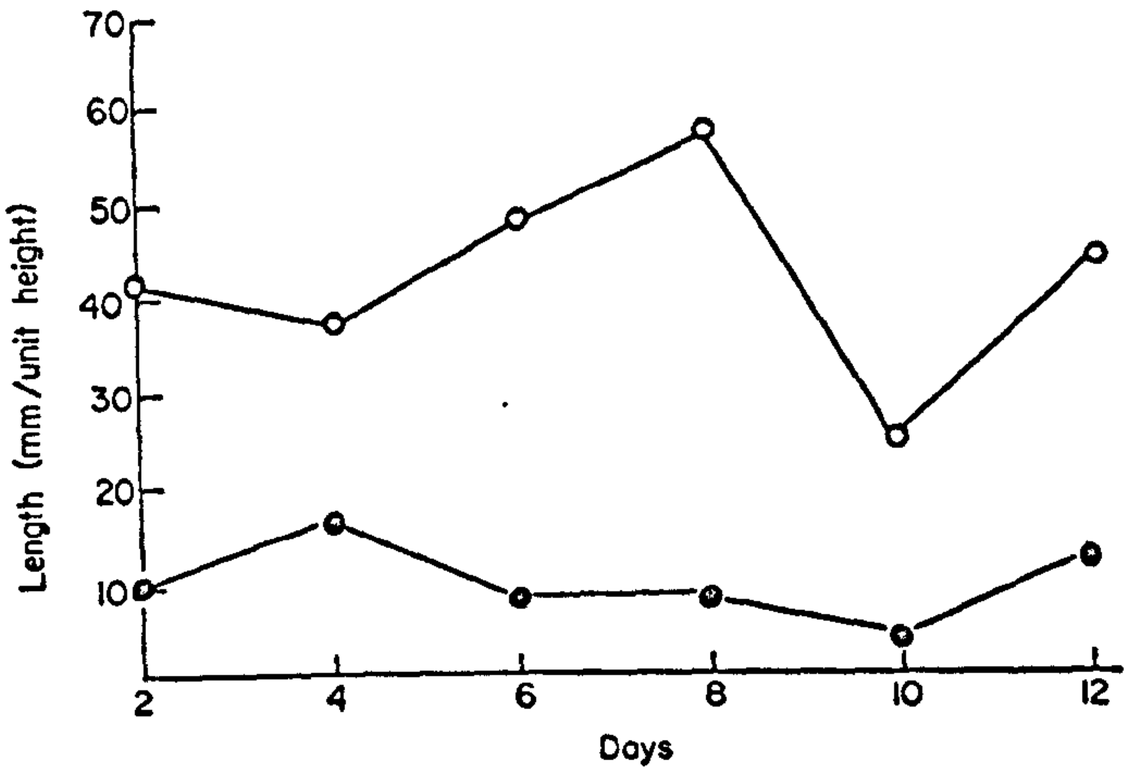


FIG. 4. The lengths of total faecal pellets (O) and liver strings (O) produced every 2 days when snails were fed on a natural diet.

Furthermore, examination of both normal and cleaned *Elodea,* on which the snails had been allowed to graze, showed no apparent damage as a result of this grazing.

Faecal output of snails fed on the green filamentous algae and those fed on diatoms was also similar to output on normal *Elodea*, though liver string production of snails fed on filamentous algae was slightly but significantly greater than the rest. It is tempting to suggest that this food type may therefore be assimilated more readily than the other food types offered.

A comparison of the data presented in Fig. 4 with that presented by Carriker (1946) for *Lymnaea stagnalis appressa* indicates that the length of faecal string produced by this snail was more variable from day to day than that produced by *L. pereger.* A similar observation has been made by Hunter (1953), who attributed this specific difference to the fact that Carriker's animals were fed on a massive diet of lettuce in the laboratory which would require more spasmodic feeding by comparison with *L. pereger* feeding on what he terms a 'diatom film' in nature. It should be pointed out, however, that Carriker correlates such fluctuation to some extent with oviposition, whereas snails under the temperature regimen used in the present experiments did not oviposit.

The other possibility raised at the beginning of this section was that *L. pereger* may have been selecting the most suitable substratum on which its preferred food material occured in greatest abundance. To test this hypothesis starved snails were offered a choice between normal *Elodea* and some other food material. The choice was offered in a 36 cm diameter pneumatic trough, filled with fresh water previously filtered through sintered glass. Food choices were supported on two 4% agar strips, seeded with sterilized grit and attached to the sides of the trough. These strips were each large enough to cover completely half the side walls of the trough.

To prevent possible orientation to light, the sides of the trough were blackened and the trough uniformly illuminated by a light source of 1000 lux fitted above it. Furthermore, the water was not aerated, to prevent possible orientation to the aerator. Water temperature was maintained at 12 ± 3° C.

Food choices offered with the normal *Elodea* were, cleaned *Elodea*, *Elodea* extract, a mixed culture of diatoms, a mixed culture of filamentous green algae, and the agar–grit medium on its own as a control. This required the use of five separate troughs and since each food choice regimen was replicated four times, a total of twenty troughs was used altogether. Ten snails (height, 10–12 cm) were placed in the middle of each trough and left for 24 hr. At the end of this period, the number of individuals found on each food choice other than normal *Elodea*, were counted. This number was expressed as a mean percentage of the total number of individuals added to each trough,,for the four replicates. Such a percentage essentially provides an index of the relative attractiveness (index of attractiveness) of each choice as compared with that of the standard, normal *Elodea*. These indices of attractiveness are presented in Table 1.

TABLE 1. Indices of attractiveness (and their standard errors) for various food choices

Choice other than *Elodea*	Control agar–grit	Clean *Elodea*	*Elodea* extract	Fil. green algae	Diatoms
Index of attractiveness	0	20	75	70	42·5
Standard error	0	8·1	17·3	11·5	5

The 'indices of attractiveness' of each food choice indicate that their relative attractiveness to *Lymnaea pereger* is :
Elodea extract› filamentous green algae› diatoms› clean *Elodea*› control agar. Standard errors, however, indicate that means for filamentous green algae, and *Elodea* extract, are not significantly different, so that the relative attractiveness of each becomes *Elodea* extract and filamentous greens› diatoms› clean *Elodea*› control agar.

When the index of attractiveness is greater than 50 it indicates a greater attractiveness to the food choice than to normal *Elodea*; when less than 50 an attractiveness lower than to normal *Elodea*. Thus the order of relative attractiveness becomes, *Elodea* extract and filamentous green algae› normal *Elodea*› diatoms› clean *Elodea*› control agar.

This order of attractiveness corresponds to the results from the previous experiments which suggested that filamentous green algae had greatest nutritive value, whereas *Elodea* tissue had least. It can therefore be concluded that *Lymnaea pereger* is probably exerting some selection for that substrate offering the most suitable food. This conclusion, however must be treated cautiously since there was nothing to suggest

that *Elodea* extract was any more nutritive than normal *Elodea* yet here it has a higher index of attractiveness.

A clue to the reason for this apparent anomaly may lie in a consideration of the mode by which *Lymnaea pereger* exerts food selection. Pieron (1908) suggested that snails may not select food material by special sensory mechanisms, and Bovbjerg (1965, 1968) has reported that individuals of the lymnaeid snail, *Stagnicola reflexa*, do not move along any sensory gradient towards preferred food when this is of a vegetable nature. Instead, they move randomly but continuously, until they come into contact with some suitable food material, when movement is inhibited or reduced. Such behaviour ultimately results in the aggregation of snails around the preferred food material, but selection is essentially random.

If one supposes that *Elodea* extract and normal *Elodea* are equally suitable as food for *Lymnaea pereger*, one would expect aggregation of this species, due to reduced locomotion, to occur equally on each of the food types. With a large number of snails and replicates one would therefore have expected an index of attractiveness in order of 50, for *Elodea* extract. That this was not obtained may merely be due to a chance deviation from the expected value due to the relatively small numbers of snails and replicates used in these experiments.

DISCUSSION

The general form of the gut in *Lymnaea pereger* is characteristic of a gastropod herbivore. A consideration of the crop contents of individuals taken directly from the field indicated that the herbivorous mode was microphagous rather than macrophagous.

Graham (1955) has pointed out that any digestive system which ultimately depends, as in *L. pereger*, on intracellular digestion must present the digestive cells with small particles of food. This may be achieved either by means of extensive preliminary digestive processes, as in macrophagous feeders, or by strictly adhering to a microphagous habit. This microphagous habit seems to apply in *L. pereger* and implies that the unspecialized radula is incapable of any comminution of food material prior to its ingestion. It is probable that the radula can scrape only small loosely attached particles into the buccal cavity and that any necessary fragmentation is achieved by the muscular action of the grit-filled gizzard, so that the type of food which can be ingested is essentially limited by the nature of the radula.

The importance of fine particles of grit in the gizzard has been demonstrated by Colton (1908) for *L. columella*. He noted that in the absence of grit, food was able to pass through the gut 'unmolested'. Similar observations have been made by Carriker (1946) and Heidermanns (1924).

Turner (1926), in apparent contrast to the hypothesis presented here, has reported that both *L. pereger* and *L. stagnalis* do best in the laboratory when cultured on the rotting leaves of lettuce and watercress. Two factors should be noted, however, that both the watercress and lettuce were used in a partially decomposed state and that these two plants have a softer and more delicate texture than *Elodea*.

The chloroplasts of higher plants are similar in both size and shape to algal unicels so that theoretically they ought to be ingested by the radula action of *Lymnaea pereger*, just as easily as epiphytic algae. It is presumably the plant cell wall, forming a protective envelope around the intracellular chloroplasts, which prevents this from occurring under normal conditions, but when this envelope is soft or partially decomposed, the chloroplasts would obviously be more easily obtained by normal radular action. Boycott (1936) has pointed out that, like terrestrial slugs and snails, freshwater snails can make use of cultivated plants like lettuce, though more readily when they are partly decayed. Furthermore, continued erosion by the radula on such envelopes, in the absence of epiphytes, cannot be discounted as a possible means of ultimate release of plant cell contents.

The feeding experiments emphasize that *L. pereger* ingests epiphytic organisms rather than macrophytic tissue. They also demonstrate that green filamentous algae appear to be selected in preference to diatomaceous species. This again may be correlated with the nature of the envelopes surrounding these two groups of algae.

It is probable that it is this protective case of diatoms which makes their utilization more difficult than the unprotected cells of filamentous green algae. Here it is presumably the relative inefficiency of the gizzard which limits utilization of food. Thus though data in Fig. 3 indicate that diatoms were being ingested in larger quantities than filamentous forms, they probably contributed less to the productivity of this population. This type of situation may not be confined to *L. pereger* since Bovbjerg (1965) has shown that *Stagnicola reflexa* tends to aggregate, in nature, on patches of the green filamentous alga, *Spirogyra*. Furthermore, Eisenberg (1966), working on the population regulation of *Lymnaea elodes*, suggested that such regulation was mediated through food limitation, and that this limitation was one of quality rather than quantity.

It should also be noted that Paine and Vedas (1969), working on the calorific values of marine benthic algae and their postulated relations to invertebrate food preferences, have shown that on a dry-weight basis green algae contain on average a greater potential energy content (Kcal/g dry-weight) than other algal types. On an ash-free dry-weight basis, however, the above workers found that diatoms contain the greatest potential energy store (Kcal/ash-free g dry-weight), presumably because these organisms contain vast amounts of inorganic material in their outer shell. Thus on a dry-weight basis one would expect green algae to be more nutritious than diatoms, whereas on an ash-free dry-weight basis the reverse would be the case. It is suggested, therefore, that even though in absolute terms diatoms are seemingly more nutritious than green algae, the fact that they have a high ash content incorporated within a protective exoskeleton make their utilization by snails more difficult. Thus, in this case, it is the quality of the envelope around the food which is important rather than the potential energy contained within the envelope.

Taylor (1896) has pointed out that plants have developed special protective devices against herbivores, so that although herbivorous molluscs are apparently living in the midst of plenty, they are in fact only able to eke out a precarious existence. The present work suggests that the protective envelopes surrounding the cell contents

of *Elodea* and diatomaceous algae are just such protective devices and that because macrophytic and diatomaceous species often contribute to the bulk of primary productivity in bodies of fresh water, it would be easy to see how such a situation could result in density limitations on natural populations of *Lymnae pereger*. It is also tempting to suggest that the occurrence of an unspecialized radula throughout the whole of the Lymnaeidae may mean that this type of population limitation is generally applicable throughout all members of this family, since such a radula obviously limits the type of food which can be ingested by snails. In this connection, it is interesting to quote Boycott (1936) who says 'it seems quite possible that the abundance of a mollusc in a locus of limited size may depend on the food supply, though whether the occurrence of any species is so determined is problematical.'

ACKNOWLEDGMENTS

I wish to express my sincere thanks to Dr J. B. Jennings, Department of Zoology, Leeds University, for his many constructive suggestions made during the course of this work, and for reading and criticising the manuscript. My gratitude is also expressed to Miss L. J. Chapman for her helpful encouragement.

SUMMARY

Consideration of the gut form of *Lymnaea pereger obtusa* (Kobelt) suggests that it is a herbivorous feeder with an unspecialized radula. Investigation of crop contents of individuals taken directly from the field supports this suggestion but indicates that *L. pereger* ingests epiphytic algae rather than macrophytic tissue.

These findings were corroborated by laboratory feeding experiments in which the faecal products of individuals fed on pure cultures of different algae, and on both normal and epiphyte-free *Elodea*, were compared. The experiments also indicated that *Lymanaea pereger* assimilates green filamentous algae better than diatomaceous species, and other experiments designed to test the selectivity shown by *L. pereger* with respect to different foods indicated that this species preferred green filamentous algae to diatoms.

The apparent inability of *L. pereger* to ingest coarse macrophytic tissues, and its less efficient assimilation of diatoms has been correlated with the protective envelopes surrounding these two potential food types. On the basis of the suggestion made by Taylor (1896) regarding the effectiveness of protective devices in plants against herbivorous molluscs, and by Eisenberg (1966) that populations of *L. elodes* are limited by food quality rather than quantity, a general theory on population regulation in Lymnaeid snails is proposed. This theory is based on the unspecialized nature of the radulae of the Lymnaeids and the quality of the envelopes surrounding the herbivorous material which is potentially available as food to these molluscs.

REFERENCES

BOVBJERG, R. V., 1965. Feeding and dispersal in the snail *Stagnicola reflexa* (Basommatophora: Lymnaeidae). *Malacologia*, **2**, 199–207.

BOVBJERG, R. V., 1968. Responses to food in Lymnaeid snails. *Physiological Zoology*, **41**, 412–423.

BOYCOTT, A. E., 1936. The habitats of fresh-water Mollusca in Britain. *Journal of Animal Ecology*, **5**, 116–186.

CARRIKER, M. R., 1945. Morphology of the alimentary system of the snail *Lymnaea stagnalis apressa* Say. *Transactions of the Wisconsin Academy of Science*, **38**, 1–88.

CARRIKER, M. R., 1946. Observation on the functioning of the alimentary system of the snail *Lymnaea stagnalis appressa* Say. *Biological Bulletin. Marine Biological Laboratory, Wood's Hole*, **91**, 88–111.

COLTON, H. S., 1908. Some affects of the environment on the growth of *Lymnaea columella* Say. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **60**, 410–448.

EISENBERG, R. M., 1966. The regulation of density in a natural population of the pond snail *Lymnaea elodes*. *Ecology*, **47**, 890–906.

ELLIS, A. E., 1926. *British Snails*. Oxford, Clarendon Press.

ENRIQUES, P., 1902. Il fegato dei Molluschi e le sue funzione. *Mitteilungen aus der zoologischer Station zu Neapel*, 281–406.

GRAHAM, A., 1955, Molluscan diets. *Proceedings of the Malacological Society of London*, **31**, 144–159.

HEIDERMANNS, C., 1924. Uber der Muskelmagen der Susswasserlungen- schnecken. *Zoologische Jahrbücher (Abtellung Allgemeine Zoologie und Physiologie der Tiere)*, **41**, 335–424.

HUNTER, W. R., 1953. On migrations of *Lymnaea peregra* (Müller) on the shores of Loch Lomond. *Proceedings of the Royal Society of Edinburgh*, B, **65**, 84–105.

HYMAN, L. H., 1967. *The Invertebrates*, Vol. 6. *Mollusca* 1. New York, McGraw Hill.

KOBELT, W., 1881. *Catalog der im Europäischen Faunengebiet lebenden Binnenconchylien*. Kassel.

PAINE, R. T. and VEDES, R. L., 1969, Calorific values of benthic marine algae and their postulated relation to invertebrate food preference. *Marine Biology*, **4**, 79–86.

PIERON, H., 1908. La localisation du sens de discrimination alimentaire chez les Limnées. *Compte renduo Lebmadaire de l'Académie des Sciences, Paris*, **147**, 279–280.

TAYLOR, J. W., 1896. *A Monograph of the Land and Freshwater Mollusca of the British Isles*. Leeds, Taylor Bros.

TURNER, F. M., 1926. The rate of growth of *Lymnaea peregra*. *Naturalist*, 231–235.

WEST, G. S. and FRITSCH, F. E., 1927. *A Treatise on the British Freshwater Algae*. Cambridge, University Press.

PUBLICATIONS APPENDIX

II

A Method for Determining the Surface Areas of Stones to Enable Quantitative Density Estimates of Littoral Stonedwelling Organisms to be made.

Journal : Hydrobiologia.

Submitted : April 1971.

Accepted : June 1971.

Published : vol. 40, 1972. p. 37-50.

Hydrobiologia, vol. 40, 1, pag. 37—50, 1972.

A Method for Determining the Surface Areas of Stones to Enable Quantitative Density Estimates of Littoral Stonedwelling Organisms to be made.

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Introduction

The ecologist has always encountered great difficulty when attempting to make quantitative density estimates of stone-dwelling littoral fauna, be it in marine, lentic or lotic habitats. Up to now five major sampling techniques have been employed for this purpose:

a. The removal of animals from a defined area of bed, usually by some mechanical device, (e.g. the area defined by bottomless boxes and cylinders Jonásson (1948), Welch (1948), the Surber sampler method Moffet (1936), Surber (1937), the "Pfahlkratzer" Steiner (1919), Wundsch (1936).

b. The removal of stones singly from the bed and fitting them together in jigsaw-like fashion within a defined area on the bank (e.g. Hunter (1953)).

c. The removal of individual stones at random, and counting the relevant organisms on each (Schräder (1932), Müller (1953).

d. the planting of an artificial bottom of prescribed area, allowing for colonisation and removing for faunal estimation (e.g. Moon (1935), Britt (1955), Albrecht (1953), Mundie (1956).

e. The use of time rather than space limited techniques (e.g. Jones, 1941, 1943, 1948).

The difficulties inherent in each of the above sampling techniques have been reviewed by Macan (1958). Basically, techniques a. and

Received April 29, 1971.

b. suffer from the disadvantage that they relate density of organganisms to the area of the bottom, not the area actually available in terms of stone surface. Since the actual area available is probably more representative of the true habitat of stone-dwelling organisms, and since this may in no way be related to the area of bottom, a considerable indefinable error may be introduced into such estimates. That is, when density estimates are made using techniques a. and b. a mean (mean number of organisms/sampling unit) will be obtained with an associated variance and this variance will contain two components, firstly, a component due to the degree of aggregation shown by the population under study and secondly, a component due to the fact that each individual sample may contain differing amounts of stone surface or true habitat. That component due to aggregation is of considerable ecological importance whereas that component due to variation of amount of true habitat contained within each sample is not. Furthermore, techniques a. and b. by conflating these two components, make their separation impossible, and render the means and variances thus obtained of questionable significance.

Technique d. suffers from the obvious disadvantage of artificiality, and the long time interval required for the planted bottom to become fully colonised. Because of these difficulties some workers, notably JONES (1941, 1943, 1948) have reverted to technique c. Time limited censuses, however, can never provide absolute estimates of density and because of variability in censors, fauna collected and habitats, such estimates can never be considered fully comparative.

