INTERNATIONAL COUNCIL FOR
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Shellfish Committee

THE OCCURENCE OF "WINTER" AND "SUMMER" EGGS IN THE BROWN SHRIMP (CRANGON CRANGON) AND THE IMPACT ON RECRUITMENT.

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Summary

Crangon crangon has a spawning period of about 46 weeks. Berried females with ripe eggs are present in all months of the year but their numbers vary greatly. For this study, the number of ripe eggs present in each month of the years 1978-1980 in the shrimp populations in four main areas of the coastal zone of the Netherlands and Belgium was correlated with the annual fluctuations of the shrimp stock.
Much attention has been paid to the difference between large "winter" eggs spawned in relatively small numbers and the more numerous but smaller "summer" eggs produced by the same stock, a phenomenon considered unique among Malacostraca. The possible factors inducing the development of these two types of eggs and their biological relevance are discussed in the light of the clear stock-recruitement relation occurring annually in spring in the four described shrimp stocks.

Introduction

The reproductive cycle of the brown shrimp (Crangon crangon) is characterized by two phenomena, the occurrence of two clearly distinguishable types of eggs and a very long spawning period covering more than ten months of the year. The two types of eggs were described by Havinga (1930), who found that eggs spawned from the end of October till the beginning of March had a diameter of 0.43 mm. The average diameter of unripe eggs spawned in this period was 0.51 mm. Because these eggs are spawned mainly during winter they were named winter eggs. The eggs spawned from March till September were named summer eggs. These eggs had a minimum diameter of 0.37 mm while the average diameter of unripe eggs (without pigment)

was 0.42 mm.
The very long spawning period of Crangon crangon was described by Ehrenbaum (1890) for several locations in the German Waddensea. Havinga (1930) repeated this part of Ehrenbaum's work for Dutch coastal waters and Tiews (1954) carried out comparable research in the fishing area of Büsum (Germany). All these three authors gave percentages of berried females in samples of adult females, showing a maximum in April and a minimum in October. The percentages of berried females in October given by Havinga and Tiews were 4.5 and 2.9 respectively. For April the percentages given by these authors were 72 and 93.2. Boddeke and Becker (1979) made a quantitative study of the fluctuations of the brown shrimp stock on the fishing grounds of Den Oever (Netherlands). They pointed out that percentages of berried females from samples do not reflect quantitatively the reproduction cycle of the brown shrimp due to the great fluctuations in the stock of mature female shrimps, being often six times higher in October than in March-April. They stated also that the percentage of berried females with ripe (dark) eggs in samples of adult females from the fishing area of Den Oever never exceeded 50 % in 1973-1974.
On basis of reliable landing statistics and a weekly sampling programme of the landings in 1973-1974 of consumption shrimps (practically only adult females) in which body length and in the case of berried females the stage of development on the eggs were defined, two series of data were produced, giving relative figures for the number of shrimps over 52 mm and numbers of ripe eggs present in each month of the years 1970-1975, both expressed in catches per fishing day. This implicates that both series have the same measure of accuracy. This is a more favourable situation than in comparable studies on certain fish stocks where data on the production of eggs (Western stock od mackerel) and larvae (North Sea herring stocks) are derived from survey catches and estimates of recruitment are based on commercial landings.
By determining the cross correlation function between these two series a very constant ratio (2.55×10^{-3}) was found between the numbers of ripe eggs in the period January-September and the number of consumption shrimps 4-5 months later. The fast growth rate suggested by the cross correlation corresponds well with data on growth of Crangon crangon in nature (Boddeke, 1975). In the present study, fluctuations of the production of ripe eggs and the number of consumption shrimps are shown for the coastal zone of the Netherlands and Belgium divided in four main areas, to demonstrate possible local differences in the relation between production of ripe eggs and recruitment in general and for both winter and summer eggs in particular.

Methods

During 1977 and 1978 extensive research was done on the numbers of eggs by berried females of different body length over the entire year in fishing areas from the Westerscheldt in the south till the Danish coast in the North. This was considered necessary because the data given by Havinga (1930) about the number of eggs carried by shrimps of different sixe are not very detailed and do not show a possible influence on the spawned numbers of eggs by the difference in size of winter and summer eggs.
Also a decrease of the egg number during the long incubation period could be expected. For this reason the relationships between body length and egg number in the various parts of the year used for recruitment calculations were based on counts of ripe eggs only.
These data on the number of ripe eggs carried by females in different

parts of the year were combined with results of a monthly sampling programme of the landings in the most important shrimp harbours of the Netherlands: Lauwersoog, Den Oever, Harlingen, Colijnsplaat and Breskens. Every month four samples from different ships were taken in these harbours and the average number of shrimps in one kilogram was defined. The monthly catch per fishing day given in kilogrammes by landing statistics could be expressed in numbers of shrimps and numbers of eggs landed in each harbour. Landing statistics on shrimps in the Netherlands not only give numbers of fishing days and catches per fishing day for each harbour but also for statistical rectangles. This enabled us to correct the catch per fishing day of (mostly small) boats fishing in inshore waters in comparison with on average larger boats mainly fishing offshore. The catches per fishing day in the Zealand estuaries, the Waddensea and the offshore areas in April and October were correlated with the density estimates of consumption shrimps derived from the biannual survey on juvenile flatfish and brown shrimps carried out in the same months since 1969. The highly significant linear regressions as shown in figure 1 made it possible to correct the catch per fishing day in inshore waters to make the catch per fishing day a true expression of the density of the stock in the entire fishing area.

After examining the results of these calculations for the different harbours it was decided to split the coastal area of the Netherlands in four areas. (figure 2). The northern area covers the rectangles 5214, 5213 a small part of 5212 and the adjacent coastal area. It is mainly fished from Lauwersoog. The north western area (3304 and 3305) covers partially 5212, 5211, 5210 and the coastal zone till IJmuiden. It is fished from Harlingen and Den Oever.

The south western area covers 3303, 3202 and 5209 and is fished from Colijnsplaat, Stellendam and Scheveningen.

The southern area covers 5208, 3201, 3101 and is fished from Breskens and Belgian harbours. Belgian landing statistics could be included in this study thanks to the kind cooperation of dr. F. Redant (Oostende).

Results

Numbers of summer and winter eggs.

The considerable difference in size between winter and summer eggs (minimum diameters 0.43 and 0.37 mm resp.) as mentioned by Havinga made it likely that this difference should reflect in the number of winter and summer eggs spawned by females of equal size.

To solve this question samples of 25 berried females carrying unripe eggs without pigment were collected in the Westerscheldt on 24-1-'78 (winter eggs) and on 7-6-'78 (summer eggs).

After counting of the eggs the relation between the number of eggs (N) and the body length^3 (L^3) was defined.

Date	regression	n	r
24-1-1978	$N = 456.3 + 10.8\ L^3$	18	0.73
7-6-1978	$N = 495.6 + 18.4\ L^3$	23	0.58

In these two regressions, the interception of the Y axis is very similar but the slope of the regression lines differs greatly.

From these two regressions the average number of eggs carried by females of 60 mm is 2786 and 4461 respectively.

For an estimate of the volume of eggs direct after spawning we consider a shrimp egg a sphere. The contents of the smallest winter egg is: $0.523 .\ 0.43^3 = 0.0416\ mm^3$. The total volume of the spawned eggs of shrimps of 60 mm is $2786\ .\ 0.0416 = 115.8\ mm^3$.

For summer eggs the total average volume of eggs spawned by a female of 60 mm is $0.523\ .\ 0.37^3\ .\ 4461 = 118.2\ mm^3$.

This calculation shows that there is a very strict relation between size and numbers spawned for winter and summer eggs.

Size of larvae born from winter and summer eggs.

Among fishes and crustaceans eggsize and the size of newborn larvae are normally related. To define the relation between the size of winter and summer eggs and the larvae born from these eggs, females with fully ripe winter eggs were collected on 5-2-'81 in the western Waddensea and with fully ripe summer eggs on 12-6-'81 in the Easterscheldt.
The shrimps were placed in aquaria on the laboratory in IJmuiden. Larvae were born in the following days and measured alive direct after hatching.

Of both groups 25 larvae were measured. The variation in length within the two groups was neglectable. The larvae born from summer eggs were on average 2.14 mm long, the larvae born from winter eggs 2.44 mm.
If we compare the ratio between the length of these larvae (1: 1.14) with the ratio between the diameters of the smallest summer and winter eggs observed by Havinga (1: 1.16) it is clear that a strict relation exist between the size of winter and summer eggs and the larvae hatching from these eggs.
The reason for the difference in size between "summer" en "winter" larvae must be sought in the low production of phytoplankton in winter (Kat 1977). Phytoplankton production reaches a peak in April in the southern North Sea. The larger size of the winter larvae will make their changes of survival in winter and early spring better.
A severe winter with low seawater temperatures in February will slow down the incubation of the eggs being related to temperature (Havinga 1930). Because the phytoplankton bloom in April is not related to the water temperature but to day length the longer incubation period of the winter eggs in a cold winter will very likely increase the survival change of the larvae. The negative correlation between the seawater temperature in February and shrimplandings in August-October of the same year has been demonstrated earlier (Boddeke 1975).

Relation body length/number of eggs.

Counts of the eggs carried by berried females in all months of the year and originating from different areas made clear that no geographic differences in fecundity exists in the coastal area of the Netherlands. The geometric regressions shown in figures 3-6 can beconsidered representative for the relations between body length and number of ripe eggs in the mentioned period of the year. Following these regression lines a berried female of 60 mm carries in the period December-March 2113 ripe winter eggs while a berried female of the same length carries 3823 ripe summer eggs in the period May-September.
April and October-November with average numbers of eggs for a berried female of 60 mm of 3472 and 2375 respectively, have an intermediate position. In April a mixing occurs between berried females with ripe winter and summer eggs. The regression line showing the relation between body length^3 and the number of ripe eggs for this reason lies between the lines showing the same relation for unmixed winter and summer eggs.
Ripe eggs in October and in the beginning of November must be considered summer eggs but are spawned in abnormal low numbers. These eggs are spawned in August or September when no fertile males are present. As was recently demonstrated by Bosschieter (1979) sperma is stored in the oviducts of the females. This makes it possible that spawning of fertile eggs takes place in August-September without direct preceding of a copulation (Boddeke, 1975b). The sometimes very low numbers of ripe eggs observed on berried females in October and November suggest that for the scarce females with ripe eggs in these months the stored amount of sperma limits the number

of spawned fertile eggs.

Fluctuations in stocksize and egg production.

In figures 7-10 the monthly production of ripe eggs and density of the stock of adult (female) shrimps, both expressed in numbers caught per corrected fishing day are shown. Although the landings of consumption shrimps normally show a peak in October the peak in the density of consumption shrimps is more often in September. This discrepancy is caused by a difference in fishing pattern (more fishing in inshore waters in September than in October) and on average smaller size of the shrimps landed in September.

From north to south the average level of the stock decreases regularly although this is better demonstrated by the difference in the highest stock densities reached in autumn than by the minimum levels in spring (table 1). In spring 1979 the shrimp stock in the northern area fell to a lower level than the smaller southern stock but reached again a much higher density in the following autumn.
It seems likely to connect the capacity of the stock to recover from spring to autumn to the availability of nursery areas, shallow silty tidal areas where the larvae settle down after their pelagic stage.
The north of the Waddensea offers large nursery areas in comparison with the south where the western stock has lost the Grevelingen recently (Boddeke 1978) and the south-western stock is supplied from the Westerscheldt which estuary (just as the Easterscheldt) has only very limited areas suitable as nursery grounds for juvenile shrimps.
Very remarkable is the difference in the two Waddensea populations suggesting a more favourable ratio between nursery grounds and total distribution area for the northern stock than for the north-western stock.
In connection to this, it is interesting to note that by the closing of the Zuider Zee in 1931 the western Waddensea lost a very large nursery area of which the importance for the north-western shrimp stock was demonstrated by the very considerable decrease of the shrimp landings in the western Waddensea after 1931. (Boddeke 1978).
The decrease of the stock of adult shrimps from aurumn to spring is in all four areas impressive but can differ greatly from year to year and per area, due to differences in levels of predation and fishing intensity and supplementary recruitment. (Boddeke and Becker 1977).
Recruitment during this period must mainly stem from winter eggs who form a stabilizing factor to the stock. In the western area where the share of the winter eggs in the annual egg production is very considerable compared with the two Waddensea populations the stock does not reach such low levels in spring as sometimes is the case elsewhere.
Ripe winter eggs produced in March-April contribute also to the recovery of the stock of adult shrimps from June on.
For this purpose the stock recruitment relations were calculated for the four areas between the numbers of ripe eggs in March-June and the corresponding numbers of adult female shrimps four months later (July-October), (figures 11-14). To demonstrate this relation the formula of Beverton and Holt $R = \frac{1}{a + b/P}$ was applied, in which P is the number of ripe eggs in month x and R is the number of adult shrimps in month x + 4. To calculate the parameters a and b the formula recommended by Paulik and Ricker

$\frac{P}{R} = b + aP$ was used. (Ricker 1975).

The results show the different levels on which the four stocks reach their maximum size.
With nursery grounds as the limiting factor to these shrimp populations these stock recruitment relations indicate that a regular production of ripe eggs over the entire year is much more effective to recruitment than a peak production in a short period.
By these two types of eggs (an unique phenomenon among Malacostraca) a production of ripe eggs in practically all months of the year and the sex change of (small) males by which all adult individuals contribute to the production of eggs, the recruitment mechanism of the brown shrimp is admirably adapted to the limited capacity of nursery areas and to very high mortality levels.