Technique c. shows the greatest promise, since here one is sampling actual habitat. The main difficulty in using this technique quantitatively, however, has been that of measuring the surface areas of the irregularly shaped stones so obtained, e.g. MÜLLER (1953) merely uses the product of the two longest dimensions of each stone as the rough index of their surface area. It is the purpose of this paper to suggest a relatively simple technique which will overcome this difficulty and to suggest statistical procedures which are most appropriate for use with this technique.

A detailed description of a method which allows the accurate determination of the surface areas of irregularly shaped stones is given first, and then, since this method would be difficult to accomplish in the field, practical and statistical procedures are described for correlating surface area with some more easily measured linear, stone parameter.

Methods

Stones for the study were obtained from a portion of the east shore of Malham Tarn in Yorkshire (Grid ref. 34897666) i.e. that part which is adjacent to "Ha Mire" Plantation and is delimited by two walls which are built into the tarn to a depth of 1 metre. This shore is 200 metres long and has a solid limestone base, with a variable depth of glacial drift and weathering debris over it. Wave action has in fact produced an extremely varied shore, composed of stones, ranging in size from small pebbles to large boulders. These rest loosely on top of one another.

The shore was divided into three sectors (A, B, C) each of which had approximately the same area. A haphazard collection of 100 stones from each sector revealed a considerable degree of inter-sector heterogeneity with respect to the frequency distribution of both stone shape and size. Stones obtained in the collection were subjectively classified as either cuboid, round, flat, or irregular,

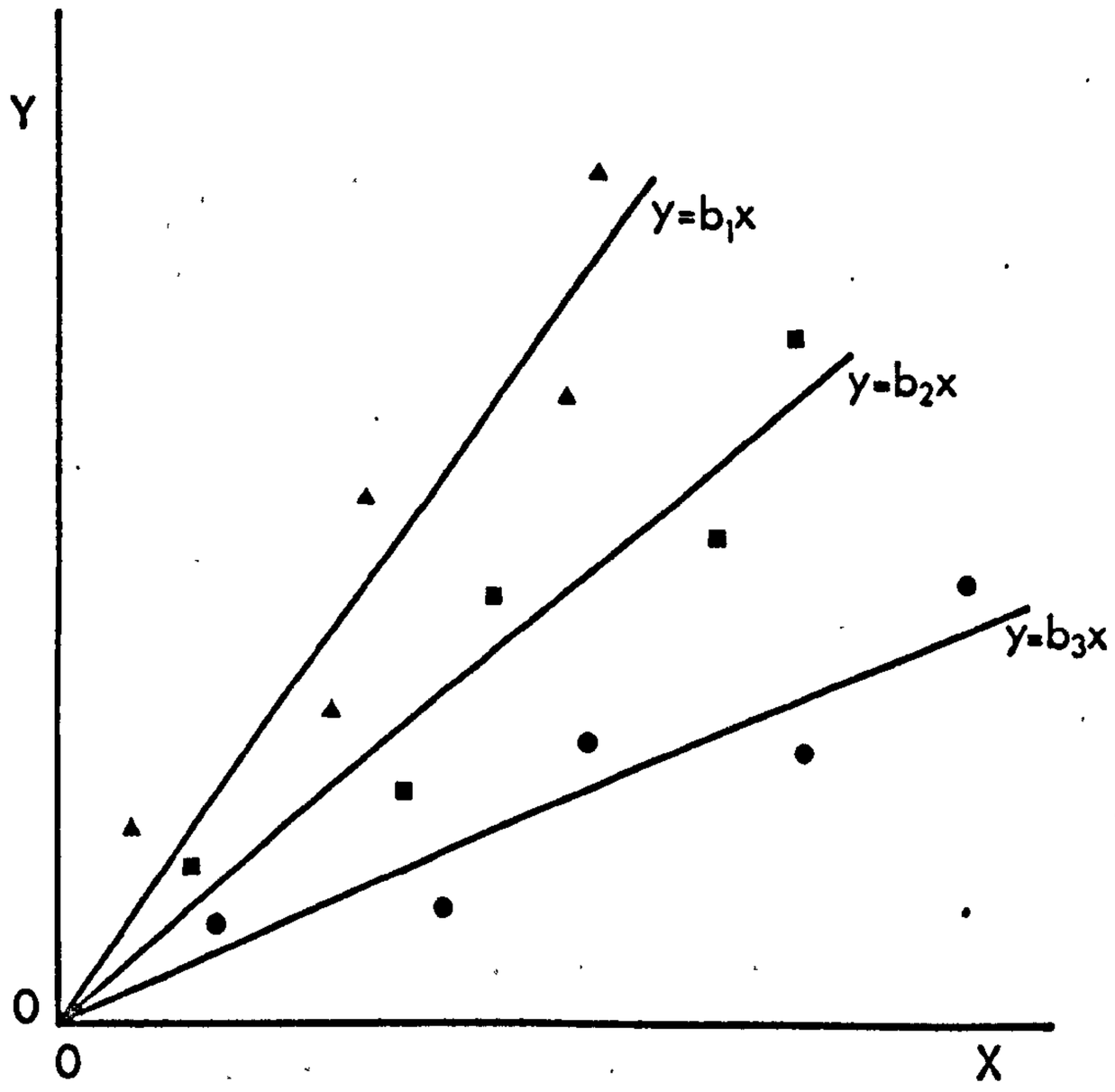

Fig. 1. Graph showing the hypothetical relationship between surface area (y) and some other linear parameter (x) in a population of stones which is comprised of three subpopulations each being characterised with a unique shape and thus a unique value of b, (b_1, b_2, b_3).

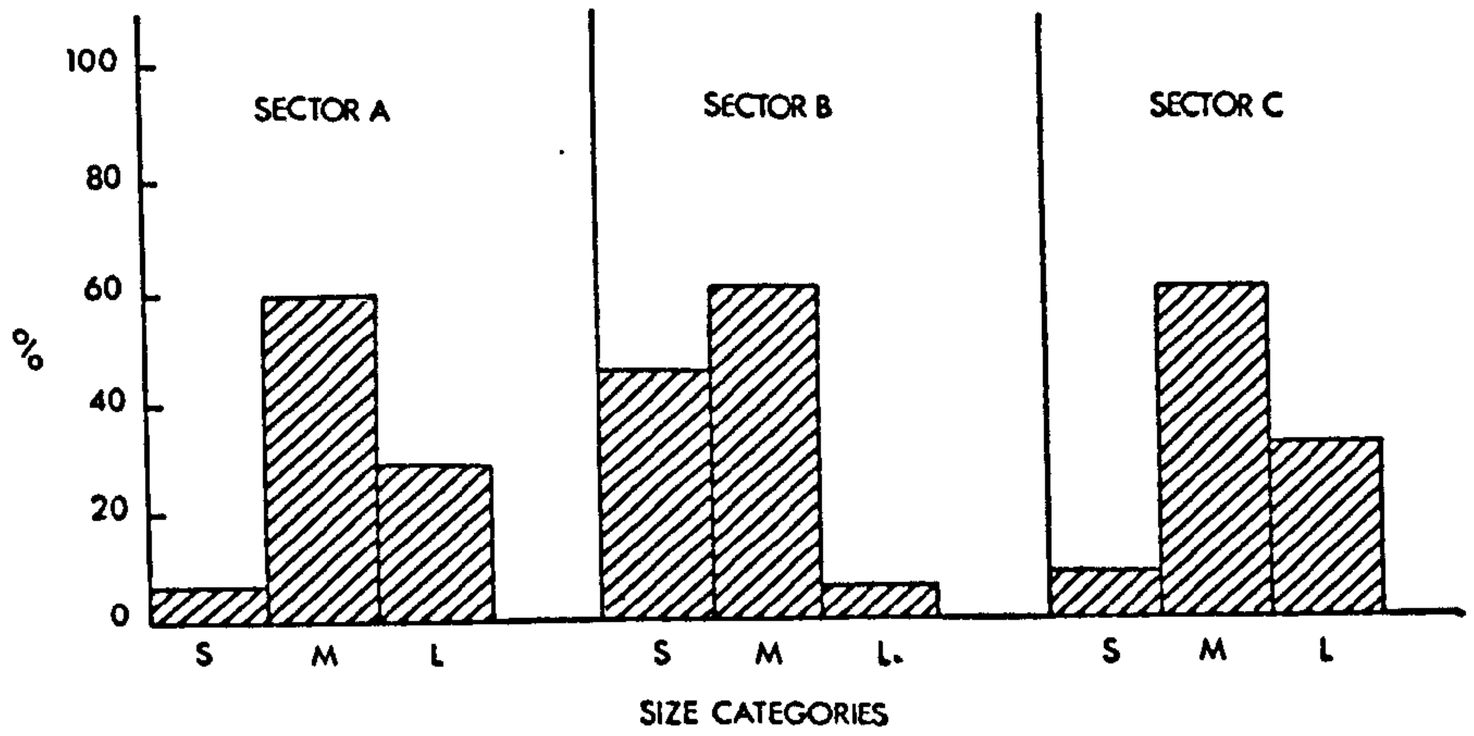

Fig. 2. Histograms showing the SIZE frequency distributions of stones in three sectors on "Ha Mire" shore.

and put into the size classes large, medium and small, on the basis of the size of their perimeter (Figs. 1 & 2). Furthermore, a casual inspection within each sector indicated a lack of homogeneity in either stone shape or size distribution. This situation will be fairly typical in littoral regions where different parts of the same shore are subjected to differing degrees of weathering. This lack of intra- and intersector homogeneity renders sampling techniques of the "types a. and b." of little meaning, for reasons stated in the introduction.

In order to obtain a truly representative sample of stones from "Ha Mire" shore, a random sample was made. This was achieved by dividing the shore on a map into a number of equally spaced longitudinal and lateral divisions. The positions for stone collection were then fixed by a series of 50 random co-ordinates.

Stones so collected were taken back to the laboratory when their greatest length and longest perimeters were measured (cm). These parameters were chosen since it was considered that they would provide the maximum amount of information about stone size, with the minimum amount of effort, they could easily be measured under field conditions, and their definition would be subject to least confusion.

After drying, 3 coats of a rubber latex solution, ("Revultex")* were applied to the stones as evenly as possible, the last coat being thickened with size. Following this procedure stones were left to dry for one week at room temperature (approximately 18°C).

*Makers: P. K. Dutt & Co. Ltd., Clan Works, Howard Rd., Bromley, Kent, England.

It soon became apparent that perfectly even coating with the latex would be impossible, so that the simple computation of stone surface area from the weight of mould required to cover them would not be feasible. Consequently, following the one week drying period the moulds were carefully removed from the stones in two halves. Each half mould was turned inside out and weighed dry (W_1). That surface of mould which mirrors the stone surface was then immersed in a "Teepol" solution, (a standard solution of "Teepol" in 500 cc of distilled water) so that it would be coated with an even surface layer of water. After making sure that the other side of the mould was completely dry, it was reweighed (W_2) so that:

$(W_2 - W_1)g$ = weight of surface layer of water 1

This procedure was then repeated on a series of ten standard bodies of uniform shapes (cuboids, spheres, and cylinders of various sizes) and with known surface areas. From these standards it was possible to compute the mean weight of surface layer of water per square centimetre of mould, and this was found to be .0020 $\pm$ .00012 g. Using this figure as a conversion factor it is then possible to calculate the surface area of the irregularly shaped stones. i.e.:

$$\frac{(W_2 - W_1)\ g}{(.002)\ g} = \text{Surface area } (cm^2) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ 2$$

Harrod & Hall (1962) also used a "Teepol" solution of the same strength as the one used here in estimating the surface areas of aquatic plants. Here moulds were not required since aquatic plants, unlike porous limestone rocks, do not absorb water over their surface area. In one of their experiments, however, Harrod & Hall used a polythene model of a Hydrangea leaf, which is to some extent comparable to the moulds used in this work, and the weight of surface films per square cm of polythene model, .0024 $\pm$ .0013 g/cm^2 (my calculation from their Fig. 1b.), obtained agrees well with the results published in this paper.

Results

The results from the above procedures provide two measures of stone size i.e. an estimate of their surface area (SA) and a measure in terms of some other linear parameter (longest length, L, largest perimeter, P, longest length x largest perimeter, LP). The latter are easily measured in the field, the former can only be measured in the laboratory. It was necessary, therefore, to try to establish a functional relationship, of the type:

$y = bf(x)$ 3

(where y = surface area, x = some other linear parameter, b = a constant). between surface area and the linear parameters.

Normally, however, a population of stones on a shore will consist of individuals with a wide variety of shapes. The shape of stones will obviously affect the relationship expressed by equation 3., such that the value of b will vary with stone shape. It is thus apparent that with respect to this functional relationship, the total population of stones could be divided into a number of subpopulations, each containing individuals with the same unique shape, and each having a unique value of b. In theory a separate regression equation could be derived for each shape category, and since each must have a common origin, zero (i.e. when x is zero y must be zero) the resultant regression lines would diverge from the origin zero. (Fig. 3). In practice the erection of separate regression lines would

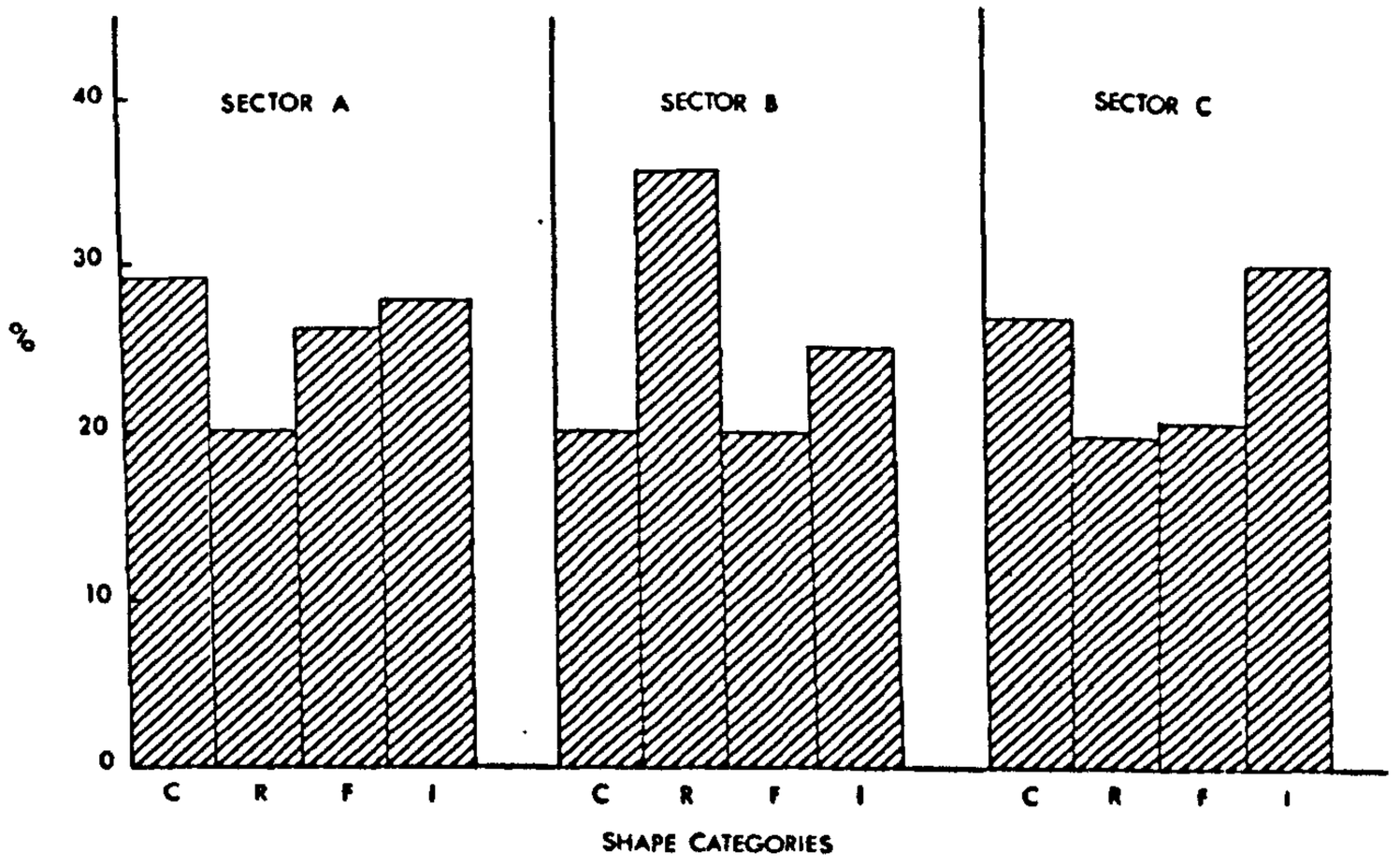

Fig. 3. Histograms showing the shape frequency distribution of stones in three sectors on "Ha Mire" shore.

be impossible or at least inconvenient, and a single line is calculated. Nevertheless, divergence of components must result in a divergent scatter of points from zero, and consequently a variance of y for a given value of f (x) which is dependent on f (x). This can be seen by inspection of Figs. 3 & 4. Since either variance or some function of variance e.g. standard deviation must be dependent on f (x) and remembering the constraint that the regression line must pass through the origin, the regression relationship between surface area and other linear parameters cannot be calculated justifiably by the normal least squares method.

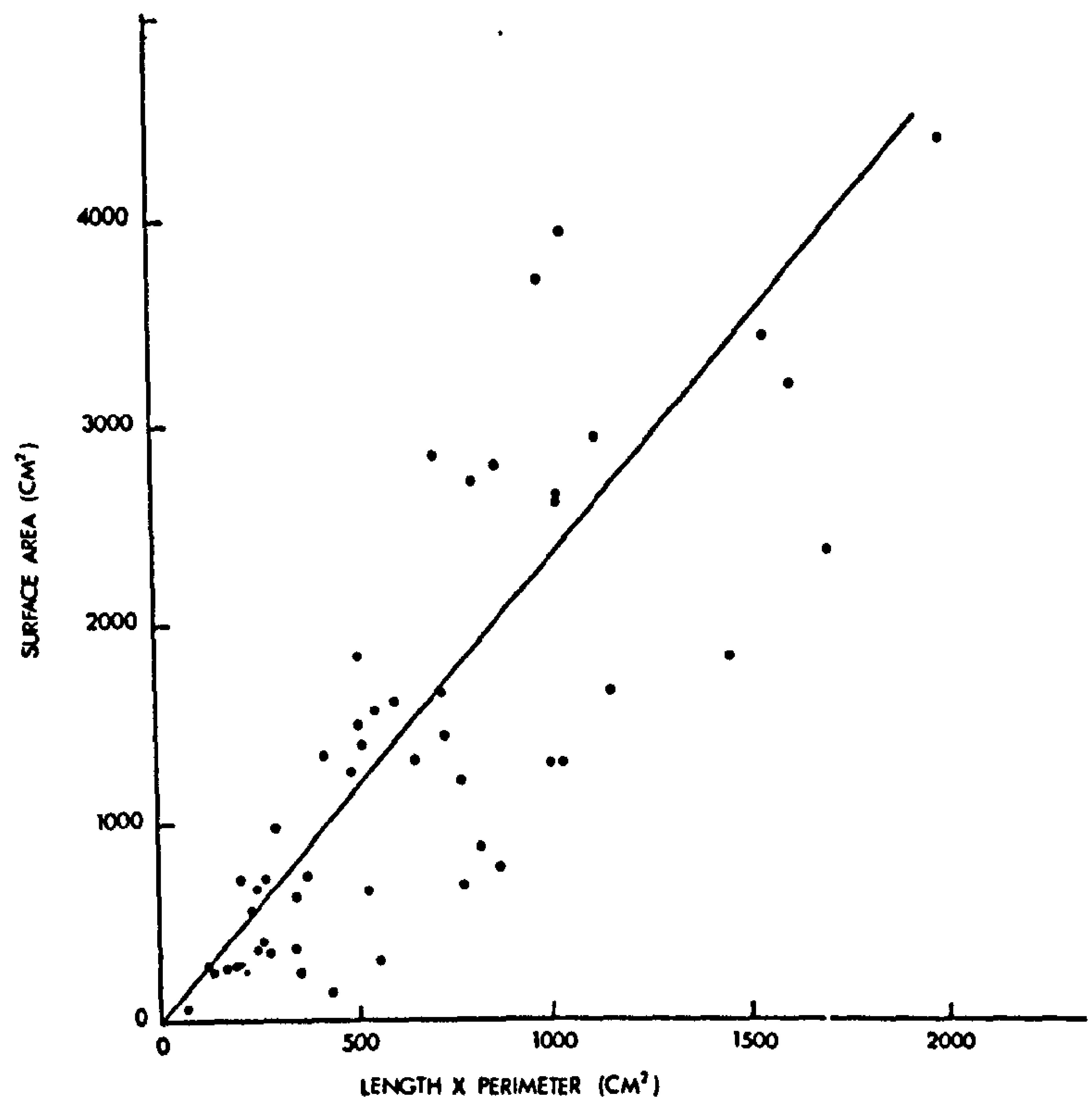

Fig. 4. Graph showing the relationship between SA and LP of stones on "Ha Mire" shore. The regression line represents equation 10 (see text).