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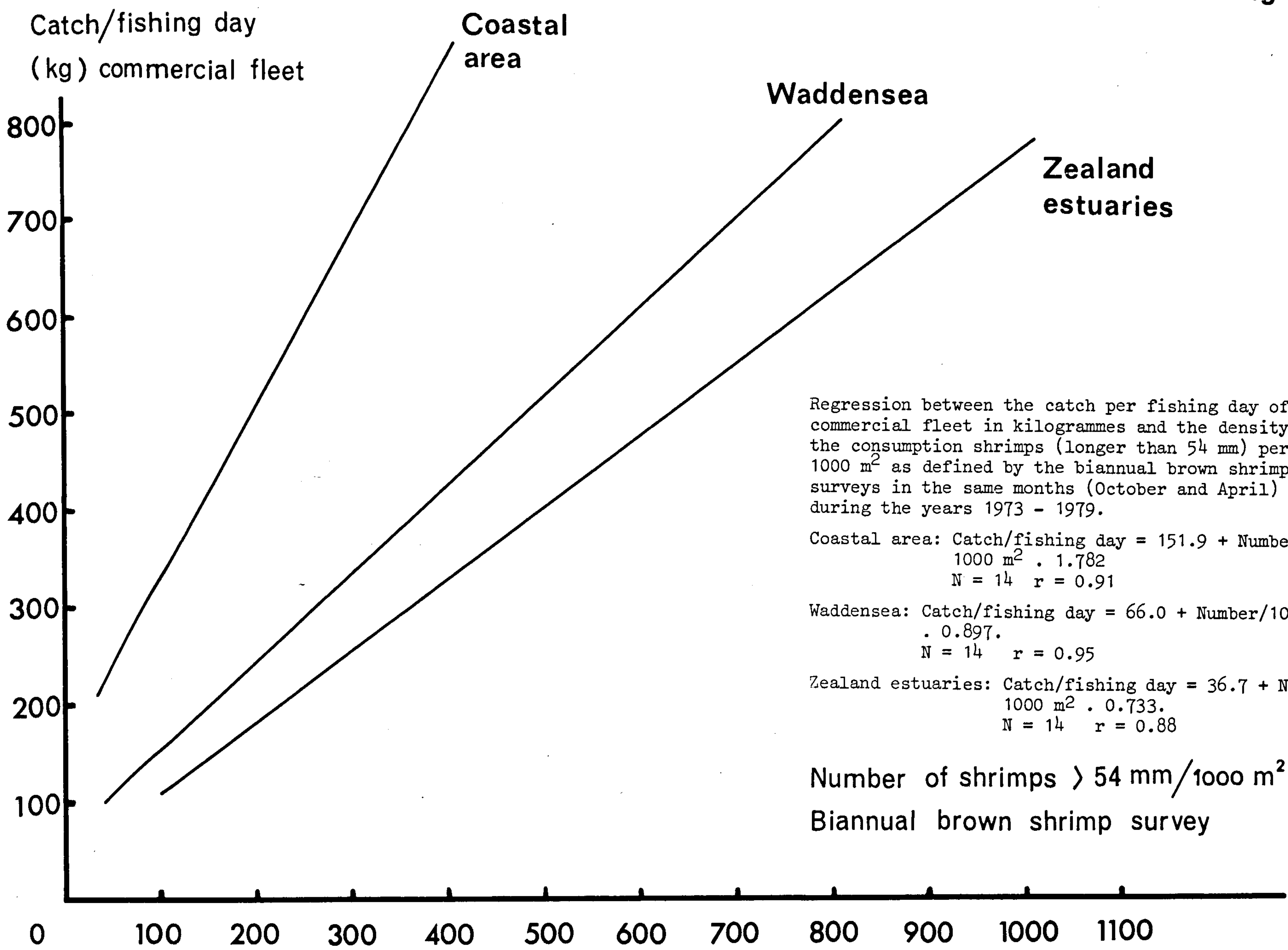
Table 1.

Catch per corrected fishing day in numbers of adult female shrimps.

	Lowest level			Highest level		
	1978	1979	1980	1978	1979	1980
Northern Area	59.443	55.458	211.864	416.806	685.035	782.725
N.W. Area	37.197	77.608	142.651	409.842	593.580	594.340
Western Area	64.964	100.633	177.635	305.257	382.080	408.481
South West Area	23.625	74.638	77.644	232.508	251.812	213.032