It can however be shown (see Appendix) that:

a. if variance is independent of f (x), but the regression line must pass through the origin (zero), then

$$b = \frac{\Sigma xy}{\Sigma x^2} \qquad (4)$$

$$\text{var.} = \frac{\hat{\sigma}}{\Sigma x^2} \qquad (5)$$

(See equations 12A—15A in Appendix).

b. if variance (S^2) is proportional to f (x), then

$$b = \frac{\Sigma y}{\Sigma x} \qquad (6)$$

$$\text{var.} = \frac{\hat{\sigma}}{\Sigma x} \qquad (7)$$

(See equations 16A—19A in Appendix).

c. if standard deviation ($\sqrt{S^2}$) is proportional to f (x), then

$$b = \frac{(\Sigma y/x)}{n} \qquad (8)$$

$$\text{var.} = \frac{\hat{\phi}}{n} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 9$$

(See equations 20A—23A in Appendix).

Using all these statistics the relationship between surface area (y) and each of the other linear parameters (x), has been computed (See Table I).

TABLE 1. Regression equations relating SA to L, P, and LP of stones on 'Ha Mire' shore. Confidence limits represent one standard error.

x	METHOD	Equation y=a+bx		't'(df=48) Comparing b with zero	P
1.	normal 'least squares'	y= -819.1+150.9(±48)x		3.20	+
L. 2.	S^2 independent of x but passing through origin.	y= 101.84(±16.5)x	*	6.20	++
3.	$S^2 \propto x$	y= 95.89(±15.4)x	*	6.23	++
4.	$\sqrt{S^2} \propto x$	y= 85.30(±16.0)x	*	5.33	++
1.		y= -1477.3+66.5(±7.01)x		3.30	+
P. 2.		y= 39.63(±5.24)x	*	7.56	++
3.		y= 36.24(±4.48)x	*	8.10	++
4.		y= 32.99(±5.44)x	*	6.06	++
1.		y= 518.0+1.4(±.35)x		4.00	++
LP. 2.		y= 1.94(±.38)x	*	5.00	++
3.		y= 2.22(±.26)x	*	8.50	++
4.		y= 2.17(±.28)x	*	7.80	++

* a=0

df= degrees of freedom (n-2)

+: p=.01 ++: p= .001

The regression equations so obtained (Table I) are all significant at the 1% level at least, but in all cases the normal least squares method is less significant than the other methods used. Furthermore considering separately all the equations for x = L., x = P., and x = LP., it can be seen by reference to the "t" values that most confidence can be placed in equations derived from the assumption that variance is proportional to f (x), which has shown to be the most reasonable on theoretical grounds.

A consideration of the "t" values associated with all the equations listed in the table indicates that most confidence can be placed in equation LP3 i.e.:

$$y = 2.22\ (\pm\ .26)\ x \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 10$$

and this is therefore the most appropriate to use on subsequent sampling occasions for converting LP (field parameter) to surface area.

Conclusions

It has been possible to obtain an equation expressing the relationship between stone surface area and some other parameter which is easily assessed under field conditions i.e. equation 10. It is not claimed, however, that either the parameter chosen or the relationship derived will have applicability to all shores. The form of the relationship will presumably depend to a large extent on the prevailing geological and weathering conditions, both of which will affect stone size and shape distributions. Nor is it claimed that the parameters chosen were necessarily the best, from the point of view of showing closest correlation with stone surface area e.g. stone weight or volume may have provided closer fits. Nevertheless, these parameters chosen were those which could be most easily measured under field conditions.

It is clear, then, that equation 10 merely provides a convenient empirical relationship between surface area and LP for one particular shore. This relationship must obviously be re-established for all new shores considered, but since using the technique described above, this can be achieved within at least a month, the objection is not prohibitive.

Having established the above relationship from an initial "calibrating" sample, and assuming that this original sample is sufficiently representative of the whole shore, it is possible to use the "calibration equation" in subsequent independent samples involving estimations of the density of organisms inhabiting stones on that shore. This can be achieved by simply using technique c. (see Introduction) which now has the added power of being associated with a method by which the surface areas of the individual stones can be estimated.

Analysis of raw data

It is clear that the sampling technique proposed will provide raw data of the following kind:

sample no.	1.	2.	3.	k.
no. of organisms/stone	x_1	x_2	x_3	x_k
observed size of stone (e.g. LP).	a_1	a_2	a_3	a_k
calculated size of stone (e.g. SA from the empirical equation $A = kf(a)$).	A_1	A_2	A_3	A_k

This raw data may be manipulated in various ways to obtain a value for the mean number of organisms per unit area of habitat, and each method must be critically examined, so that the most effective is chosen. These methods may be summarised as follows:

$$\frac{\Sigma\left(\frac{x}{a}\right)}{k} = \bar{x}_{1a} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 11$$

$$\frac{\Sigma x}{\Sigma a} = \bar{x}_{2a} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 12$$

$$\frac{\Sigma\left(\frac{x}{A}\right)}{k} = \bar{x}_{1A} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 13$$

$$\frac{\Sigma x}{\Sigma A} = \bar{x}_{2A} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 14$$

where: $\bar{x}_{1a}$ and $\bar{x}_{2a}$ = the mean numbers of organism per unit observed size.

and $\bar{x}_{1A}$ and $\bar{x}_{2A}$ = the mean numbers of organism per unit area (calculated size).

In order to obtain the values $\bar{x}_{1A}$ and $\bar{x}_{2A}$, all the observed stone sizes (a_1 to a_k) must be converted using the empirically derived equation $A = kf(a)$, to surface area values, (A_1 to A_k). This has the disadvantage of repeatedly introducing the error associated with this conversion into the ultimately obtained mean, and should obviously be avoided. This leaves estimates of the type $\bar{x}_{1a}$ and $\bar{x}_{2a}$, and it is now necessary to consider how the variances associated with these estimates should be computed.

The sample obtained will contain a large number of stones which will show a considerable variation in observed size i.e. there is no fixed sampling unit. Thus in calculating a mean from the sample, one is essentially determining the mean relationship between numbers of organisms per stone and stone size, and this can be expressed as follows:

$$x = bf(a) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 15$$

where, $b = \bar{x}_{1a}$ or $\bar{x}_{2a}$

This equation can clearly be identified with equation 3., so that equations 11 and 12 can be identified with equations 8 and 6 respectively, and their associated methods of variance estimation i.e. equations 9 and 7.

The problem remains as to which of the estimates $\bar{x}_{1a}$ and $\bar{x}_{2a}$ is most appropriate, and this will clearly depend on the population considered and its associated dispersion pattern. Thus if the sample is divided up into a number of subgroups, where each subgroup contains all stones of the same or similar sizes, and the mean num-

ber of organisms per stone with variance is estimated by conventional means for each subgroup; then $\bar{x}_{1a}$ is most appropriate when standard deviation is dependent on the mean, whereas $\bar{x}_{2a}$ is most appropriate when variance is dependent on the mean.

For purposes of comparison it is necessary to convert estimates of the type $\bar{x}_{1a}$ and $\bar{x}_{2a}$ to an expression of the type mean number of organisms per unit area. This can simply be achieved by:

$$\frac{\bar{x}_{1a}}{b} = \bar{X} \quad \ldots\ldots 16$$

where b is obtained from the empirically derived equation relating observed stone size to surface area (e.g. equation 3 or $b = 2.22\ x$ from the results obtained here). Each of the expressions $\bar{x}$ and b have been associated with variance i.e. S_x^2 and S_b^2 respectively, so that the variance of $\bar{x}$ becomes:

$$\frac{1}{(b)^2}\left[S_x^2 - \left(\frac{\bar{x}_{1a}}{b}\right) S_b^2\right] \quad \ldots\ldots 16$$

(variance of a ratio).

Summary

1. Surface areas of irregularly shaped stones were determined by coating the stones with a rubber latex solution, removing the mould and calculating the weight of an even film of water which covered the surface of the mould which mirrored the stone surface.

2. Similar work on standard bodies of known surface area revealed that .0020 ($\pm$ .00012) g of water film covered 1 cm^2 of mould. This factor was then used in estimating the surface areas of the stones.

3. It was recognised that this procedure could not be carried out in the field, neither would it be convenient for large repetitive samples so that the possibility of correlating stone surface area with some other parameter which could be more easily measured, was investigated.

4. A relationship was found to exist between surface area and the product of the stones longest length and largest perimeter i.e. $y = 2.22\ (\pm .26)\ x$ (where y = surface area and x = LP). It was not possible to obtain this relationship by normal least squares method.

5. A sampling procedure based on this technique and using the individual stones as the sampling unit was suggested.

6. The statistical treatment of raw data which would be obtained from such a sample was discussed.

Acknowledgements

I am indebted to Professor B. L. Welch, of the Department of Mathematics, Leeds University, for invaluable assistance with the statistical part of this work. My gratitude is also expressed to Dr. E. Broadhead for advice during the course of the work and for reading and criticising the manuscript, and to my wife for assistance in collecting the stones, and for typing the manuscript.

The work was carried out under the tenure of a N.E.R.C. studentship.

Appendix

Methods of Calculating b in the relationship y = bf (x)

If there is some functional relationship between two variables by $y = Bf(x)$, the expected value of y for a given value of x will be given by:

$$E(y/x) = Bf(x) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 1A$$

and Variance (var.) $(y/x) = \text{ø}f(x)$ $\ldots\ldots\ldots\ldots\ldots\ldots$ 2A

where ø = some constant

now, assuming var. (y/x) is dependent on some function of x

$$\therefore \quad \frac{1}{\text{var. } (y/x)} = \frac{1}{\text{ø}f(x)} = \frac{1}{\text{ø}} w_x \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 3A$$

where $w_x = \dfrac{1}{f(x)}$

Now B is obtained by minimising

$S = w_x (y - \bar{y})^2$ with respect to B $\ldots\ldots\ldots\ldots\ldots\ldots$ 4A

or $S = w_x (y - Bx)^2$ $\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$ 5A

$$\therefore b = \frac{\Sigma w_x xy}{\Sigma w_x x^2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad 6A$$

where b = sample estimate of B

$$\therefore \quad \text{var. } b = \frac{\text{ø}}{(\Sigma w_x x^2)} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 7A$$

$$\text{and estimated var. } b = \frac{\hat{\text{ø}}}{(\Sigma w_x x^2)} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 8A$$

where $\hat{\text{ø}}$ = sample estimate of ø

$$= \frac{S_{\text{min.}}}{n-1} = \frac{\Sigma w_x (y - bx)^2}{n-1} \ldots\ldots\ldots\ldots \quad 9A$$

$$\therefore n-1\ \hat{\text{ø}} = (\Sigma w_x y^2) - b(\Sigma w_x x^2) \ldots\ldots\ldots\ldots\ldots\ldots \quad 10A$$

Substituting from equation 6A:

$$n-1\ \hat{\text{ø}} = \Sigma (w_x y)^2 - \frac{(\Sigma w_x xy)^2}{(\Sigma w_x x^2)} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad 11A$$

Applying this to particular cases: —

a. *in particular if variance is independent of f (x) i.e. the same for all values of x*

Since var. (y/x) = ø 12A
(by substituting f (x) = 1 and $w_x = 1$ in equation 1A).

then $b = \frac{\Sigma xy}{\Sigma x^2}$ (Substituting in equation 6A) 13A

and estimated var. $b = \frac{\hat{\sigma}}{(\Sigma x)^2}$ (Substituting in equation 7A) 14A

where (n—1) $\hat{\sigma} = (\Sigma y^2) - \frac{(\Sigma xy)^2}{\Sigma x^2}$ (Substituting in equation 11A) 15A

b. *in particular if variance is directly proportional to x*

Since var. (y/x) = øx 16A
(by substituting f (x) = x and wx = 1/x in equation 1A).

then $b = \frac{\Sigma y}{\Sigma x}$ (Substituting in equation 6A) 17A

and estimated var. $b = \frac{\hat{\sigma}}{(\Sigma x)}$ (Substituting in equation 7A) 18A

where (n—1) $\hat{\sigma} = \Sigma (\frac{y^2}{x}) - \frac{(\Sigma y)^2}{\Sigma x}$ (Substituting in equation 11A) 19A

c. *in particular if standard deviation is proportional to* x

Since var. (y/x) = øx² 20A
(by substituting f (x) = x² and $w_x = 1/x$ in equation 1A).

then $b = \frac{(\Sigma y/x)}{n}$ (Substituting in equation 6A) 21A

and estimated var. $b = \frac{\hat{\sigma}}{n}$ (Substituting in equation 7A) .. 22A

where (n—1) $\hat{\sigma} = \Sigma (\frac{y^2}{x^2}) - \frac{(\Sigma y/x)^2}{n}$ (Substituting in equation 11A) 23A

References

Albrecht, M. L. - 1953 - Die Plane und andere Flämingbäche. *Z. Fisch.* 1: 389—476.

Britt, N. M. - 1955 - New methods of collecting bottom fauna from shoals or rubble bottoms of lakes and streams. *Ecology* 36: 524—525.

Harrod, J. J. & Hall, R. E. - 1962 - A method for determining the surface areas of various aquatic plants. *Hydrobiologia* 20: 173—178.

Hunter, W. R. - 1953 - On the growth of the fresh-water limpet, *Ancylus fluviatilis* Müller. *Proc. Zool. Soc. Lond.* 123: 623—636.

HUNTER, E. R. - 1961 - Life cycles of four fresh-water snails in limited populations in Loch Lomond, with a discussion of intraspecific variations. *Proc. Zool. Soc. Lond.* 137: 135—171.
JÓNASSON, P. M. - 1948 - Quantitative studies of the bottom fauna. In Berg, K. Biological studies on the River Susaa. *Folia. limnol. scand.* 4: 204—208.
JONES, J. R. E. - 1941 - The fauna of the river Dovey, West Wales. *J. Anim. Ecol.* 10: 12—24.
JONES, J. R. E. - 1943 - The fauna of the river Teifi, West Wales. *J. Anim. Ecol.* 12:
JONES, J. R. E. - 1948 - The fauna of four streams in the "Black Mountains" district of South Wales. *J. Anim. Ecol.* 17: 75—80.
MACAN, T. T. - 1958 - Methods of sampling the bottom fauna in stony streams. *Mitt. int. Ver. Limnol.* 8: 1—21.
MOFFETT, J. W. - 1936 - A quantitative study of the bottom fauna in some Utah streams variously affected by erosion. *Bull. Univ. Utah.* 26: 1—32.
MOON, H. P. - 1935 - Methods and apparatus suitable for an investigation of the littoral region of digotrophic lakes. *Int. Rev. Hydrobiol.* 32: 319—333.
MÜLLER, K. - 1953 - Produktionsbiologische Untersuchungen in nordschwedischen Fliessgewassern. Teil 1. Der Einfluss der Flossereiregulierungen auf dem quantitativen und qualitativen Bestand der Bodenfauna. *Rep. Inst. freshwat. Res. Drottningholm.* 34: 90—121.
MUNDIE, J. H. - 1956 - A bottom sampler for inclined rock surfaces in lakes. *J. Anim. Ecol.* 25: 429—432.
SCHRÄDER, T. - 1932 - Über die Möglichkeit einer quantitativen Untersuchung der Boden und Ufertierwelt fliessender Gewässer. *Z. Fisch.* 30: 105—125.
STEINER, G. - 1919 - Untersuchungsverfahren und Hilfsmittel zur Erforschung der Lebewelt der Gewässer: *Z. Fisch.* 30: 105—125.
SURBER, E. W. - 1937 - Rainbow trout and bottom fauna production in one mile of stream: *Trans Amer. Fish. Soc.* 66: 193—202.
WELCH, P. S. - 1948 - Limnological Methods. Blakiston, Philadelphia. pp. 381.
WUNDSCH, H. H. - 1924 - Die quantitative Untersuchung der Bodenfauna und -flora in ihrer Bedeutung für die theoretische und angewandte Limnologie. *Verh. int. Ver. Limnol.* 2: 13—59.

PUBLICATIONS APPENDIX

III

A New Radiotracer Technique Involving 14C and 51Cr for Estimating the Assimilation Efficiencies of Aquatic Primary Consumers.

Journal : Oecologia.

Submitted : January 1972.

Accepted : February 1972.

Published : In conjunction with Dr. C.R. Fletcher.
vol. 9, 1972. p. 155-170.

Oecologia (Berl.) 9, 155—170 (1972)

A New Radiotracer Technique Involving ^{14}C and ^{51}Cr, for Estimating the Assimilation Efficiencies of Aquatic, Primary Consumers

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Received January 3, 1972

Summary. Gravimetric, radiotracer, and indicator methods currently available for estimating assimilation efficiencies, have been reviewed and their associated limitations have been discussed. It was concluded that the basic assumption implicit to gravimetric and indicator techniques, i.e. that all material contained within the faeces is derived from the food, does not generally hold. Radiotracer techniques are not based on this assumption but are time consuming. Consequently a new radiotracer technique analogous to indicator methods has been developed. In this technique the concentration of a non-absorbed indicator is expressed in terms of a radiotracer, ^{14}C, which can be absorbed but which, at least initially, is only present in the food, rather than expressing it in terms of dry weight. ^{51}Cr has been used as the non-absorbed indicator.

Use of these two isotopes in conjunction not only enables a distinction to be made between faecal material derived from food, and that derived from metabolic secretions but also facilitates estimation of assimilation efficiencies from small samples of faeces only. The new technique requires simply, measurement of the ratio ^{14}C:^{51}Cr in samples of both food and faeces.

The applicability of conditions necessary for operation of the new technique has been tested on two species of freshwater gastropod, one feeding on epilithic algae, the other on bacteria, and its effectiveness has been tested by reference to results obtained from another, more conventional method involving ^{14}C only.

Introduction

Most population energy studies are organised around the energy budget equation which, in its basic form may be expressed as

$$C - F = D = P + R + U$$

(symbols from Petrusewicz, 1967b). Component D (absorbed energy) can be derived indirectly from terms on the right hand side of the equation (e.g. Fischer, 1966; Klekowski *et al.*, 1966; Shushkina *et al.*, 1968). Independent and direct estimation of D from terms on the left hand side of the equation, however, provides not only a useful check but also enables a deeper understanding of the energy flow and production processes operating within the population.

Component D is usually expressed as a fraction of C (consumption) i.e.

$$\left(\frac{C-F}{C}\right)\times C=D, \tag{2}$$

and this fraction $(C-F)/C$, in the form of a percentage, is generally, but erroneously called the assimilation efficiency. Because of the wide acceptance of this term, however, we shall continue to use it.

The techniques already available for estimating assimilation efficiencies can be divided into three main groups, i.e. gravimetric, radiotracer and indicator. Gravimetric techniques involve estimating absorption from the difference between weight of food consumed and weight of resultant faeces (e.g. Smith, 1959; Phillipson, 1960a, b; Fewkes, 1960; Lawton, 1970). Radiotracers on the other hand, have been used in a variety of ways depending on the type of radiotracer employed, and on the relationship between actual body burden and equilibrium body burden of radioisotope in the organism concerned. Thus with ^{85}Sr, a gamma emitter, uptake of isotope can be monitored in whole, living animals when, according to Hubbell *et al.* (1965), absorption of ^{85}Sr appears to be equivalent to absorption of food, at least in terrestrial isopods. The more logical isotopes to use, however, are ^{3}H and ^{14}C, since carbon and hydrogen are the two most abundant elements in organic material. But since both emit $-\beta$ particles of only moderate penetrating power and energy, measurement of absorption is only possible either postmortem or by collection of faeces from the labelled diet and measuring the difference between the amount of isotope eaten and that egested (e.g. Hargrave, 1970, for ^{14}C).

Whereas both gravimetric and radiotracer techniques require quantitative collection of faeces, or at least in the latter case complete removal of non-absorbed isotope from the gut, indicator techniques have been developed to allow estimation of assimilation efficiencies using small samples of faeces only. The methods involve measuring the increase in concentration of an inert, non-absorbed substance as it passes through the gut. The non-absorbed substance may either be part of the food e.g. ash (Conover, 1966), or may be added by the experimeter e.g. chromic oxide (Corbet *et al.*, 1960; McGinnis and Casting, 1964a, b).

The assumption that all organic material contained within the faeces is derived entirely from the food is implicit to the use of both gravimetric and indicator methods. This assumption is never exactly true, however, since all animals lose some metabolic secretions in the faeces and such losses will result in an underestimation of assimilation efficiencies, especially when faeces are either used as a major vehicle for excretion e.g. the insects, or when faeces are inextricably mixed with urine e.g. birds, or when faecal pellets are compacted by metabolic secretions e.g. mucus in

snails. The methodological difficulties involved in dinstinguishing between excreta and egesta have lead to the replacement of the term absorption (D) by the term assimilation (A) in Eq. (1) i.e.

$$A = C - FU \tag{3}$$

$$A = P + R \tag{4}$$

(Petrusewicz, 1967a; Johannes and Satomi, 1967). Although this reorganisation of the equation is theoretically sound, and apparently more feasible, this should not detract from attempts to partition FU, since the latter will give a more complete picture and will furthermore be essential to physiological ecologists interested in efficiencies of utilization of different food types.

Radiotracer techniques allow this partitioning, but at present are rather time consuming requiring total removal of isotope from the gut. It is the purpose of this paper to suggest a new radiotracer technique allowing measurement of absorption, but not requiring quantitative collection of faeces.

Theory of New Technique

The indicator technique allows computation of assimilation effeciencies from a small sample of faeces (see introduction), by use of the following equation:

$$\text{Assimilation efficiency} = \left\{1 - \frac{\text{conc. indicator in food/unit dry wt.}}{\text{conc. indicator in faeces/unit dry wt.}}\right\} 100. \tag{4}$$

This technique, however, can be improved upon considerably by expressing the concentration of non-absorbed indicator in terms of some other substance which can be absorbed but which, at least initially, is only present in the food, rather than expressing it in terms of dry weight. The assimilation efficiency thus obtained would not contain the error associated with metabolic losses in the faeces. ^{14}C can be used as such a substance i.e. to label the food and thus distinguish between non-absorbed material and secretions in the faeces provided that the ^{14}C body burden of the organism concerned never becomes significant.

To alleviate the necessity of weighing and to transform all terms of Eq. (4) into the same units it would also be more convient to use a radioisotope as the non-absorbed indicator when, since decay rate of an isotope is proportional to its mass, and assuming decay of the two isotopes can be distinguished, Eq. (4) becomes:

$$\text{Assimilation effeciency} = 1 - \left\{\frac{\text{cpm non-absorbed indicator (food)/cpm } ^{14}C \text{ (food)}}{\text{cpm non-absorbed indicator (faeces)/cpm } ^{14}C \text{ (faeces)}}\right\} 100. \tag{5}$$

Using ^{14}C to label the food means that the assimilation efficiency so obtained will be essentially that of carbon, but since carbon is ubiquitously distributed throughout the biomass of all organisms, this efficiency will be approximately equivalent to the assimilation of ash free dry weight.

A review of the literature suggested that ^{51}Cr (in its trivalent, least toxic form, Bowen, 1966) would be most suitable as the non-absorbed indicator, since in the vertebrates at least, it appears to be little absorbed, McKenzie *et al.* (1959), Utley *et al.* (1970). The Lanthanide, ^{144}Ce also appears to have suitable properties (V. T. Bowen cited in Odum *et al*, 1963) but is more objectionable to use than ^{51}Cr which because of its medical applications is also cheap and easy to obtain (i.e. as $^{51}CrCl_3$ in isotonic solution).

^{14}C and ^{51}Cr disintegrations can easily be distinguished in mixtures of these two isotopes by the use of suitable sensing equipment as ^{14}C emits only-β particles which can be sensed using either a Geiger-Müller or liquid scintillation counters whereas ^{51}Cr emits only γ rays which can be sensed using γ crystal scintillation apparatus.

Assimilation efficiencies, however, can only be determined from the ratios of ^{14}C to ^{51}Cr in food and faeces providing that the following conditions are satisfied:

1. That ^{14}C and ^{51}Cr are uniformly distributed throughout the food material.
2. That ^{14}C and ^{51}Cr move along the gut at similar rates.
3. That ^{51}Cr is not absorbed to any significant extent.
4. That the non-absorbed indicator is all present in the faeces (i.e. is not readily leached out).

These assumptions and the new technique have been tested experimentally using two species of freshwater gastropod, *Ancylus fluviatilis* (Mull.) and *Planorbis contortus* (Linn.), since freshwater gastropods produce faeces that are copiously coated in mucus, and which contain excretory particles, Carriker (1946), Calow (1970). *A. fluviatilis* is a microherbivore feeding on epilithic diatoms, whereas *P. contortus* is a bacterial feeder (Calow, unpublished). These two species, therefore, afforded an opportunity to test the new technique on animals utilising different foods. Furthermore, the result obtained by the ^{14}C, ^{51}Cr technique have been compared with results obtained from the more usual techniques which involve ^{14}C only.

Materials and Methods

a) General Techniques

Snails for the study were collected from Malham Tarn in Yorkshire, where both species are found on rocks in the littoral region. The dominant food organisms

present in this habitat with respect to *A. fluviatilis* are epilithic diatoms (mainly *Navicula* sp.), and with respect to *P. contortus* are epilithic bacteria (particularly a gram-positive *Micrococcus* and a gram-negative rod, hereafter called species D and E respectively). Food organisms used in the experiments described below are limited to these groups.

Navicula sp. initially isolated from the tarn was cultured in Allen and Nelson's (1910) medium suitably modified for freshwater organisms and enriched with sodium metasilicate (200 mg/l). Stock cultures were maintained at 20° C under a natural illumination regimen. Both groups of bacteria were initially isolated from rocks in the tarn, on nutrient agar (pH 7.0), stored in stock on agar slopes (4° C in the dark), and cultured for experimental purposes in Knight and Proom's (1950) basal liquid medium, using glucose (25 g/l) as the organic source.

Radioisotopes were obtained from the Radiochemical Centre, Amersham, England. ^{51}Cr was measured using a well type γ scintillation counter and timer scaler (Ekco Electronics types N664B and N610A). ^{14}C was measured by collecting the labelled food organisms or broken up faeces on millipore filters (dia. 2.5 cm, pore size, 5 μ for algae, 0.8 μ for faeces or bacteria) which were dried for 6 h at 40° C and counted on aluminium planchettes using a EW3H thin end window Geiger Müller tube, attached to a probe unit, with a paralysis time of 400 μsecs, and timer scaler (Ekco Electronics types N558B and N530G).

The degree of self absorption of ^{14}C-β-particles from such sources was checked by counting various volumes of suspensions of each ^{14}C-labelled food source, and was found to be less than 5% for up to 15 ml of algal suspension (1.2 mg wet weight of algae) or 20 ml of the bacterial culture (2.0 mg wet weight of bacteria). The volume routinely filtered was chosen to be 5 ml of suspension so errors due to self absorption should be less than 1.5%. The self absorption of faecal material was tested by adding various quantities of inactive faecal suspension to 5 ml aliquots of labelled food culture before filtering, and showed that up to 5 mg wet weight of faeces caused less than 2% self absorption.

The G. M. tube registered some counts from ^{51}Cr γ rays and comparison of dried filter discs carrying pure $^{51}CrCl_3$, ^{51}Cr labelled bactera and algae, revealed that the G. M. tube responded to 3%, 2.45% and 2.5% respectively of the counts registered by the γ scintillation counter. The difference between pure isotope and the labelled food organisms was assumed to be due to the non-uniform distribution of the former on the disc, and G.M. counts for ^{14}C were corrected for ^{51}Cr present by subtracting 2.5% of the γ scintillation count rate.

^{51}Cr counts were either expressed as a fraction of a standard of ^{51}Cr counted at about the same time, or corrections for decay were made. ^{14}C counts were corrected for paralysis time, background, and ^{51}Cr-γ-rays in that order.

b) Sorption of ^{51}Cr by Bacteria and Algae

To each of the three cultures, *Navicula* in Allen and Nelson's medium (50 cm^3) and bacteria D and E in Knight and Proom's medium (50 cm^3), was added ^{51}Cr as $^{51}CrCl_3$ in sterile, isotonic, saline solution (100 μCi/100 cm^3 culture). After thorough mixing, a 5 cm^3 aliquot was immediately removed from each culture, centrifuged and 3 cm^3 of the resultant, clear supernatant transferred to a 5 × 1 cm pyrex tube for counting over a period of 300 sec. This initial sample was kept separately as standard at 4° C and both algae and bacterial cultures were maintained at 20° C, the former under natural illumination conditions, the latter in the dark.

At given time intervals after the addition of isotope, further 5 cm^3 aliquots were removed from the cultures and dealt with as above. The standard sample was counted at the same time, so that a comparison between standard and subsequent

samples would enable measurement of uptake of ^{51}Cr from the ambient media by bacteria and algae, without requiring correction for decay of ^{51}Cr. All samples other than the standard were returned to cultures after counting, and manipulations were carried out in the usual sterile manner.

To test the rate of loss of the label from algae and bacteria, 5 ml aliquots were removed from separate cultures after 48 h exposure to ^{51}Cr and drawn through millipore filters. The retained organisms were washed five times with sterile distilled water, and transferred to tubes containing 5 ml of filtered tarn water. The cells are retained on the filters by both mechanical and Van der Waal's forces (Millipore Filter Corp., 1964), and this was found to be facilitated by drawing air through the filter for 30 sec after washing. At intervals after immersion (12, 24, and 36 h), the filters and water were assayed separately for ^{51}Cr.

c) Absorption of ^{51}Cr by Snails and Leaching from Faeces

Two groups of ten individuals (various sizes) of both species, were starved at 10° C for three days. Each group was then transferred to a plastic petri dish (5 cm diameter, 2 cm depth), containing filtered tarn water and discs of Whatman's no. 1 filter papers, through which had previously been drawn the relevant labelled food type (i.e. ^{51}Cr-*Navicula* in the case of *A. fluviatilis* and ^{51}Cr-bacteria D, in the case of *P. contortus*). These petri dishes were sealed over with plankton net, secured with elastic bands and immersed in tanks of aerated, filtered tarn water. Snails were then left to feed for 24 h at 10° C.

Following this period, snails were removed from chambers, washed thoroughly in running tap water and transferred to vials for counting. Subsequently the snails were transferred to clean petri dishes containing no food source in which they were left to empty their guts. At approximately 6 h intervals faeces were removed from the chambers and counted, so that the loss of ^{51}Cr in the faeces could be followed and a comparison between total counts lost with initial counts of whole snails would provide an estimate of absorption of ^{51}Cr by snails.

Some of the labelled faeces were retained, suspended in filtered tarn water and counted. At specified time intervals, for 48 h after this initial count a 3 cm^3 sample of water was removed from above the faeces and counted also. This procedure enabled estimation of loss rate of ^{51}Cr from faeces.

d) Consumption Rates and Assimilation Efficiencies

The *Navicula* cultures used in this group of experiments were on average two weeks old, and had been grown in the presence of ^{14}C as $NaH\,^{14}CO_3$ (1 μCi/10 cm^3 of culture) for at least one week, and ^{51}Cr (form and concentration as before) for at least 24 h before use. Both types of bacterial culture were on average 1 week old and had been grown in the presence of ^{14}C as uniformly labelled ^{14}C-glucose (1 μCi/10 cm^3 culture) and ^{51}Cr (usual form and concentration) for the same time intervals as specified for algae. Snails used in the experiments were of constant size (*P. contortus* 2–3 mm diameter; *A. fluviatilis* 4–5 mm long) and had been acclimatised and starved at 10° C for 3 days. All experiments were carried out at 10° C.

Labelled food was offered to snails on millipore filters since these retain cells during immersion, thus enabling a comparison of food present before and after feeding. All food types were dealt with in the following way. A 5 cm^3 aliquot of a ^{51}Cr-, ^{14}C-, culture was drawn through the millipore filter using a filter pump, retained cells being subsequently washed twice with 10 cm^3 of sterile distilled water. Food laden filters were then transferred to feeding chambers consisting of inverted

polythene vial stoppers with diameters just sufficient to accommodate filters (i.e. 2.5 cm dia., 1.25 cm deep). Several such stoppers had previously been stuck on to glass plates for ease of handling, and the whole plate was immersed in aerated, filtered tarn water. A single snail was inserted in each chamber which was then sealed over with a square of plankton net and secured with an elastic band. Two or three filters from each batch i.e. carrying either *Navicula*, bacterium D, or bacterium E were used as controls, and were treated in exactly the same way as the other filters except that they were not subject to grazing by snails.

Following a specified time interval (24 h for *A. fluviatilis* and 6 h for *P. contortus*) snails were removed from the chambers, washed in tap water, and transferred for gut clearance to clean chambers containing no food, and left for a further 96 h with faeces being removed from these chambers at ca. 12 h intervals. After removal of faeces from the initial feeding chambers (these being thoroughly washed in distilled water and stored at 4° C), filters were removed, dried and counted for 100 sec for ^{14}C. Finally, faeces which had been removed from gut emptying chambers over the first 12 h period were counted for ^{14}C and ^{51}Cr disintigrations together with the controls carrying the food organisms. Faeces collected from gut emptying chambers between the 12–96 h interval were treated similarly but only counted for ^{14}C disintigrations. Recounting control food discs with faecal discs meant that no correction for the decay of ^{51}Cr was necessary in the final calculations although the slightly longer drying period for controls could have resulted in a greater loss of ^{14}C from these discs as compared with the others (Wallen and Geen, 1968). Comparison of ^{14}C disintigrations for the control at initial counting i.e. with food discs with decay rate at final counting, however, showed that this effect was insignificant (mean % reduction in c.p.m. over 12 h drying, ca. 1.78).

The faeces initially extracted from the feeding chambers were also homogenised, filtered, dried, and counted in the Geiger Müller apparatus. Since 96 h represents the outside limit for gut emptying in both species of snail (Calow, unpublished) the sum of c.p.m. for faeces obtained from the feeding chamber, together with those obtained from gut emptying chamber over the first 12 h and the subsequent 12–96 h interval represents the total c.p.m. lost in the faeces. The difference between this value and total c.p.m. lost from the food discs provides a further independent estimate of assimilation with which to compare assimilation efficiencies derived from the ^{14}C, ^{51}Cr technique using a smaller sample of faeces.

Results

a) Sorption of ^{51}Cr by Algae and Bacteria

Figs. 1 and 2 demonstrate that both the bacteria and algae used in these experiments are capable of sorbing ^{51}Cr, though it is impossible to say from the results whether this is true active absorption or merely passive adsorption. Of general note is the close similarity in all uptake curves, and of particular relevance, from the point of view of the present work, is the fact that under the conditions used, ca. 40–50% of ^{51}Cr is taken up in 24h by both algae and bacteria, but little more thereafter. This degree of labelling, however, is perfectly adequate for subsequent experiments.

With respect to loss of ^{51}Cr from labelled cells, Table 1 shows that this occurs at a relatively low rate and to no appreciable extent over the first

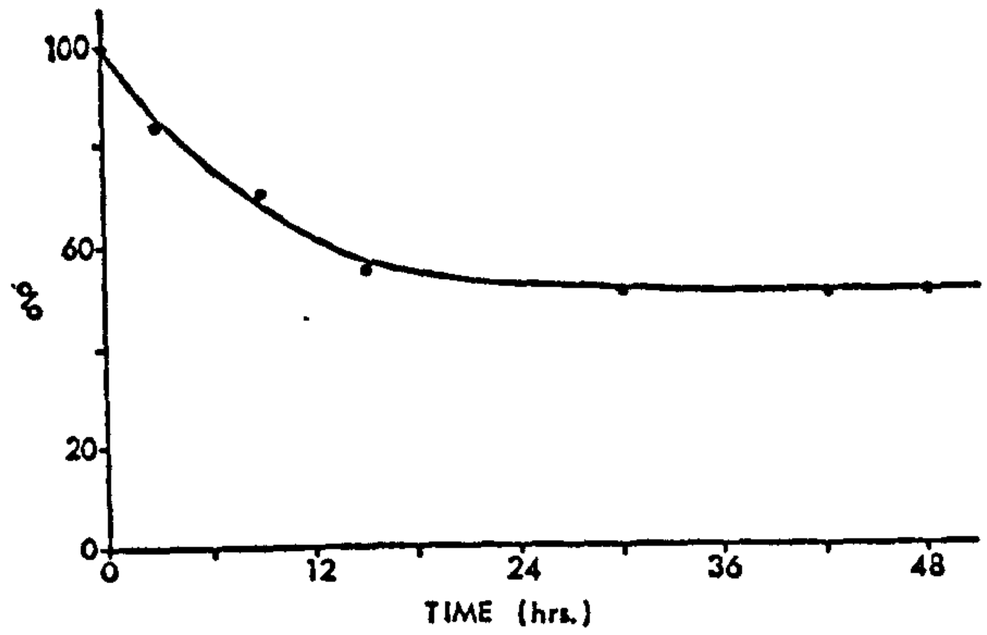

Fig. 1. The percentage reduction of ^{51}Cr activity in ambient medium containing *Navicula* sps.

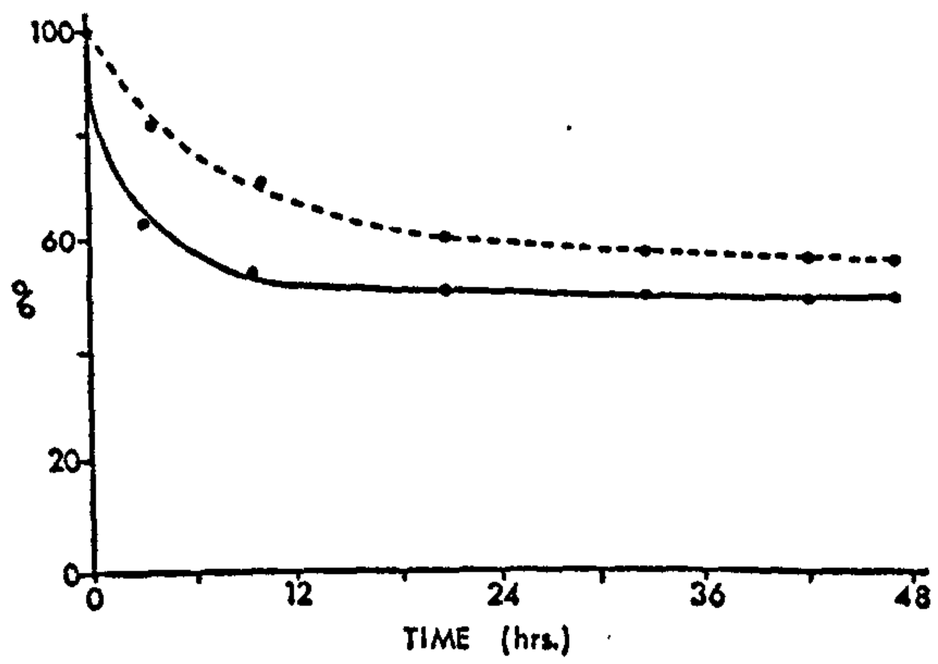

Fig. 2. The percentage reduction of ^{51}Cr activity in ambient media containing bacteria D (broken line) and E (continuous line)

Table 1. Loss of ^{51}Cr from labelled *Navicula* and bacteria as a percentage

	T_0	T_0+12 h	T_0+24 h	T_0+48 h
Navicula	0	0.44	0.88	1.80
Bacterium D	0	0.70	2.00	3.90
Bacterium E	0	0.50	1.00	2.80

24 h after removal of organisms from culture, so that little difficulty should be provided by ^{51}Cr passing into solution in the experimental feeding chambers.