fig 1

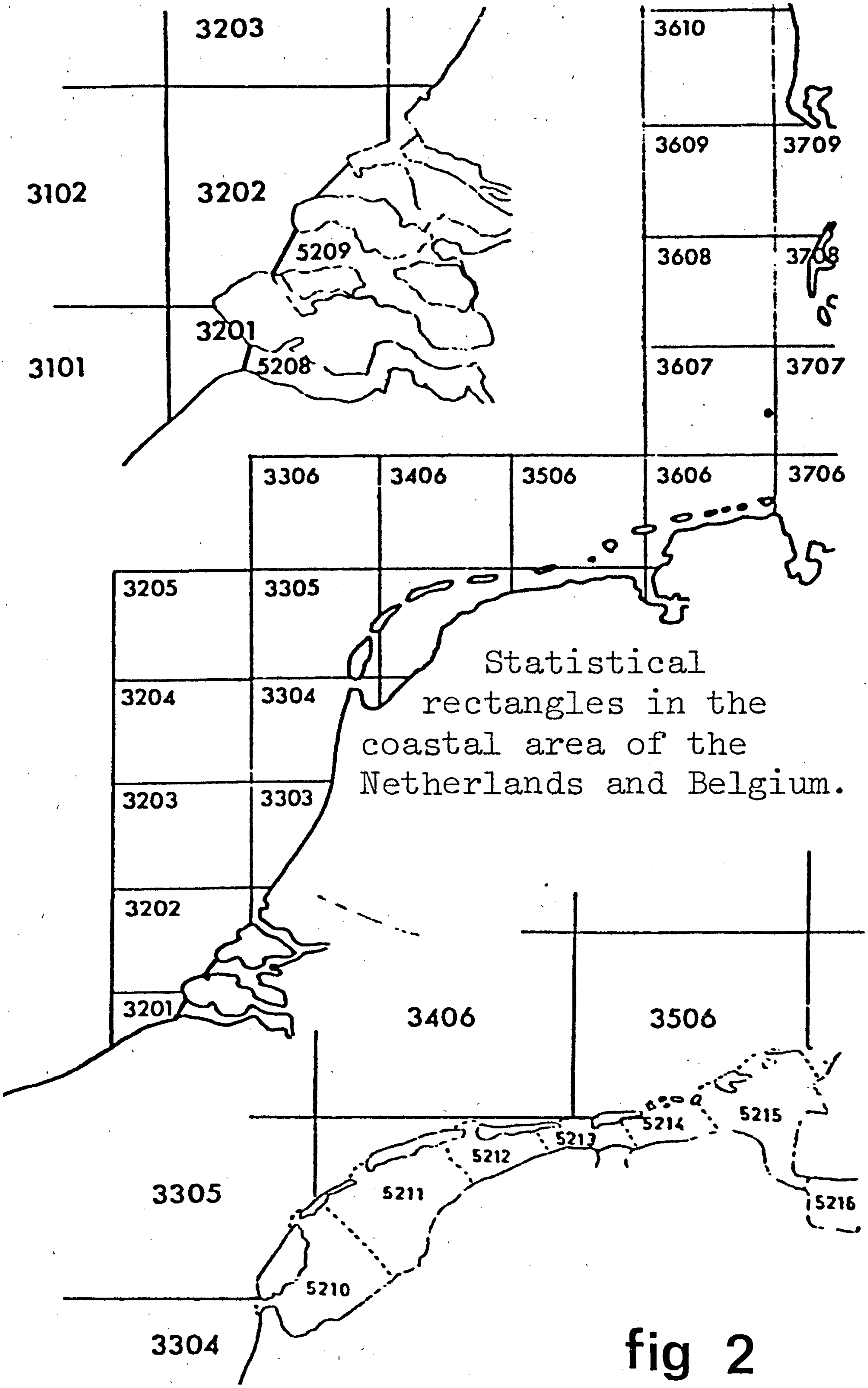


Regression between the catch per fishing day of the commercial fleet in kilogrammes and the density of the consumption shrimps (longer than 54 mm) per 1000 m^2 as defined by the biannual brown shrimp surveys in the same months (October and April) during the years 1973 - 1979.

Coastal area: Catch/fishing day = 151.9 + Number/1000 m^2 . 1.782
N = 14 r = 0.91

Waddensea: Catch/fishing day = 66.0 + Number/1000 m^2 . 0.897.
N = 14 r = 0.95

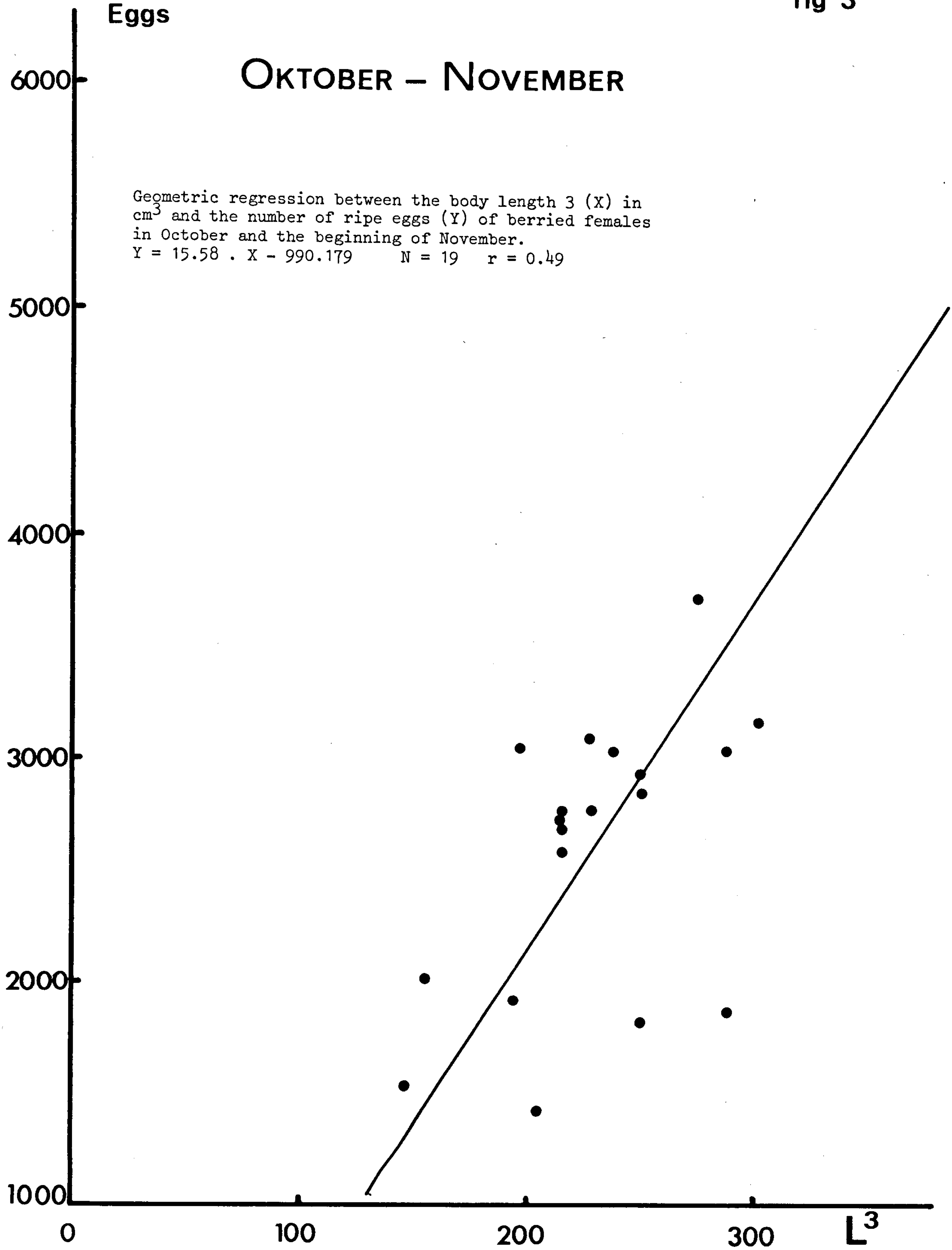
Zealand estuaries: Catch/fishing day = 36.7 + Number/1000 m^2 . 0.733.
N = 14 r = 0.88



Statistical rectangles in the coastal area of the Netherlands and Belgium.

fig 2

fig 3



Geometric regression between the body length 3 (X) in cm^3 and the number of ripe eggs (Y) of berried females in October and the beginning of November.
Y = 15.58 . X - 990.179 N = 19 r = 0.49

fig 4.