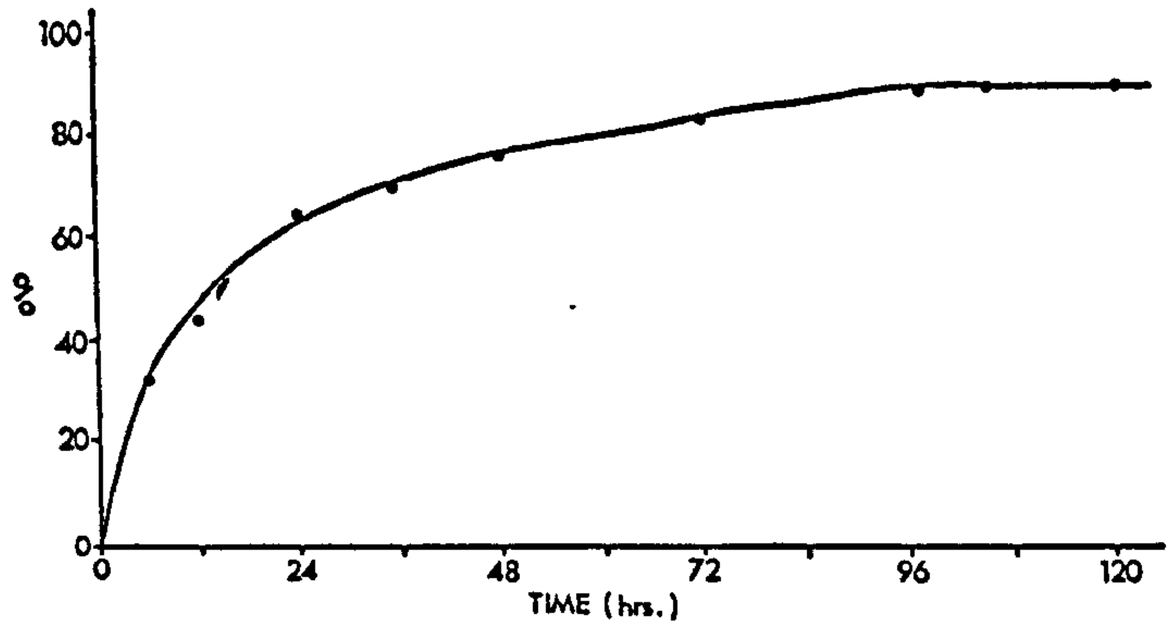

Fig. 3. The cumulative percentage recovery of ^{51}Cr in the faeces of *A. fluviatile* after feeding a meal of ^{51}Cr-*Navicula*

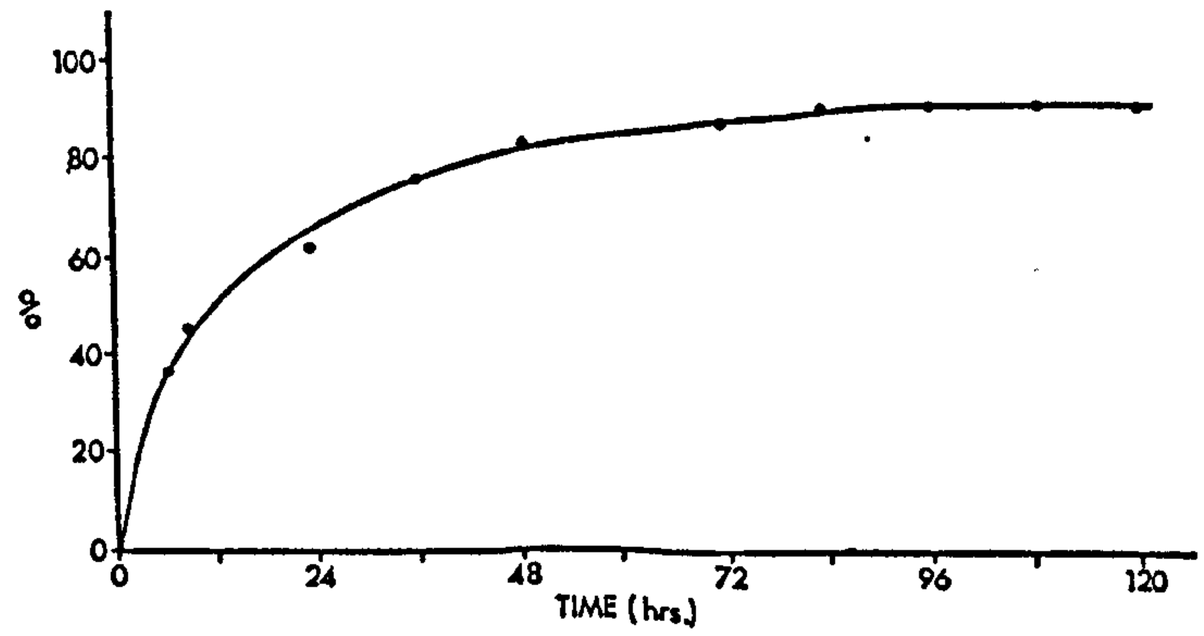

Fig. 4. The cumulative percentage recovery of ^{51}Cr in the faeces of *P. contortus* after feeding a meal of ^{51}Cr-bacterium D

b) Absorption of ^{51}Cr by Snails and Leaching from Faeces

Figs. 3 and 4 demonstrate the accumulative percentage recovery of ^{51}Cr in the faeces of the two species of snail and show that total recovery of ^{51}Cr was 90.2 and 90.0% in *A. fluviatilis* and *P. contortus* respectively. This indicates that some ^{51}Cr is absorbed by these snails (i.e. 9.8 and 10.0%) and that a suitable correction must be made for this in final calculations of assimilation efficiencies. A correction factor of 10% has been used for both species.

Of more general significance is the peculiar but similar shapes of the two curves (fitted by eye) in Figs. 3 and 4. This peculiarity is probably due to the fact that the faeces of fresh water snails consist of two major components, the gizzard string containing food derived directly from the

stomach, and the liver string containing the remains of food diverted to the hepatopancreas for intracellular digestion (Calow, 1970; Carriker, 1946). It would appear that during starvation these two components are defaecated at different rates, the faecal pellets consisting of predominantly liver string after the first 12 h in *A. fluviatilis* and after the first 6–9 h. in *P. contortus*. Work is continuing on this particular problem.

Less than 0.5% of the ^{51}Cr was ever detected in the water samples covering labelled faeces obtained from either of the two snail species. This suggests that leaching of ^{51}Cr from labelled faeces does not occur at least to any appreciable extent over the first 48 h. after removal from feeding chambers.

c) Assimilation Efficiencies and Consumption Rates

Table 2, column 3, contains assimilation efficiencies calculated on the basis of Eq. (5), and corrected for absorption of ^{51}Cr by snails. A specimen calculation of the assimilation efficiency of *P. contortus* fed on bacterium D is presented in the appendix. Column 4 of Table 2 contains assimilation efficiencies based on ^{14}C counts lost from filter discs with those retrieved in faeces collected over a 96 h period after cessation of feeding. There is, as can be seen, a close correlation between assimilation efficiencies using these two techniques.

Table 2. Assimilation efficiencies and ingestion rates for both species of snail on the various food types

1. Snail species	2. Food type	3. Assimilation efficiency (new technique)	4. Assimilation efficiency	5. Ingestion rate (μgm. dry *wt.*/day)[a]
A. fluviatilis	*Navicula* sps.	88.00	86.10	154.60
P. contortus	Bacterium D	96.54	92.00	180.20
	Bacterium E	84.78	81.64	293.40

[a] Average of 5 experiments.

Column 5 of Table 2 contains ingestion rates based on loss of ^{14}C counts from feeding discs, and the specific activity of the different food organisms. This information is included to demonstrate that the new technique proposed allows simultaneous measurement of the absorption and consumption parameters necessary for inclusion in Eq. (1).

Discussion

The technique described above for estimating assimilation efficiencies is only applicable provided that the conditions listed in section 2 of this paper are fulfilled. These conditions must obviously be re-established for all new situations in which the technique is to be used.

The first major consideration, however, must be choice of the non-absorbed indicator substance which should be convenient to obtain, handle, and measure. It must also be easily and uniformly incorporated within the food material(s) to be tested, and of course, it should not be assimilated to any appreciable extent by the experimental animals. ^{51}Cr appeared to be the most likely substance to fulfil these requirements although lack of relevant information in the literature necessitated tests on the possibility of labelling food organisms with this isotope and on the possible absorption of ^{51}Cr by snails. Other substances may also be suitable e.g. ^{144}Ce.

The results have demonstrated that at least some freshwater algae and bacteria can be labelled with ^{51}Cr, though it is impossible to know whether this is by passive adsorption or active absorption, nevertheless, both processes are likely to produce relatively homogenous distribution of isotope throughout the food material so that the nature of the process is irrelevant to present considerations. It is also difficult to know how widespread the phenomenon of ^{51}Cr uptake is in freshwater microflora. The work of Timofeyeva-Resovskaya (1963), for example, suggests only limited uptake whereas the work of Foster (1963), suggests considerable concentration of ^{51}Cr in algae taken from a ^{51}Cr polluted river. Furthermore, some workers have claimed chromium to be one of the non-essential trace elements e.g. Fruton and Simmonds (1959), and yet it has been implicated in various key biochemical reactions by other workers, e.g. Strickland (1965), Schwarz and Mertz (1959). Further research is obviously required on uptake of ^{51}Cr by aquatic microflora, and tests on uptake should always be carried out prior to using ^{51}Cr in the way suggested here.

Results from experiments on absorption of ^{51}Cr by snails indicated that these organisms are able to absorb a limited amount (i.e. ca. 10%) of the ^{51}Cr ingested. Limited absorption of ^{51}Cr also appears to occur in snails of the genus *Stagnicola* (Foster, 1963), and has been demonstrated in the marine worm *Hermione* (Chipman, 1966). Foster's (1963) data, however, suggests that the extent of ^{51}Cr concentration depends on trophic position, organisms occupying higher positions on the trophic pyramid being least able to concentrate this isotope. The net effect of limited absorption of the, "non-absorbed" indicator on the technique proposed here is the necessity to estimate a suitable correction factor in the way described (see Materials and Methods, section C). A secondary

outcome of these experiments, i.e. measurement of rate of loss of ^{51}Cr from animals fed a ^{51}Cr labelled diet has been the realisation of the utility of ^{51}Cr labelled food in studying gut emptying rates under different conditions, and such techniques are being currently used in this laboratory.

Of the other conditions listed in section 2 of this paper, uniform ^{14}C distribution was ensured by metabolic incorporation, the absence of leaching of ^{51}Cr from labelled faeces was demonstrated (see section b, Results), and the condition that ^{14}C and ^{51}Cr move along the gut at similar rates was alleviated to some extent by ignoring the initial faecal pellets produced (i.e. those from the feeding chambers) and by allowing contact between snails and labelled food for a period which was long enough for snails to clear at least half of their gut contents. It is important, however, that the contact time between snails and labelled food is not excessively long otherwise complications arise from the release of isotopes by algae, and from the rising body burden of isotopes within the snails.

As noted in the last section, assimilation efficiencies estimated from the ratio of ^{14}C:^{51}Cr in food and faeces (Column 3, Table 2) are directly comparable with assimilation efficiencies estimated from the difference between ^{14}C lost from the food discs and ^{14}C appearing in the faeces (Column 4, Table 2). This provides the experimental verification of the new technique. The assimilation efficiencies presented in Table 2 are essentially those of organic carbon, but as noted in section 2 of this paper, this will closely approximate to the assimilation efficiency of ash free dry weight. With respect to the values of these efficiencies, similar but slightly smaller results have been obtained by Hargrave (1970), working on the assimilation of algae and bacteria by the amphipod, *Hyalella azteca*. His efficiencies were 75% for *Navicula* sps., 82.5% for *Pseudomonas* sps., 78% for *Vibrio* sps., and 60% for *Flavobacter* sps. The technique of Hargrave was essentially similar to the one used here, i.e. involving ^{14}C, except that no indicator substance was used, so that complete gut emptying was required.

As far as we are aware the efficiencies of Hargrave and the ones presented here are the only ones available for bottom dwelling, aquatic invertebrates using bacteria as food. A limited amount of information is available regarding the assimilation efficiency of bacteria by zooplankton e.g. Saunders (1969) and Monakov and Sorokin (1961), but these appear to be lower than those shown in our data for *P. contortus* and Hargraves (1970) for *H. azteca* i.e. ca. 13.5–51.8%.

The new technique described then, allows relatively rapid estimation of assimilation efficiencies (or more properly, absorption efficiencies) in the sense defined by Eqs. (1) and (2) of the introduction. This is possible

because use of ^{14}C enables a distinction to be made between faecal material derived from the food, and that derived from intestinal secretions. Furthermore, use of a non-absorbed indicator such as ^{51}Cr means that total faecal production from a particular feed need not be observed.

Johannes and Satomi (1967) however, have raised two further relevant objections to measuring absorption rather than net assimilation in the sense defined by Eqs. (3) and (4) of the introduction. These are that in aquatic organisms some unabsorbed food may be released from the anus in solution rather than in the faeces, and that when using isotopes like ^{14}C, exchange of ^{14}C labelled compounds from the food in the gut lumen with unlabelled compounds in the gut wall may occur. Loss of ^{14}C compounds from the anus in solution does not appear to occur in snails, however, since spot checks on water covering snails in gut emptying chambers revealed no significant ^{14}C activity, even though these animals were presumably expiring $^{14}CO_2$. With respect to the exchange of material across the gut wall, whereas this phenomenon certainly occurs, especially with amino acids (Whittam and Wheeler, 1970), it must be expected that under the conditions operating in vivo, the extent of exchange will be considerably less than the amount being absorbed, so that its effect on estimation of assimilation efficiencies is probably very small and will tend to produce slight overestimates.

Finally, although the new technique has been primarily developed for application to aquatic invertebrates, its application can undoubtably be extended to other trophic and habitat situations. It may for example have particular relevance in agricultural practice, where considerable difficulty is experienced in measuring assimilation efficiencies because faeces are often inextricably mixed with excretory materials, e.g. in poultry.

Appendix

Calculation of assimilation efficiencies from the data derived from a comparison between ^{14}C:^{51}Cr counts in food and faeces (see Results, section C).

a) Raw data:

	G.M. tube (c.p. 100 sec)	Scintillation counter (c.p. 300 sec)
Background	34	2811
Control	647	15360
Background	33	2879
Faecal disc 2[a]	59	5476

[a] Faecal sample obtained in first 12 h after removal of snails from food, see Materials and Methods, section d.

b) Correction to c.p.s. and for paralysis time:

Method of correction for paralysis:

$$N_t = \frac{N_o}{1-(N_o \times T)}$$

where

N_t = corrected counts.
N_o = observed counts (c.p.s.).
T = paralysis time (sec).

N.B. this correction need only be applied when c.p.s. > 20, when the correction is ca. 1% N... data is not corrected in the following:

Background	1.34	9.37
Control	6.47	51.20
Background	0.33	9.60
Faecal disc 2	0.59	18.25

c) Correction for background:

Control	6.13	41.83
Faecal disc 2	0.26	8.65

d) Correction for γ ray detection by the G.M. tube:

Method of correction: By subtraction of 2,5% of scintillation counts from G.M. tube counts (see Materials and Methods, section a).

Control	5.08	41.83
Faecal disc 2	0.04	8.65

e) Correction for absorption of ^{51}Cr by snails:

Method of correction: By increasing the faecal disc counts by 10% (see Results, section b).

Control	5.08	41.83
Faecal disc 2	0.04	9.61

f) Calculation of assimilation efficiency:

Method – by use of Eq. (4):

$$\text{Assimilation efficiency} = 1 - \frac{0.04/9.61}{5.08/41.83} \times 100$$
$$= 96.54\%$$

References

Allen, E., Nelson, E. W.: On the artificial culture of marine plankton organisms. J. marine biol. Ass. 8, 421–474 (1910).

Bowen, H. J. M.: Trace elements in biochemistry, 241 p. London-New York: Academic Press 1966.

Calow, P.: Studies on the natural diet of *Lymnaea pereger obtusa* (Kobelt) and its possible ecological implications. Proc. malac. Soc. Lond. 39, 203–215 (1970).

Carriker, M. R.: Observations on the functioning of the alimentary system of the snail *Lymnaea stagnalis appressa*. Say. Biol. Bull. Woods Hole 91, 88–111 (1946).

Chipman, W. A.: Some aspects of the accumulation of ^{51}Cr by marine organisms. Radioecological concentration processes, eds. B. Aberg and F. P. Hungate, p. 931–941. Oxford-London-Edinburgh-New York-Toronto-Sydney-Paris-Braunschweig: Pergamon Press 1966.

Conover, R. J.: Assimilation of organic matter by zooplankton. Limnol. Oceangr. 11, 338–345 (1966).

Corbett, J. L., Greenhalgh, F. D., McDonald, I., Florence, E.: Excretion of chromium sesquioxide administered as a component of paper to sheep. Brit. J. Nutr. 14, 289–299 (1960).

Fewkes, D. W.: The food requirements by weight of some British *Nabidae* (Heteroptera). Entomol. exp. appl. 3, 231–237 (1960).

Fischer, Z.: Food selection and energy transformation in larvae of *Lestes sponsa* (Odonata) in Asiatic waters. Verh. int. Verein. theor. angew. Limnol. 16, 600–603 (1966).

Foster, R. F.: Enviromental behaviour of chromium and neptunium. Radioecology, eds. V. Schultz and A. W. Klement, Jr., p. 569–576. New York and Washington: Reinhold Publishing Corp. and The American Institute of Biological Sciences 1963.

Fruton, J. S., Simmonds, S.: General biochemistry, 1077 p. New York: Wiley 1959.

Hargrave, B. T.: The utilisation of benthic microflora by *Hyalella azteca* (Amphipoda). J. Anim. Ecol. 39, 421–437 (1970).

Hubbell, S. P., Sikora, A., Paris, O. H.: Radiotracer, gravimetric, and calorimetric studies of ingestion and assimilation ratios of an isopod. Hlth Phys. 11, 1485–1501 (1965).

Johannes, R. E., Satomi, M.: Measuring organic matter retained by aquatic invertebrates. J. Fisheries Res. Bd. Can. 24, 2467–2471 (1967).

Klekowski, R. Z., Shushkina, E. A.: Ernährung, Atmung, Wachstum und Energie-Umformung in *Macrocyclops albidus* (Jurine). Verh. int. Verein. theor. angew. Limnol. 16, 399–418 (1966).

Knight, B. C. J. G., Proom, H.: A comparative survey of the nutrition and physiology of mesophilic species in the genus Bacillus. J. gen. Microbiol. 4, 508–538 (1950).

Lawton, J. H.: Feeding and food energy assimilation in larvae of the Damselfly, *Pyrrhosoma nymphula* (Sulz.) (Odonata; Zygoptera). J. Anim. Ecol. 39, 669–689 (1970).

McGinnis, A. J., Kasting, R.: Chromic oxide indicator method for measuring food utilisation in a plant feeding insect. Science 144, 1464–1465 (1964a).

McGinnis, A. J., Kasting, R.: Digestion in insects, colorimetric analysis of chromic oxide used to study food utilisation by phytophagous insects. J. agric. Fd. Chem. 12, 259–262 (1964b).

McKenzie, R. D., Anwar, R. A., Byerrum, R. U., Hoppert, C. A.: Absorption and distribution of ^{51}Cr in the albino rat. Arch. Biochem. 79, 200–205 (1959).