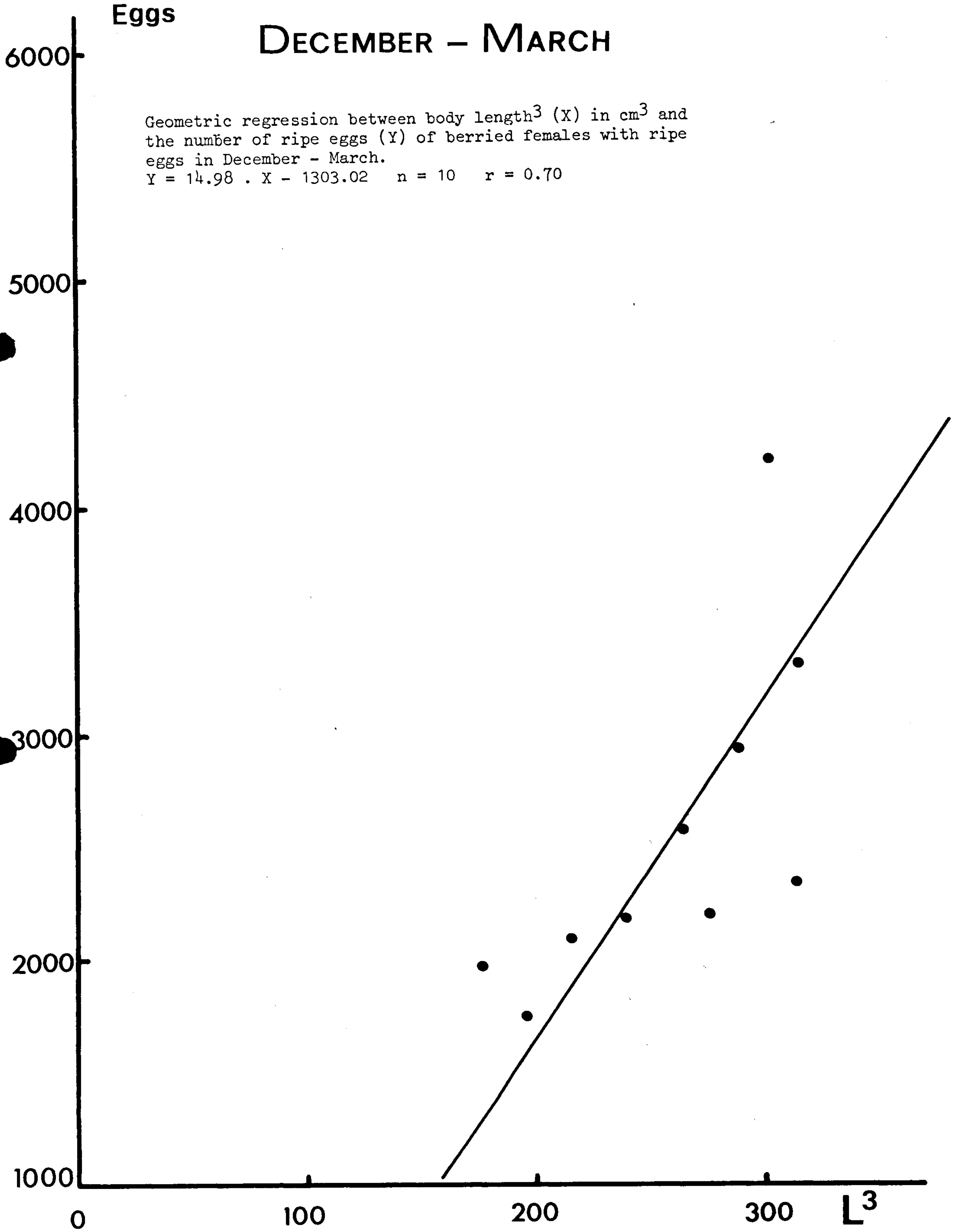
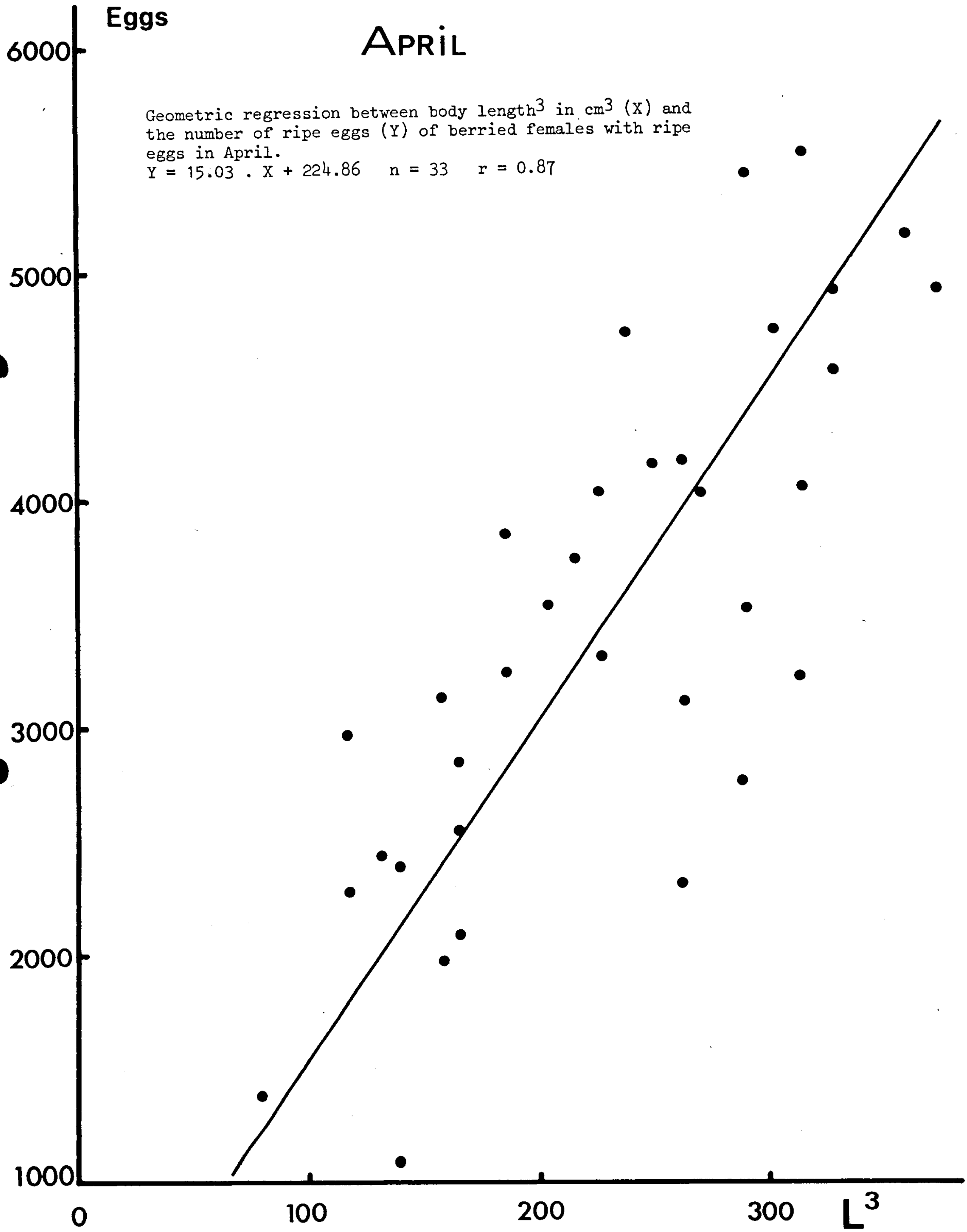

Eggs
DECEMBER – MARCH
Geometric regression between body length³ (X) in cm³ and the number of ripe eggs (Y) of berried females with ripe eggs in December - March.
Y = 14.98 . X - 1303.02 n = 10 r = 0.70
6000
5000
4000
3000
2000
1000
0
100
200
300
L³

fig 5



Eggs
APRIL
6000
5000
4000
3000
2000
1000
0
100
200
300
L3
Geometric regression between body length3 in cm3 (X) and the number of ripe eggs (Y) of berried females with ripe eggs in April.
Y = 15.03 . X + 224.86   n = 33   r = 0.87

fig 6

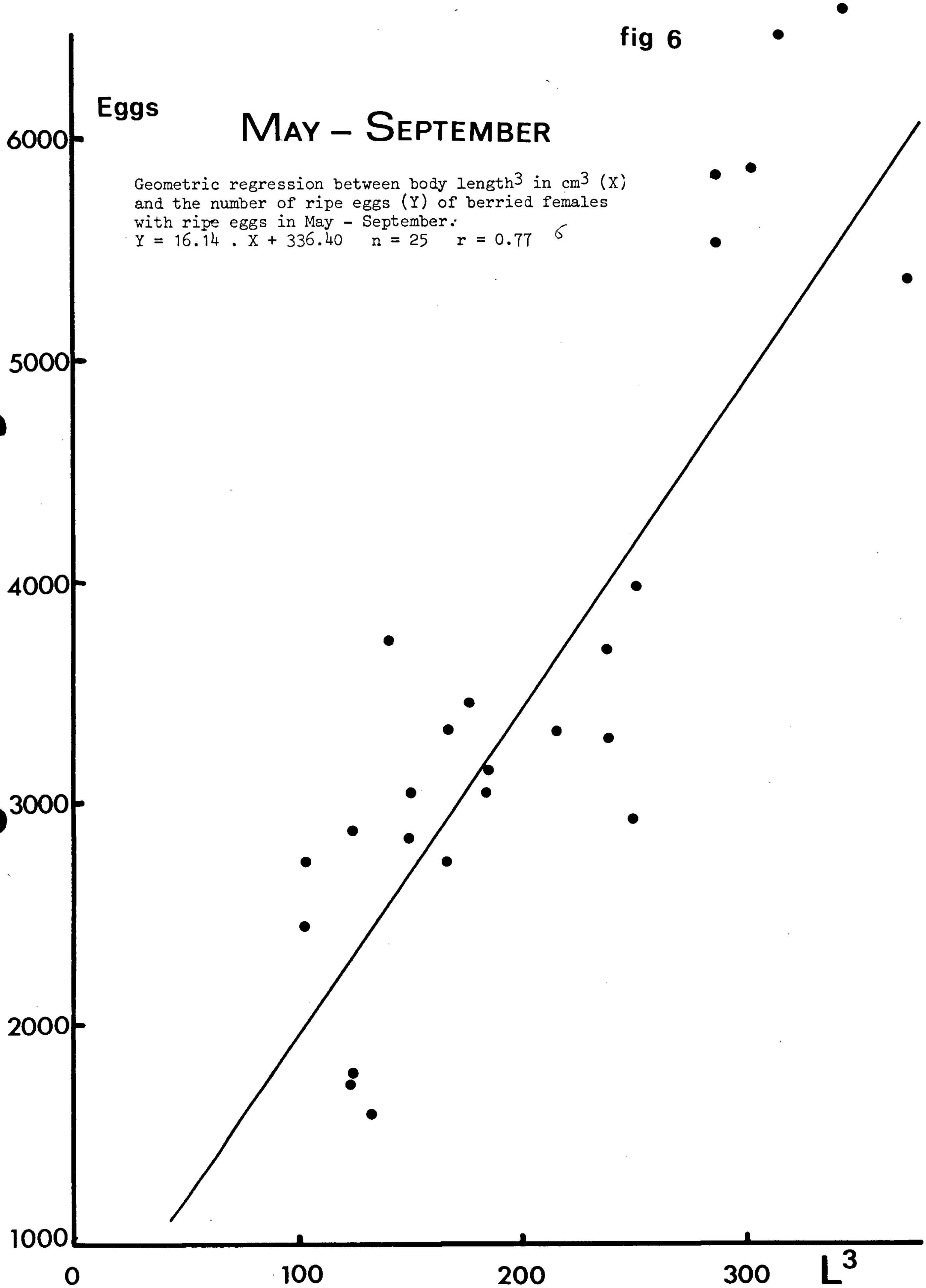
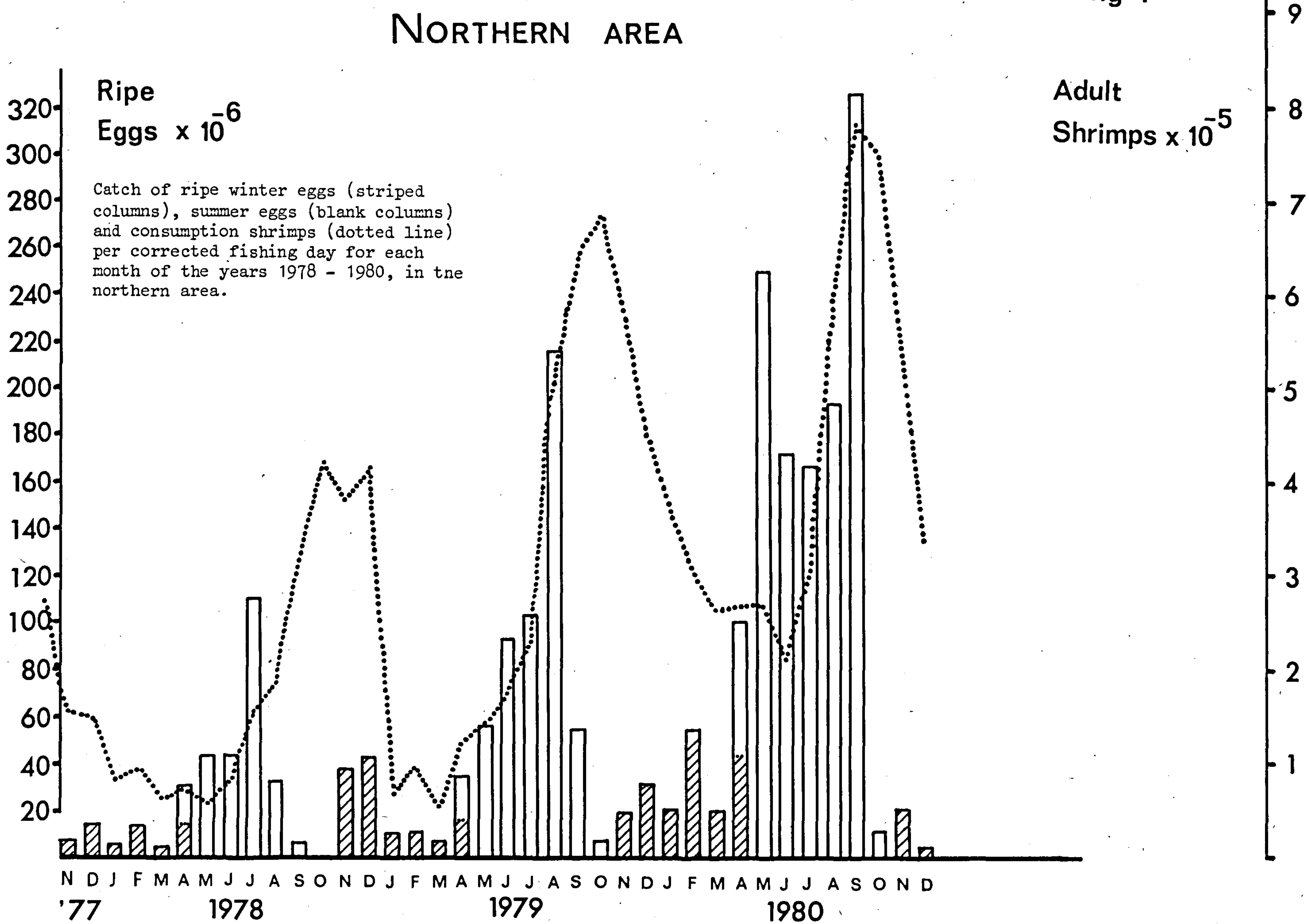