Millipore Filter Corporation: Techniques for exfoliative cytology (ADM-50), 18p. (1964).
Monakov, A. V., Soroin, Yu. I.: Quantitative data on the feeding of Daphnia. Trud. Inst. Bil. Vodokhr. 4, 251–261 (1961).
Odum, E. P., Keunzler, E. J.: Experimental isolation of food chains in an old field system with use of ^{32}P. Radioecology, eds. V. Schultz and A. W. Klement, Jr., p. 113–125. New York and Washington: Reinhold Publishing Corp. and The American Institute of Biological Sciences 1963.
Petrusewicz, K.: Concepts in studies on the secondary productivity of terrestrial ecosystems. Secondary productivity of terrestrial ecosystems, vol. 1, ed. K. Petrusewicz, p. 17–49. Warsaw: Panstwavi Wydownicwo Naukowi 1967a.
Petrusewicz, K.: Suggested list of more important concepts in productivity studies (definitions and symbols). Secondary productivity in terrestrial ecosystems, vol. 1, ed. K. Petrusewicz, p. 51–58. Warsaw: Panstwavi Wydownico Naukowi 1967b.
Phillipson, J.: A contribution to the feeding biology of *Mitopus morio* (F) (Phalangida). J. Anim. Ecol. 29, 35–43 (1960a).
Phillipson, J.: The food consumption of different instars of *Mitopus morio* (F) (Phalangida) under natural conditions. J. Anim. Ecol. 29, 299–301 (1960b).
Saunders, G. W.: Some aspects of feeding in zooplankton. Eutrophication, Chairman G. A. Rohlich, p. 556–573. Washington: National Academy of Sciences 1969.
Schwarz, K., Mertz, W.: Chromium 111 and the glucose tolerance factor. Arch. Biochem. 85, 292–295 (1959).
Shushkina, E. A., Anisimov, S. I., Klekowski, R. Z.: Calculation of production efficiency in plankton copepods. Polskie Arch. Hydrobiol. 15, 251–261 (1968).
Smith, D. S.: Utilisation of food plants by the migratory grasshopper, *Melanopus bilituratus* (Walker) (Orthoptera: Acrididae) with some observations on the nutritional value of plants. Ann. ent. Soc. Amer. 52, 674–680 (1939).
Strickland, J. D. H.: Production of organic matter in the primary stages of the marine food chain. Chemical oceanography, vol. 1, eds. J. P. Riley and S. Skirrow, p. 433–473. London-New York: Academic Press 1965.
Timofeyeva-Resovskaya, Ye. A.: Distribution of radioisotopes in the main components of freshwater bodies. Tr. inst. biol. Akad. Nauk. S. S. S. R. 30, 1–78 (1963).
Utley, P. R., Boling, J. A., Bradley, N. W., Tucker, R. E.: Recovery of radioactive chromic oxide from the bovine gastrointestinal tract. J. Nutr. 100, 1227–1232 1970).
Wallen, D. G., Geen, G. H.: Loss of radioactivity during storage of ^{14}C-labelled phytoplankton on membrane filters. J. Fisherics Res. Bd. Can. 25, 2219–2224 (1968).
Whittam, R., Wheeler, K. P.: Transport across cell membranes. Ann. Rev. Physiol. 32, 21–60 (1970).

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PUBLICATIONS APPENDIX

IV

The Relationship Between Fecundity, Phenology and Longevity: A Systems Approach.

Journal : The American Naturalist.

Submitted : February 1972.

Accepted : June 1972.

Published : In - press.

INTRODUCTION

Within the framework of the phenomenon of natural selection two intuitive statements can be formulated regarding fecundity and phenology i.e. :-

i) the fecundity of all species will be controlled to that level ensuring the maximal survival of progeny to their reproductive age.

ii) the life history pattern adopted by any species will be that which favours the production of the maximum number of surviving progeny within the phyletic and ecological circumstances in which the species occurs.

Two essentially different types of phenology can be distinguished within the sexually reproducing realms of the living world. One in which the parent reproduces once and then dies, semelparity, another in which the parent reproduces on successive occasions, iteroparity, terminology after Cole (1954). From statement ii) above both patterns must be considered as enabling maximum survival of progeny under the particular conditions of their operation, the semelparous by preventing deleterious inter-generation interaction i.e. competition and/or increasing the chances of progeny survival by production of a vast number at one time, the iteroparous by allowing advantageous intergenaration interactions i.e. parental care, cultural transmission and/or increasing the chances of progeny survival by intermittent production of small numbers over an extended period of time.

These considerations have considerable implications regarding the nature of control on fecundity as embodied in statement i), i.e. in species showing semelparity, control of fecundity is in terms only of progeny survival, whereas in species showing iteroparity control of fecundity must not only take account of progeny survival but also the subsequent survival of parents. In short semelparous organisms can, and indeed must, invest a considerably greater effort in reproduction than organisms showing more complex phenologies.

It is the aim of this paper to represent these intuitive considerations more formally within the framework of a systems model (the representation problem), to deduce properties of the system from analysis of the model (stability problem), and to present empirical information allowing the deductions to be

tested within the real world (the experimental problem).

THE REPRESENTATION PROBLEM

Representation has been achieved by simple modification of Hubbell's (1971) "Improbably Linear Bioenergetics Model", in which reproduction has been included simply as a source of negative input to the body potential energy store. The model is represented in flow diagram form in fig. 1. Each block in the diagram represents a lumped subcomponent of the system which computes an output storage or flow variable from its input variables (letters within the block represent their transfer functions). The circles are comparators which produce a new variable from the sum, or the difference between other variables. Solid lines denote variables (dimensions: energy ML^2T^{-2} or energy flow ML^2T^{-3}), wavy lines denote environmental disturbance variables whose dimensions depend on the factors involved. All variables are expressed in the complex frequency (S) domain, rather than in the time (t) domain so that operations of differentiation and integration are reduced simply to multiplication and division respectively by the complex variable S. Terminology follows that of Hubbell (1971), except for terms included within the innovation, here, of reproduction. The symbols are defined in table 1.

A central feature of Hubbell's (1971) model, is the concept of "Desired Growth Rate". It represents a recognition of the fact that growth is under endogenous control with feedback as contrasted with growth in the inorganic world which merely represents the passive outcome of building up and breaking down processes. The desired growth rate signal DG(S) is generated out of the interaction between present size P(S),(i.e. the potential energy store), and the endogenous blueprint, (i.e. genotypic representation) for the specific growth form. On the basis of the difference between the desired growth rate signal DG(S) and the actual growth rate signal AG(S), an error correcting signal GE(S) is generated which ultimately feeds back positively as AE(S) on the anabolic process (comparator 1) and negatively as RE(S) on the catabolic respiratory processes (comparator 2). Integration of GE(S) to E(S) represents the well documented phenomena of metabolic memory Brody (1945), but is probably over-simple in that it is allowed to operate without constraints suggesting that it is unrealistically

perfect. This representation will be retained for convenience of calculation. The anabolic and catabolic respiratory processes are also subject to linear positive modification from the potential energy store level and from the linear outcome of the interaction between this and correction for errors, compute signals whose difference (comparator 3) produces actual growth rate AG(S) which upon intogration represents present size P(S).

In the modified model presented here reproduction has been represented (comparator 4) as a catabolic element analagous to respiratory catabolism i.e. it is a source of energy loss. It is consequently represented as the outcome of the interaction between the potential energy store level (+Rep P(S)) and error correction (-Rep E(S)). Error correcting feedback is denoted by a broken line since it is considered that this will be operative only in organisms showing iteroparity (postulate), i.e. in semelparity the level of reproduction must represent an absolute maximum under the physiological restraints imposed by +Rep P(S) whereas in organisms showing iteroparity reproduction must represent the maximum allowed, without imparing the parental well being. The positive feedback from P(S) is represented linearly, whereas in reality it is likely to act non-linearly since reproduction is not a continuous process and P(S) will require to reach some threshold value, i.e. size at maturity (MP(S)), before reproduction, in its catabolic sense, can begin. As a first approximation this complication will be ignored. This is justified to some extent because organisms will only be considered in their reproductive condition.

THE STABILITY PROBLEM

To find the transfer function H(S) = AG(S)/DG(S) the system is solved for AG(S) as a function of DG(S), by opening the system at X. Assuming no disturbance inputs:-

1) Solution for system without error correcting feedback on reproduction (hereafter called the simple system).

$$AG(S) = A(S)-(R(S)+Rep(S)) \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots 1$$

$$= (KAP/S)(AG(S))+(KAE/S)(DG(S)-AG(S))-(KRP/S)(AG(S))$$
$$+(KRE/S)(DG(S)-AG(S))-(KRepP/S)(AG(S)) \quad \ldots\ldots\ldots\ldots 2$$

Separating variables and cross multiplying:

$$H(S)_i = \frac{AG(S)}{DG(S)} = \frac{KAE+KRE}{S+(KRP+KRepP+KAE+KRE-KAP)} \quad \ldots\ldots\ldots\ldots 3$$

Equation 3 represents a simple first order system i.e with only one pole $(S + P_i)$, where

$$P_i = (KRP+KRepP+KAE+KRE-KAP)$$

so that the pole will be located at

$$S = -P_i$$

and in order for the system to be stable (i.e. the pole to have negative real parts)

$$-(KRP+KRepP+KAE+KRE) > + KAP$$

2) Solution for system with error correcting feedback on reproduction (hereafter called the complex system).
by similar reasoning to 1.

$$H(S)_{ii} = \frac{AG(S)}{DG(S)} = \frac{KAE+KRE+KRepE}{S+(KRP+KRepP+KAE+KRE+KRepE-KAP)} \quad \ldots\ldots\ldots\ldots 4$$

Equation 4 again represents a first order system where

$$P_i = +(KRP+KRepP+KAE+KRE+KRepE-KAP)$$

so that for stability

$$-(KRP+KRepP+KAE+KRE+KRopE) > +KAP$$

Having obtained transfer functions $H(S)_i$ and $H(S)_{ii}$, it is possible to investigate the response of the two systems to hypothetical test inputs. The"test" input employed will be the unit step, x, (when $x(S) = 1/S$), so that:
letting $(KAE+KRE) = K_1$

$(KAE+KRE+KRepE) = K_2$

$(KRP+KRepP+KAE+KRE-KAP) = K_3$

$(KRP+KRepP+KAE+KRE+KRepE-KAP) = K_4$

the exposing both systems to the unit step input gives:-

$$AG(S) = \frac{1}{S} \cdot \frac{K_1}{S+K_3} \quad \ldots\ldots\ldots\ldots 5$$

and

$$AG(S) = \frac{1}{S} \cdot \frac{K_2}{S+K_4} \quad \ldots\ldots\ldots\ldots 6$$

as outputs for the simple (equation 5) and complex (equation 6) systems respectivoly. Inverse Laplace transformation on both equations, by the method of partial fractions, gives

$$AG(t) = \frac{K_1}{K_3}(1-e^{-K_3t}) \quad \text{.....7}$$

$$AG(t) = \frac{K_2}{K_4}(1-e^{-K_4t}) \quad \text{.....8}$$

and indicates that the response of actual growth rate AG(t) to a hypothetical step from 0 to 1 in DG(t) is an exponentially decelerating rise to a plateau of K_1/K_3 for the simple and K_2/K_4 for the complex with a time constant of $1/K_3$ and $1/K_4$ for simple and complex systems respectively.

Now:

$K_2 > K_1$ (by KRepE) 9

$K_4 > K_3$ (by KRepE) 10

$$\frac{K_1}{K_3} < \frac{K_2}{K_4} \quad \text{.....11}$$

since $$\frac{K_2}{K_4} = \frac{K_1 + KRepE}{K_3 + KRepE} \quad \text{.....12}$$

These inequalities allow comparison between the ability of the simple and complex models to track a desired growth rate signal input. Thus inequality (9) indicates that the response of the simple system will be more sluggish than the complex and inequality (11) indicates that AG(t) will undershoot DG(t) to a greater extent in the simple system. Both the difference between asymptotes in the two systems and the difference between the asymptote for the complex system and the reference input will depend on the value of KRepE. In short the complex system, with error control on reproduction, is able to respond more rapidly and more accurately to the desired reference input. Its accuracy and rapidity increases as KRepE increases.

Disturbance inputs will now be considered. Following the methods of Hubbell (1971), it is possible to investigate the effects of these on the two models by combining for convenience the disturbance on absorption rate and respiration into one input D(S) (see fig. 2). Thus the transfer relations between AG(S) and DG(S) with D(S) included become

$$AG(S) = \frac{K_a}{S+K_b} \cdot DG(S) - \frac{S}{S+K_b} \cdot D(S) \quad \text{.....13}$$

where $K_a = K_1$ (for simple model) or K_2 (for complex model)

$K_b = K_3$ (for simple model) or K_4 (for complex model)

and setting DG(S) to zero since our major concern lies with the relationship botween AG(S) and D(S), the transfer function becomes:

$$\frac{AG(S)}{D(S)} = \frac{-S}{S+K_b} \quad \text{.....14}$$

This term has the same order in the numerator and denominator so that the time domain equivalent of this equation will not remain finite with input of an impulse transient. Nevertheless, the frequency response of the system can be investigated by letting D(t) represent some generalised rotating vector $Ae^{j\omega t}$ (i.e. a sine wave of amplitude A, angular frequency ω and when $j = \sqrt{-1}$) so that:

$$\mathcal{L}\left[Ae^{j\omega t}\right] = \frac{A}{S-j\omega} \quad \text{.....15}$$

Substituting equation 15 in 14 and applying the method of partial fractions the amplitude of the steady state oscillation is given by:

$$AG(t) = A\omega/\sqrt{(K_b^2 + \omega^2)} \quad \text{.....16}$$

(for more complete workings see Hubbell (1971) p. 296)

From equation 16 it can be seen that the greater the value of K_b the smaller the amplitude of the output oscillations, and consequently from inequality(10) it is possible to say that the complex system is capable of better compensation for disturbances than the simple system since the actual growth rate output is affected to a lesser extent by oscillatory disturbance inputs. The efficiency of compensation increases as KRepE increases.

In summary, the major, as yet untested postulate contained within the systems model is that negative feedback on reproduction from the parental metabolic requirements only operates in species showing iteroparity (complex systems). This postulate follows from the statement made in the introduction which suggested that control of fecundity in species showing semelparity (simple

systems) need only refer to progeny survival, whereas in species showing iteroparity control must also take account of well-being of parents. On the basis of this postulate certain deductions have been made regarding behaviour of the system. In the simple variant, response to parental metabolic requirements is slow and incomplete when compared with the complex variant. Similarly, compensation for disturbances operating via the anabolic and catabolic components of the system is less efficient in the simple system. Both the efficiency of response to parental (desired growth rate) requirements, and control for perturbation in the complex system, depends on the value of the transfer function of the feedback element KRepE, or in other words, on the intensity of feedback.

THE EXPERIMENTAL PROBLEM

The most direct way of experimentally testing the above model would be to open the feedback loop carrying information regarding present growth level (P(t)) to the desired growth rate controller (KDG) of a real organism, apply a test input, observe the output and infer the intervening systems characteristics from the resultant open loop transfer function. In reality this is not possible because, firstly, the feedback loop is not accessible for breaking, and secondly, if breaking were possible, it would probably result in death of the organism concerned. A less direct method of analysis has, therefore been used here in which the response of certain real intact organism systems has been observed with respect to experimentally imposed perturbations. Whereas this technique cannot provide any absolute verification of postulates contained in the proposed model (see representation problem), it can indicate falsity of these postulates by a comparison of expected systems response (see stability problem) with actually observed systems response, and in this sense is scientifically valid.

The following data have in part been derived from the author's own experimentation, and in part from the literature. The input perturbation considered has been in terms of food supply and the output responses observed have been fecundity and adult survival. No attempt has been made to consider growth rate during egg/young production since this will necessarily

be complicated by weight (energy) losses resulting directly from loss of reproducta. In consequence it has not been possible to test those deductions concerning the speed and efficiency of adult potential energy level response with respect to perturbation (see section on stability problem). It has, however, been possible to test the deductions concerning compensation for disturbances, in this case operating via the anabolic subcomponent.

Making the assumption that mortality rate under different conditions of environmental perturbation will reflect the degree to which these perturbations are allowed to impinge on the system's dynamics, two simple predictions regarding mortality and fecundity during the application of food supply perturbations can be made (figs. 3a & 3b), based on the models of the simple and complex systems. In the simple system (fig. 3a) mortality will rise as the intensity of perturbation increases whereas fecundity will remain constant or at least gradually fall as food stores reduce with increasing starvation. In the complex model mortality will remain constant (and may be zero) whereas fecundity will rise as perturbation reduces because the differential (DG(S)-AG(S)) will reduce and hence feedback RepE will become less intense. The responses (figs 3a & b) have been represented linearly but they are not likely to behave in this simple way (e.g. fecundity in the complex model is likely to follow the "law of diminishing increments", Brody (1945) and rise at an exponentially reducing rate to a plateau). Nevertheless these simple predictions provide a clear indication as to the general type of response to be expected. Furthermore figs 3a & b represent the two extreme possibilities of response, and all possible intermediaries are to be expected between these two extremes, depending on the value of KRepE i.e. the intensity of feedback on reproduction.

These theoretical predictions can now be compared with actual data. Original observations for one annual species of animal, the freshwater snail Planorbis contortus (Linn.) are presented in fig. 4a and Hester's (1964) observations for a perrenial species of fish, the Guppy, Lebistes reticulatus (Peters) in fig. 4b. (1964) The two figures (4a & 4b) are not directly comparable because dietary stress was not measured in exactly the same terms. For my data it was measured in terms

of feeding time allowed on a constant food supply (i.e. 4 cm^2. lettuce), such that dietary stress unit 1 represents a continuous supply with replenishment every day, whereas dietary stress unit e.g. 0.5 represents 4 cm^2. lettuce supply once every other day, for one day, and so on. Experimental replicates were identical in all other respects, i.e. volume of water used (2 litres/10 snails), temperature (18 C), water chemistry (Leeds City tapwater, replenished every day), and light (natural illumination). Hester's stress units are in terms of quantity of food supplied continuously, so that unit 1 represents an amount supplied equivalent to the weght of food eaten daily under ad lib. feeding conditions, and stress unit 0.5 represents a supply of half this quantity.

The patterns of mortality and fecundity in figs 4a & b and figs. 3a & b are essentially the same. Thus behaviour of the semelparous snail under conditions of dietary stress conforms to the simple model, whereas behaviour of the iteroparous fish conforms to the complex model. Furthermore a body of circumstantial evidence exists regarding both plants ans animals which similarly lends support to the validity of the models. Basically these data consist of observations recording a negative correlation between the extent of reproduction and mortality in semelparous species, and a negative correlation between starvation and fecundity in iteroparous species. These data together with their sources are summarised in table 2.

CONCLUSIONS AND DISCUSSION

From the intuitive statement, based on considerations regarding the operation of Natural Selection on phenology and fecundity, that organisms showing semelparity can afford to invest more in a single reproductive phase than organisms showing iteroparity, a simple systems model has been constructed in which fecundity is constrained by parental growth requirements in the latter, but not in the former case. Use of Systems Control Analysis (the stability problem) allowed certain deductions to be formulated regarding the iteroparous and semelparous systems, namely, and as required from the original intuitive statement, that parental growth requirements are more accurately and more rapidly monitored in the iteroparous than the semelparous systems. Two further, less obvious deductions arise from this analysis. Firstly, that the iteroparous was less susceptible to environmentally imposed perturbation than the semelparous variant, and secondly, that both the efficiency of monitoring of parental growth requirements and the extent of perturbation effect on the system during the reproductive period depends on the intensity of feedback from parental requirements to reproductive processes. Experimental observations (the experimental problem) are presented which conform to the model.

The implications of these deductions are clear. Firstly, the operation of fecundity as a catabolic element during the breeding season, not only puts a strain on parental metabolism in semelparity, but also renders the parental system more susceptible to environmental perturbation. In short, the act of reproduction in annual organisms increase the probability of parental death and consequently may be one of the major factors preventing extension of parental life beyond the breeding season in nature. Thus, as shown for semelparous species (table 2), by preventing reproduction, or in other words cutting the feedback path between P(S) and KRepP, longevity can be increased. From this it is tempting to conclude that annual species are annual because of the selective advantages accruing from vast gamete production at one time and not vice versa (i.e. vast gamete production being required of an annual species). Secondly, the above discussion naturally leads to considering reproduction as an element of senescence in the sense of

Maynard-Smith (1958), since it increases the sensitivity of adult organisms to adverse environmental conditions. Certainly for the example given in fig. 4, P.contortus can live in constant laboratory culture, providing optimum conditions, in a state of continuous, though progressively reducing reproduction for at least 28 months, whereas in the field it has an annual life cycle (Calow, unpublished), and this observation seems to be the general experience of other workers on freshwater snails, e.g. Oldham (1929), Boettiger (1944), De Witt (1954). Furthermore variations recorded in the natural phenologies of other species of freshwater snail from half- to two-yearly cycles (e.g. Berrie, 1963, 1965) may also possibly be accounted for in these terms. Thirdly, the intensity of feedback, i.e. the value of KRepE is of central importance to the sensitivity of the parental system to perturbation during reproduction. In reality there will be no sharp distinction between the semelparous and iteroparous condition regarding feedback, but a complete gradient is likely to exist between the former and the latter reflecting a gradient in the intensity of feedback. Evolution from the semelparous to the iteroparous state will require "tightening" of the system, by increasing the intensity of this feedback i.e. movement up the gradient and a loosening of the system for evolution in the opposite direction e.g. Angiosperms (Bows, 1927).

In physiological terms feedback is likely to operate at low level intensity by preventing diversion of nutrients to developing ova and at a high level intensity by atretion of ova (e.g. Scott, 1962) or even resorption of embryos (Brambell, 1948). The rewards that might result from physiological observation on these phenomena in organisms showing different states of iteroparity or semelparity are obvious.

The overall conclusions arising from the above considerations is that natural selection is likely to favour and act primarily on vast gamete production at one time. This will result in semelparity. Advantages arising from extension of the life cycle will require secondary selection for increasing intensity of feedback on reproduction via the physiological pathways described above, and a return to shorter life cycles will require tertiary modification of this feedback.

Finally, and as a footnote, I would like to point to the

value and method of systems analysis as a means of constructing biological models. The appraoch, as I have used it, involves the incorporation of intuitive statements into a theoretical model (the representation problem). The behaviour of these theoretical models is specified with regard to standard test input signals (the stability problem). These theoretical specifications are incorporated into a formal deduction regarding the system which is then tested empirically (the experimental problem).

This sequence theoretically allows erection of a large number of models pertaining to a particular phenomenon, rejection of some during the stability analysis on grounds of feasibility and without recourse to experimentation, rejection or acceptance of others at the experimental level and finally, rejection, acceptance or modification of the original model. The final systems model is easily transferred to either digital or analogue computer for simulation and prediction.

SUMMARY

From the intuitive statement based on considerations regarding the operation of Natural Selection on phenology and fecundity, that organisms showing semelparity can afford to invest more in a single reproductive phase than organisms showing iteroparity a simple systems model has been constructed. The semelparous system is represented without, and the iteroparous is represented with, negative feedback from parental growth requirements on fecundity. At the theoretical level, Systems Control Analysis indicated that the system without feedback reacted less accurately and more sluggishly to a test parental desired growth rate input and was more sensitive to environmental perturbation. Indirect experimental and more circumstantial evidence from the literature suggested that this behaviour was typical of semelparous species in reality, and verified to some extent the systems representation adopted. Arguing from these conclusions lead to the hypotheses that reproduction in semelparity is an element of senescence and that lengthening life cycles requires an increase in intensity of feedback on reproduction. The types of feedback involved are listed.

Finally the merits of a systems theory approach are discussed.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to the following members of staff at Leeds University for their encouragement and advice; Mr. D. Knapp (Department of Applied Mathematics), Mr. C. Clark (Department of Management Studies), Professor H.W. Woolhouse (Department of Plant Sciences) and particularly to Dr. E. Broadhead (Department of Pure and Applied Zoology) for patient and meticulous criticism of the manuscript. I would also like to record the inspiration and stimulus which I have derived from the paper by S. P. Hubbell cited below. The work was carried out under tenure of a N.E.R.C. studentship.

Literature cited

- Berrie, A.D. 1963. Life cycle of Planorbarius corneus (L.). Nature Lond. 198: 805-806.

- Berrie, A.D. 1965. On the life cycle of Lymnaea stagnalis (L.), in the West of Scotland. Proceedings of the malagological Society Lond. 36: 283-295.

Bews, J.W. 1927. Studies in the ecological evolution of angiosperms. New Phytologist 26: 273-294.

- Boettger, C.R. 1µ44. Bassomatrophora. In G. Grimple and E.Wagler, (Ed.). Die Tierwelt der Nord- und Oste. 35. Leipzig.Akademisch Vergsgesellschaft, Berker und Erler Kom-Ges. 241-278.

Brambell, F.W.Rogers. 1948. Prenatal mortality in mammals. Biological Review. 23: 370-407.

Brody, S. 1945. Bioenergetics of Growth. 1st ed. Reinhold, New York. 1023 pp.

Cole, L.C. 1954. The population consequences of life history pnehomena. Quarterly Review of Biology. 29: 103-137.

Comfort, A. 1956. The Biology of Senescence. 1st ed. Routledge & Kegan Paul, London.

- De Witt, R.M. 1954. Reproduction, embryonic development, and growth in the pond snail Physa gyrina Say. Transactions of the American Microscopical Society. 73: 124-137.

Hester, F.J. 1964. Effects of food supply on fecundity in the female guppy, Lebistes reticulatus (Peters). Journal of the Fisheries Research Board of Canaca. 21: 757-763.

Hubbell, S.P. 1971. Of sowbugs and systems: the ecological energetics of a terrestrial isopod. pp.269-323. In B.C.Patten (ed.) Systems Analysis and Simulation in Ecology. Vol.1. Academic Press, London, New York.

Loeb, L. 1917. The concrescence of follicles in the hypotypical ovary. Biological Bulletin, Woods Hole, 32: 187-193.

Markus, H.C. 1934. Life history of the black headed minnow, Pimephales promelas. Copeia 70: 116-122.

Maynard, L.A. & Loosii, J.K. 1962. Animal Nutrition, 1st ed. McGraw-Hill, New York, Toronto, London. 533 pp.

Maynard-Smith, J. 1958. Prolongation of the life of Drosophila subobscura by a brief exposure of adults to a high temperature. Nature (London), 181: 496-497.

Murdoch, W.W. 1966. Population stability and life history pnehomena. American Naturalist. 100: 5-11.

Oldham, C. 1930. Fecundity of Planorbis corneus. Naturalist, London: 177-179.

Palka, J. & Spaul, E.A. 1970. Studies of feeding and digestion in the enchytraed worm Lumbricillus lineatus Mull. in relation to its activity in sewage bacteria beds. Proceedings of the Leeds Philosophical and Literary Society (Scientific Section). 10: 45-59.

Scott, D.P. 1962. Effects of food quantity on fecundity of Rainbow Trout, Salmo gairdneri. Journal of the Fisheries Research Board of Canada. 19: 715-731.

Legends to Tables and Figures

Table 1: Definition of terms in figure 1.

Table 2: Circumstantial evidence relating to the presence or absence of feedback on reproduction in semelparous and iteroparous species.

Fig. 1. Flow diagram representing the modification of Hubbell's "Improbably Linear Bioenergetics Model". (Zig-zag line represents disturbance inputs).

Fig. 2. Reorganisation of Fig. 1 to allow direct input of environmental disturbances D(S) at one point where A = KAE + KRE (for the simple system) and KAE + KRE + KRepE (for the complex system).

Fig. 3. Predictions of the relationship between fecundity (F), mortality (M), and food supply (0 = no food provided, n = superabundant food supply).

Fig. 4. Fecundity (F) and mortality (M) plotted against dietary stress, in the freshwater gastropod P. contortus (A) and the female guppy Lebistes reticulatus (B). Confidence limits for the snail represent $tS/\sqrt{n}$ when t = 2.262 for 9 degrees of freedom (n = 10) at the 95% level, s = standard deviation. (10 replicates were used each consisteing of 12 snails).

TABLE 1

VARIABLES	SUBCOMPONENT TRANSFER FUNCTIONS (Denoted fy first letter K).
DG(S) - Desired growth rate	Middle letter denotes process:-
GE(S) - growth rate error	
E(S) - integrated growth rate error	Absorption (A)
AE(S) - integrated error control of absorption	Respiration (R)
RE(S) - integrated error control of respiration	Reproduction (Rep)
RepE(S)- integrated error control of reproduction	on which output operates
A(S) - absorption rate	Final letter denotes source:-
R(S) - rate of energy dissipation via respiration	Body size (P) Growth rate error (E)
AG(S) - current growth rate	
P(S) - integrated growth rate or current size	and:-
AP(S) - body size component of respiration	KDG = desired growth rate
DR(S) - disturbance input on respiration	
DA(S) - disturbance input on absorption	

TABLE 2

A) Evidence Regarding Semelparous Species

1. Markus (1934)	Non-spawners in minnows which normally die after breeding may live for an extra year.
2. Comfort (1956)	Death in annual plants can be postponed indefinitely if reproduction is prevented.
3. Murdoch (1966)	Demonstrated in field experiments that the beetle Agonum fuliginosum survives longer when unmated.
4. Palka & Spaul (1970)	Observed starvation has little effect on cocoon production in the enchytraeid worm Lumbricillus lineatus (Mull.). Histological section revealed that gonads were the most resistant organs to starvation.

B) Evidence Regarding Iteroparous Species

1. Loeb (1917)	Demonstrated that underfeeding prevented maturation of follicles in the guinea pig and may cause atrophy.
2. Brody (1945) p.95	"While no data are available, there is no doubt that egg production in domestic fowls is related exponentially to food consumption".
3. Maynard & Loosii (1962) p.434	"It is a well recognised fact that half starved domestic animals are relatively infertile".

(Table 2 continued)

4. Scott (1962)	A higher proportion of maturing follicles undergo atrophy the greater the dietary stress in the Rainbow Trout Salmo gairdneri.

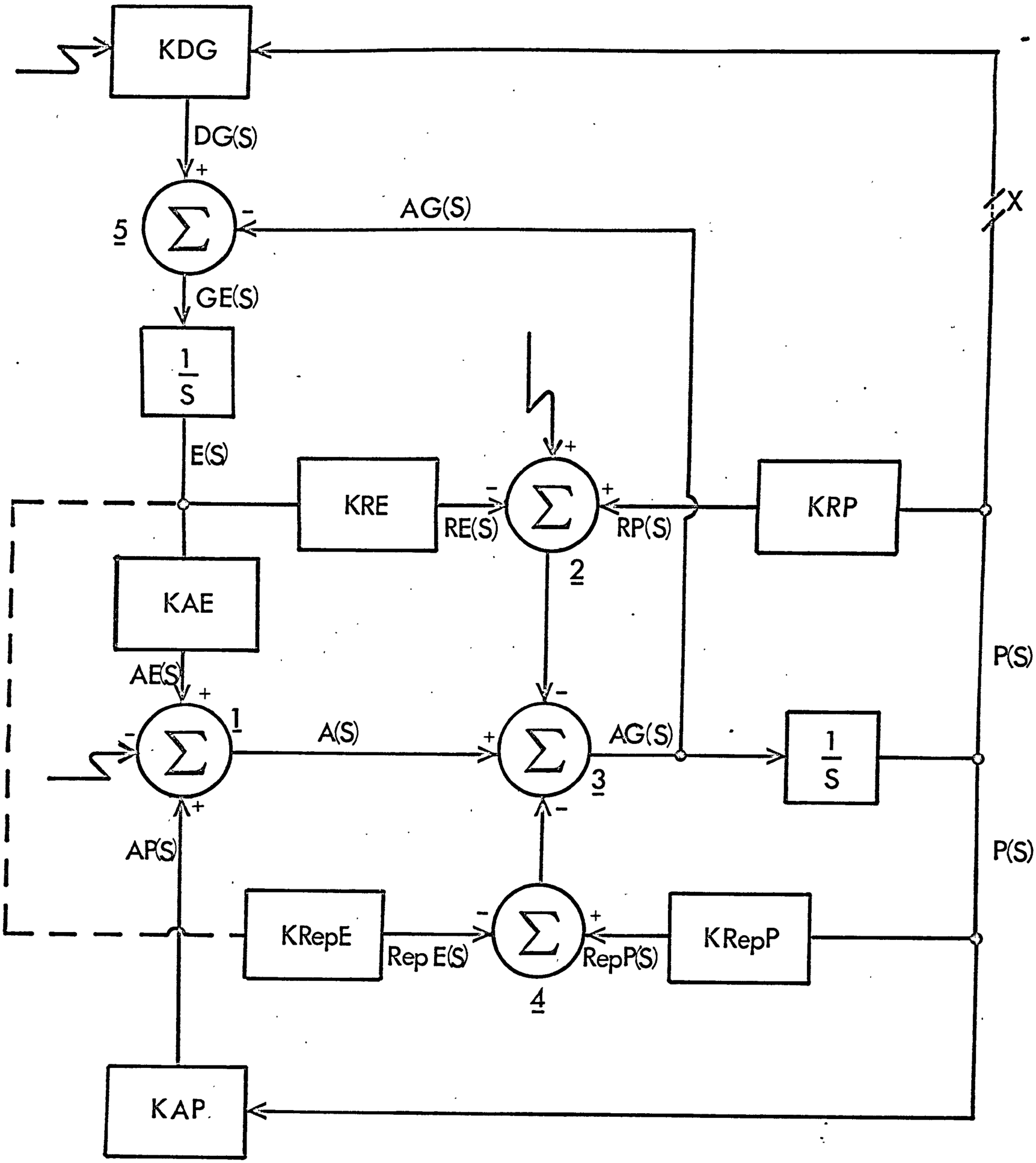

KDG
DG(S)
+
5
Σ
-
AG(S)
X
GE(S)
1/S
E(S)
KRE
-
Σ
+
RE(S)
RP(S)
KRP
2
KAE
AE(S)
+
-
1
Σ
A(S)
+
Σ
AG(S)
1/S
3
P(S)
AP(S)
+
-
P(S)
KRepE
Rep E(S)
-
Σ
+
RepP(S)
KRepP
4
KAP

FIG. 1.

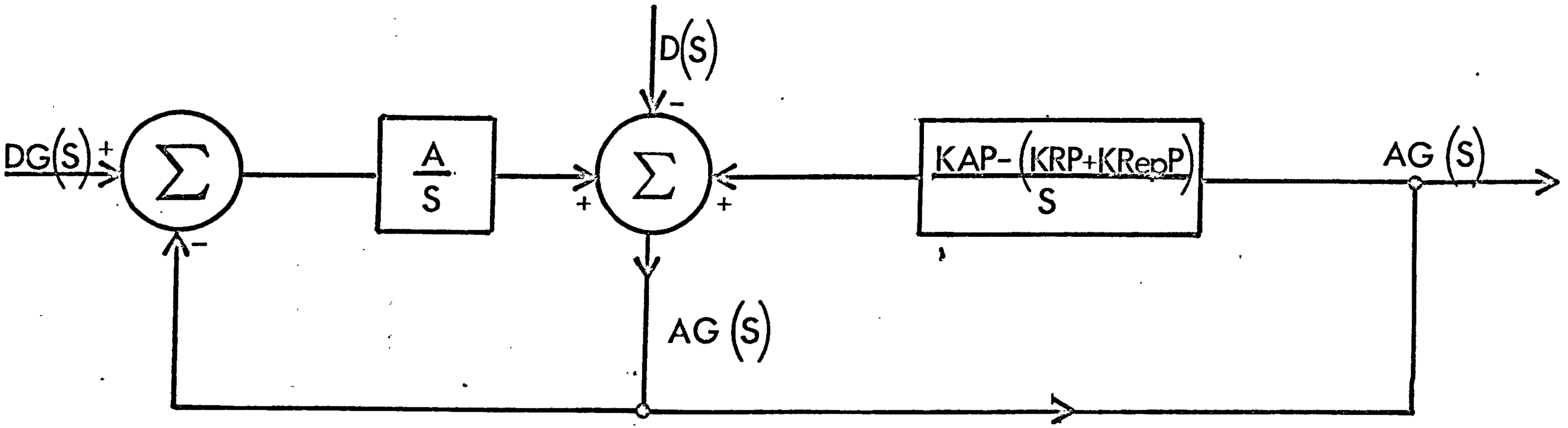


Fig. 2

FIG. 3.

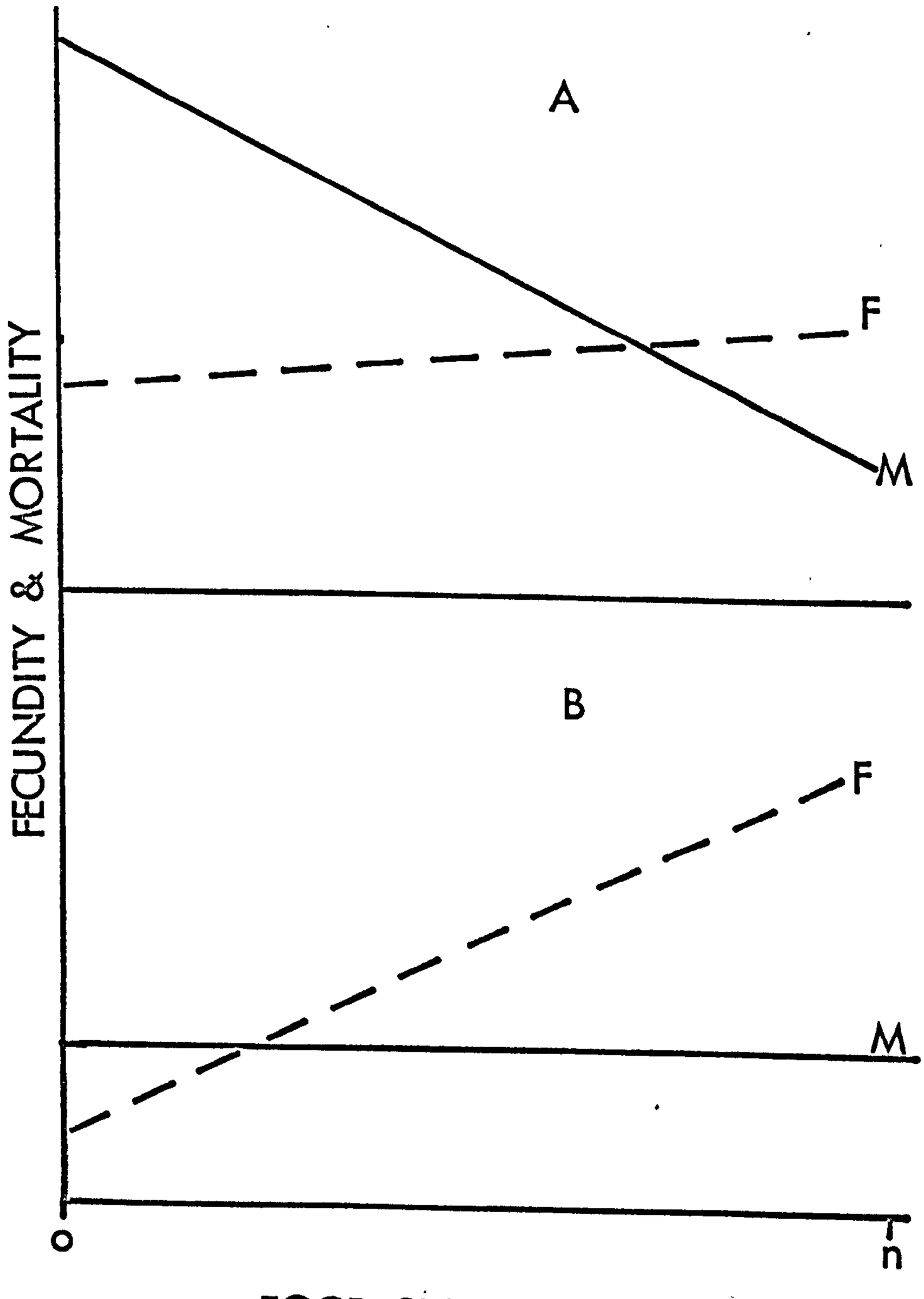
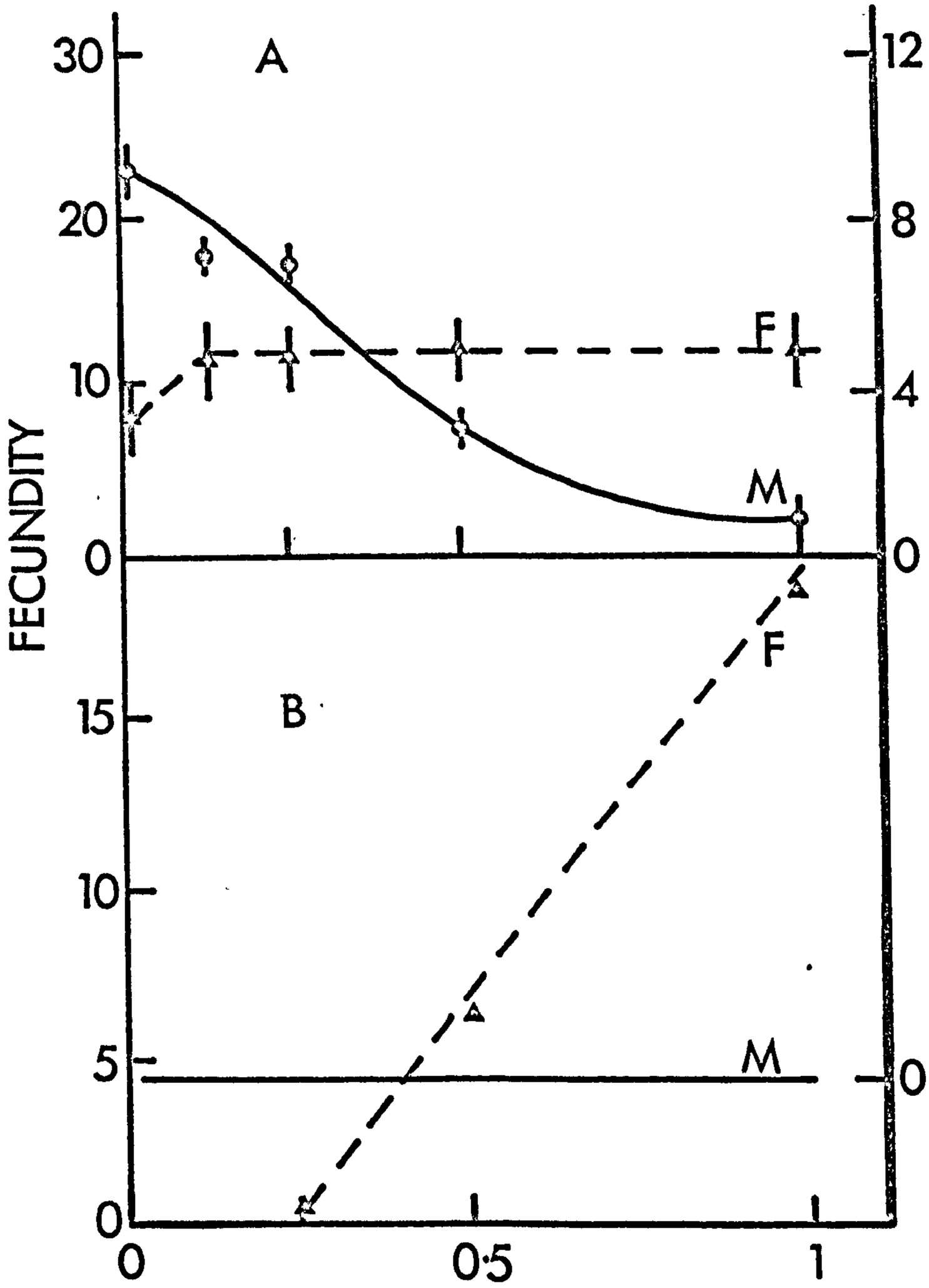