Eggs
MAY – SEPTEMBER
Geometric regression between body length3 in cm3 (X) and the number of ripe eggs (Y) of berried females with ripe eggs in May - September.
Y = 16.14 . X + 336.40 n = 25 r = 0.77
6000
5000
4000
3000
2000
1000
0
100
200
300
L3

fig 7



Catch of ripe winter eggs (striped columns), summer eggs (blank columns) and consumption shrimps (dotted line) per corrected fishing day for each month of the years 1978 - 1980, in tne northern area.

fig 8

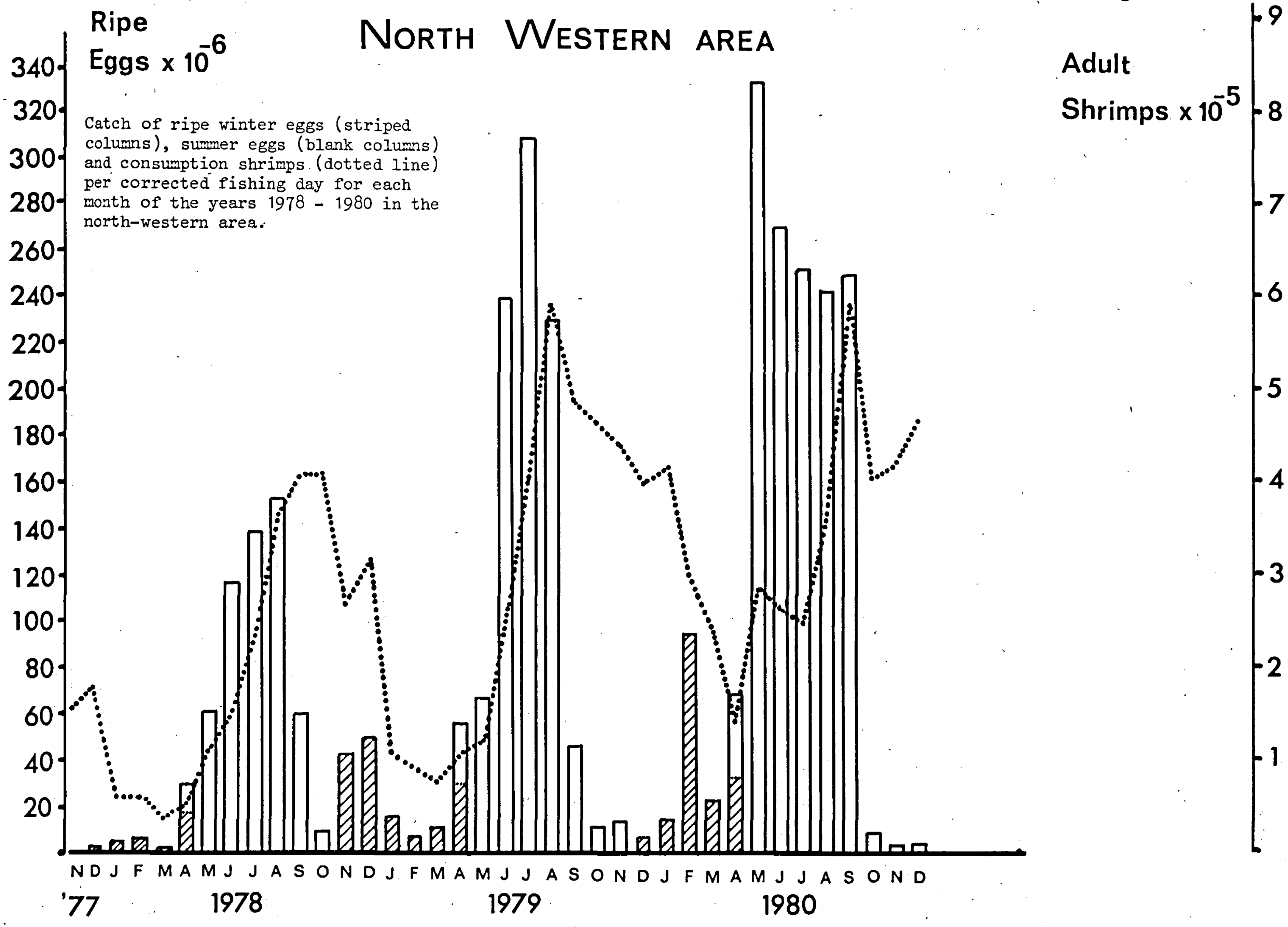
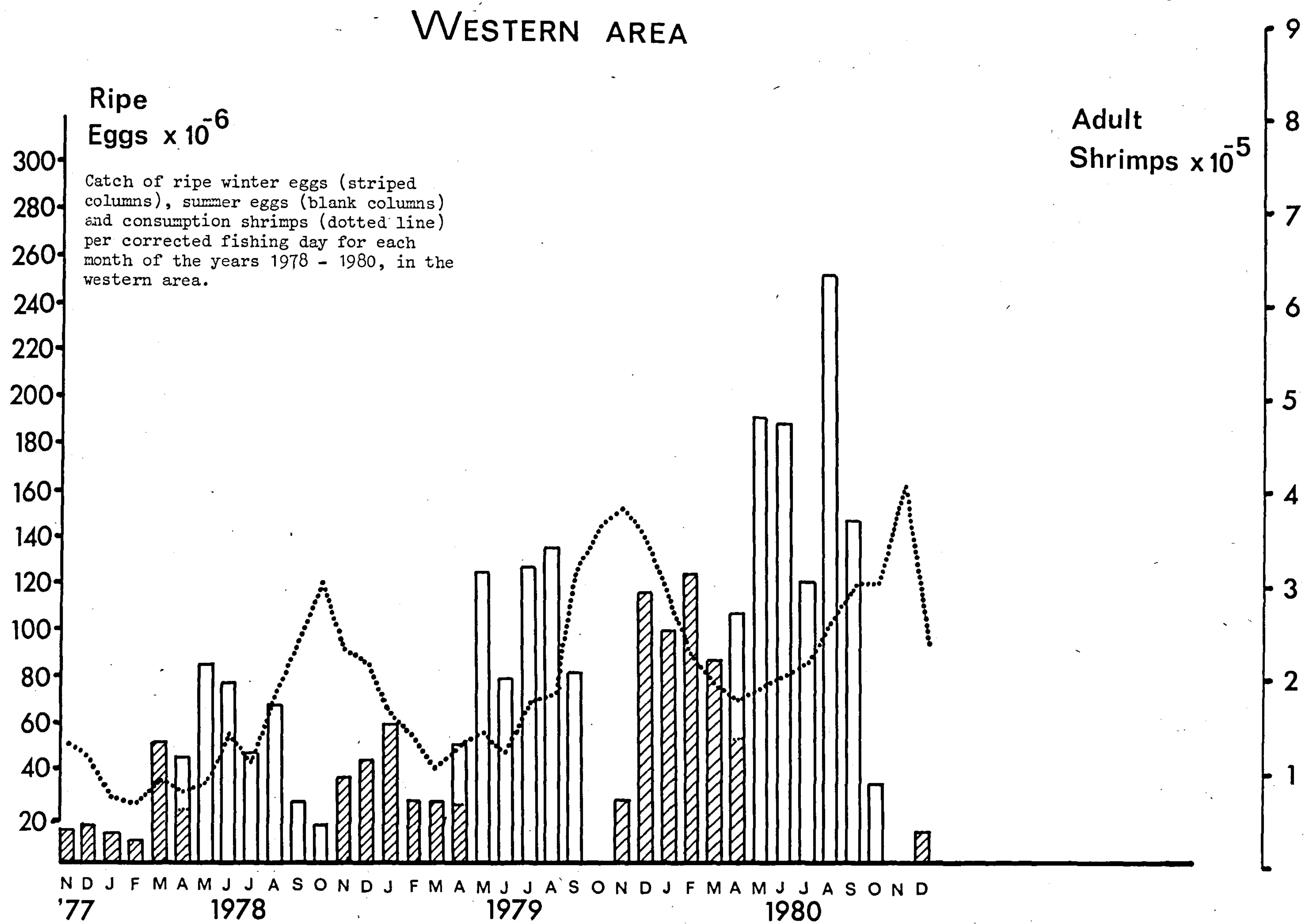