FIG. 4.


30
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MORTALITY
DIETARY STRESS

PUBLICATIONS APPENDIX

V

Potamopyrgus jenkinsi, Smith, at Malham, with Particular Reference to its Invasion Ecology.

Journal : Naturalist (Hull).

Submitted : June 1972.

Accepted : September 1972.

The following note is derived from a more detailed survey (to be published elsewhere) concerned with the species composition of gastropod communities in Malham Tarn. Work on the Mollusca at Malham began with Soppitt and Carter (1888) and was most recently carried out by Stratton (1956). The present survey was undertaken between August 1968 and August 1971 and has essentially involved a quantitative extension of Stratton's qualitative findings.

TABLE 1 shows a summary chart of snail species distribution throughout various parts of the Tarn, both in terms of results from the present survey and Stratton's own observations. FIG. 1 shows the location of sampling sites, and position of weed beds within the Tarn. It should be noted that there is only one, isolated patch of the pond-weed Elodea canadensis Michx. outside the north-west boathouse, where it has apparently remained since its introduction in July 1962 (Holmes, 1965).

Of particular interest is the case of Potamopyrgus jenkinsi. This species is the most recent molluscan colonist of fresh waters, making the transition from its original brackish location around the turn of the century. Robson (1923) has discussed reasons for this transition and its history of colonisation is well documented (see Robson, 1923 and Boycott, 1936, for England; Hunter and Warwick, 1957, for Scotland; Bondesen and Kaiser, 1949, for Denmark; and Hubendick, 1950, for the whole of Europe. Warwick (1944, 1952) suggests that there are probably several distinct races within the species).

Potamopyrgus was not recorded in Malham Tarn until 1950 (Stratton, loc. cit.) although it had been found in Conistan Tarn, 6.5 miles south of Malham, by 1928 (Fysher, 1929). Reduced dispersal rate of this species in highland, compared with lowland, areas seems to be typical (Hunter and Warwick, 1954). Its subsequent course of colonisation in the Tarn is described by Holmes (1965), from whom the following is a summary. Potamopyrgus was originally recorded from around the mouth of the inflow stream but by 1954 it had become very abundant along most of the north shores as far as "Three Trees Point", and also in the offshore Chara beds. In August 1954 some 2,000 snails were transplanted beyond the point and by the following year had begun to spread slowly. In 1958 and 1959, however, total densities of P. jenkinsi fell drastically in all locations, although between this time and Holmes's publication in 1965 Potamopyrgus was again apparently undergoing slow recovery and recolonisation. There are no further

records after 1965 until the present survey.

TABLE 1 shows that Potamopyrgus is now strictly confined to the equally limited Elodea bed, so that between 1965 and the present time its total Tarn density must again have fallen. This pattern of initial rapid invasion and dispersal, followed by dramatic reductions in density and restrictions in distribution seems to have been typical (Boycott, 1936; Macan, 1950), and it may be characteristic of any new colonist whilst finding its ecological place within the indigenous fauna (Elton, 1958).

The present association between P.jenkinsi and the Canadian pondweed may be significant. Certainly the invasion of British fresh waters by both these species seems to have been related and Robson (1923) suggests that Elodea may have prepared the way for Potamopyrgus by contributing some factor to its food supply. It should be noted, however, that Elodea appeared in the Tarn in 1962 after the initial invasion of the snail (Holmes, loc.cit.) and that Potamopyrgus does not eat weed tissue directly, only the encrusting epiphytes (Robson, loc. cit.). This latter behaviour is similar to Lymnaea pereger populations living on Elodea (Calow, 1970).

It seems likely, therefore, that Elodea merely provides a suitable refuge for Potamopyrgus either against the direct action of predators or from competition with other snails. From this point of view it is interesting to note that although other species of gastropod do occur within the Elodea bed P.jenkinsi is by far the most abundant (see FIG. 2), and also that some snails apparently find Elodea tissue toxic (Gaevskaya, 1966). Whether or not the P.jenkinsi population has ultimately become stabalised within the Tarn remains to be seen.

TABLE 1

STATION NAME	Three Trees Bay					Ha Mire Shore							North east sedge bed
Species list \ Station number	1	2	3	4	5	6	7	8	9	10	11	12	13
Subclass Euthyneura													
order Pulmonata													
Ancylus fluviatilis Müll.	X	XS	X	X	X	X	X	X					
Planorbis contortus L.	X	XS	X	X	X	X	X	X	X	X	X	X	X
Planorbis albus Müll.	X	XS				X			X	X	X	X	
Planorbis crista L.	X	XS				X			X	X	X	X	
Planorbis leucostoma Millet													X
Lymnaea stagnalis L.	X	XS	X	X	X	X	X	X		XS	XS	XS	S
Lymnaea pereger Müll.	X	XS	X	X					X	X	X		S
Lymnaea palustris Müll.		S							X	X	X	XS	S
Physa fontinalis L.		X								X	XS	XS	X
Subclass Streptoneura													
order Pectinibranchia													
Bithynia tentaculata L.		S		X		X			X	S	XS	XS	
Valvata cristata Müll.		S								X			
Valvata piscinalis Müll.		S							X	XS	XS	XS	X
Potamopyrgus jenkinsi Smith		S							X	S			

FIG. 1: Distribution of the major weed beds within the Tarn (after Phillipson, 1968, but checked in August 1969) and the position of the sampling stations.

FIG.1

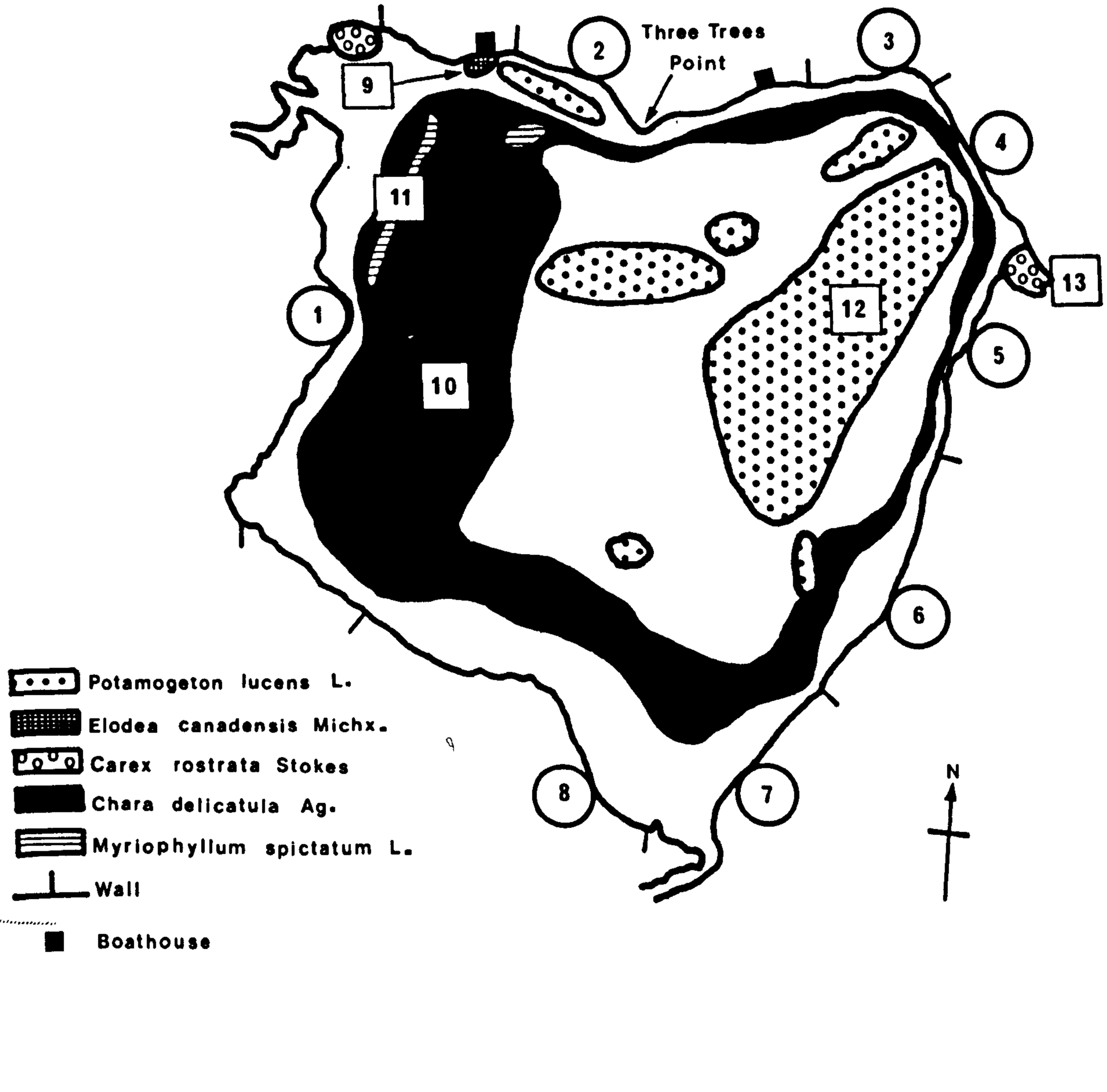
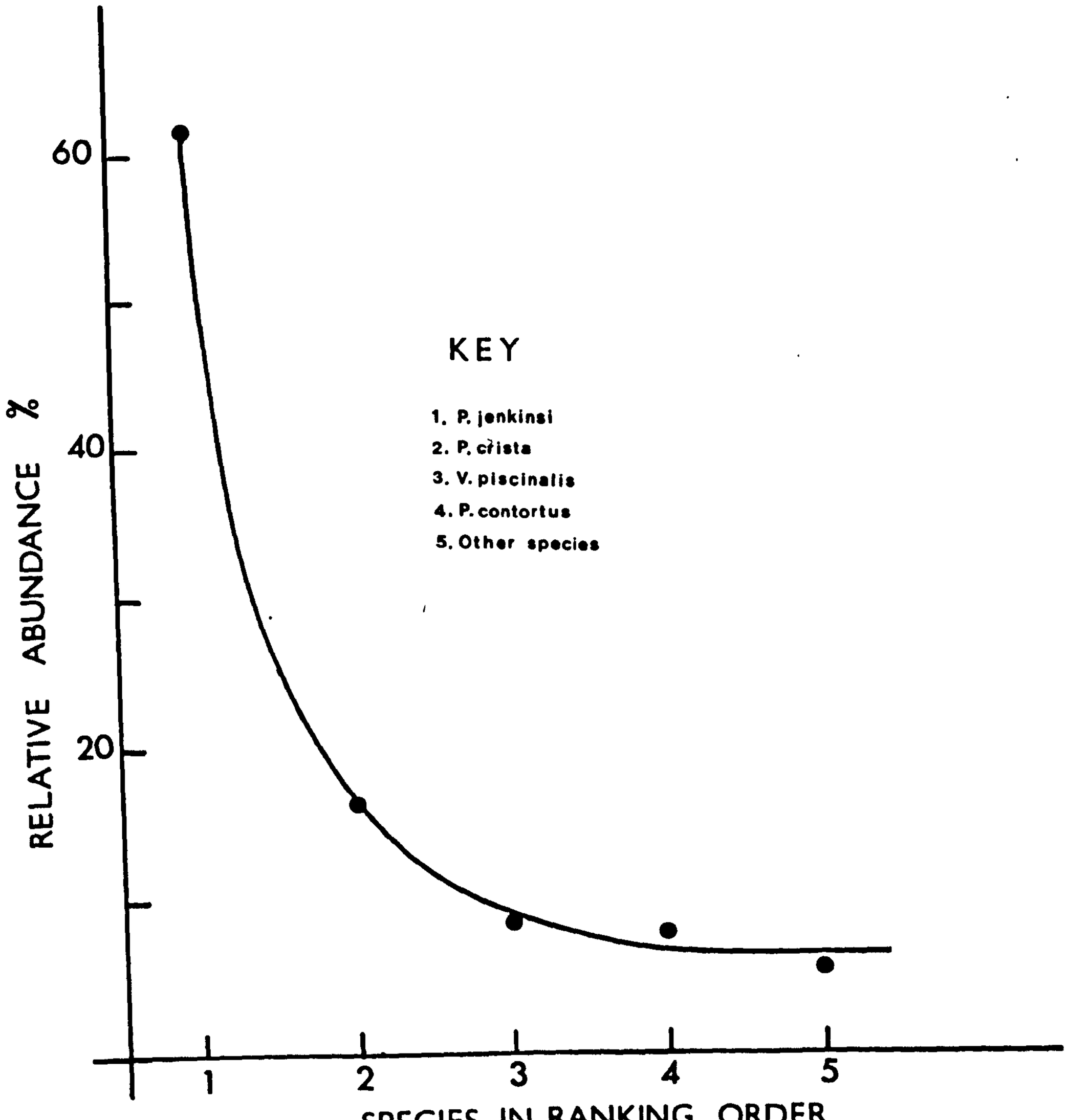

Three Trees Point
1
2
3
4
5
6
7
8
9
10
11
12
13
N
Potamogeton lucens L.
Elodea canadensis Michx.
Carex rostrata Stokes
Chara delicatula Ag.
Myriophyllum spictatum L.
Wall
Boathouse

FIG. 2 : Relative abundance :-

$$\frac{\text{no. of particular species in sample}}{\text{total no. of species}} \times \frac{100}{1}$$

plotted against the ranking order of species in the *Elodea* bed. The results are the average of 3 samples taken with a Phillipson (1968) grab in August 1969.

FIG.2


60
40
20
RELATIVE ABUNDANCE %
KEY
1. P. jenkinsi
2. P. crista
3. V. piscinalis
4. P. contortus
5. Other species
1
2
3
4
5
SPECIES IN RANKING ORDER

ACKNOWLEDGEMENTS

I would like to thank the Warden and staff of Malham Tarn Field Centre (F.S.C.) for allowing access to the Tarn and its faunal records, my wife for helping to collect the samples, and Dr, E. Broadhead for reading and criticising the manuscript. The work was undertaken under the tenure of a NERC Studentship.

REFERENCES

Bondesen, P., Kaiser, E.W. (1949). Hydrona (Potamopyrgus) jenkinsi Smith, in Denmark illustrated by its ecology. Oikos, 1, 252-281.

Boycott, A.E. (1936). The habitats of fresh-water Mollusca in Britain. J. Anim. Ecol., 5, 116-186.

Calow, P (1970). Studies on the natural diet of Lymnaea pereger obtusa (Kobelt) and its possible ecological implications. Proc. malac. Soc. Lond., 39, 203-215.

Elton, C.S. (1958). The Ecology of Invasions by Animals and Plants. Methuen, London, 181p.

Fysher, G, (1929). Mollusca at Hellifield, Yorkshire. Naturalist (Hull), 207-208.

Gaevskaya, N.S. (1966). (The Role of Higher Aquatic Plants in the Nutrition of Animals in Freshwater Basins). Moscow (N.L.L. translation by D.G. Maitland; ed. K.H. Mann; 2 vols).

Holmes, P.F.)1965). The Natural History of Malham Tarn. Field Studies, 2, 199-233.

Hubendick, B. (1950). The effectiveness of passive dispersal in Hydrobia jenkinsi. Zool. Bidrag. Uppsala, 28, 493-504.

Hunter, W. Russell., Warwick, T (1957). Records of'Potamopyrgus jenkinsi' (Smith) in Scottish fresh waters over fifty years (1905-56). Proc. R. Soc. Edinb. (B), 66, 360-373.

Macan, T. T. (1950). Ecology of fresh-water Mollusca in the English Lake District. J. Anim. Ecol., 19, 124-146.

Philipson, G.N. (1968). Ecological pyramids; a field study at Malham Tarn. School Science Review, 43, 262-278.

Robson, G.C. (1923). Parthenogenesis in the mollusc Paludestrina jenkinsi, Patt 1. J. exp. Biol., 1, 65-78.

Soppitt, H.T., Carter, J.W. (1888). Land and fresh-water Mollusca of the Upper Airedale, Yorkshire. Naturalist (Hull), 91-102.

Stratton, L.W. (1956). The Mollusca of the Malham area. J. Conch, Lond., 24, 111-138.

Warwick, T. (1944). The inheritance of the keel in Potamopyrgus jenkinsi (Smith). Nature, Lond., 154, 798-799.

Warwick, T. (1952). Strains in the mollusc, Potamopyrgus jenkinsi (Smith). Nature, Lond., 169, 551-552.