North Western area
Ripe Eggs x 10^{-6}
Adult Shrimps x 10^{-5}
Catch of ripe winter eggs (striped columns), summer eggs (blank columns) and consumption shrimps (dotted line) per corrected fishing day for each month of the years 1978 - 1980 in the north-western area.
340
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
9
8
7
6
5
4
3
2
1
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
'77
1978
1979
1980

fig 9



WESTERN AREA
Ripe
Eggs x 10^{-6}
Catch of ripe winter eggs (striped columns), summer eggs (blank columns) and consumption shrimps (dotted line) per corrected fishing day for each month of the years 1978 - 1980, in the western area.
Adult
Shrimps x 10^{-5}
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
9
8
7
6
5
4
3
2
1
N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
'77
1978
1979
1980

fig 10

South Western area

Catch of ripe winter eggs (striped columns), summer eggs (blank columns) and consumption shrimps (dotted line) per corrected fishing day for each month of the years 1978 - 1980, in the south-western area.

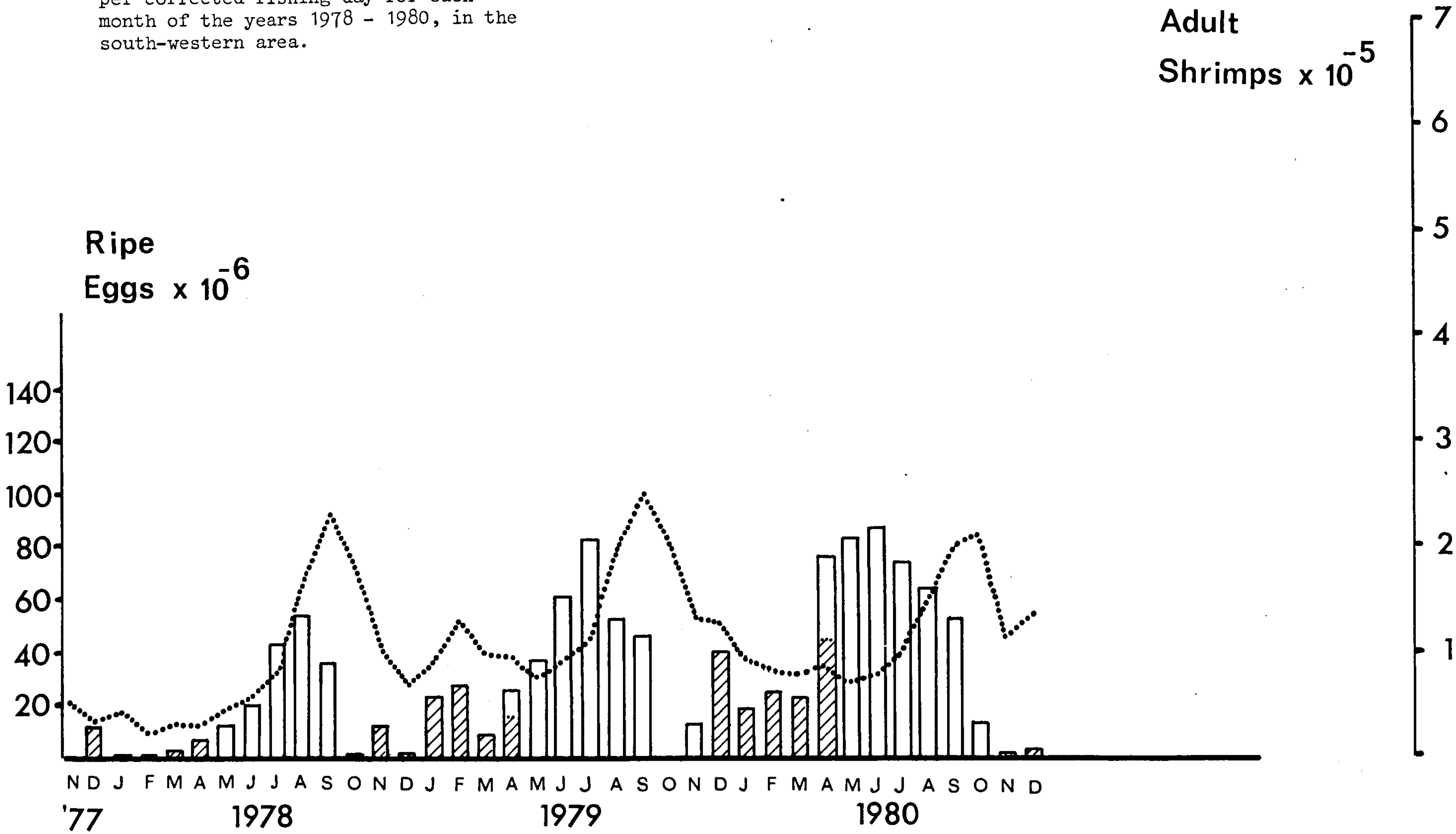
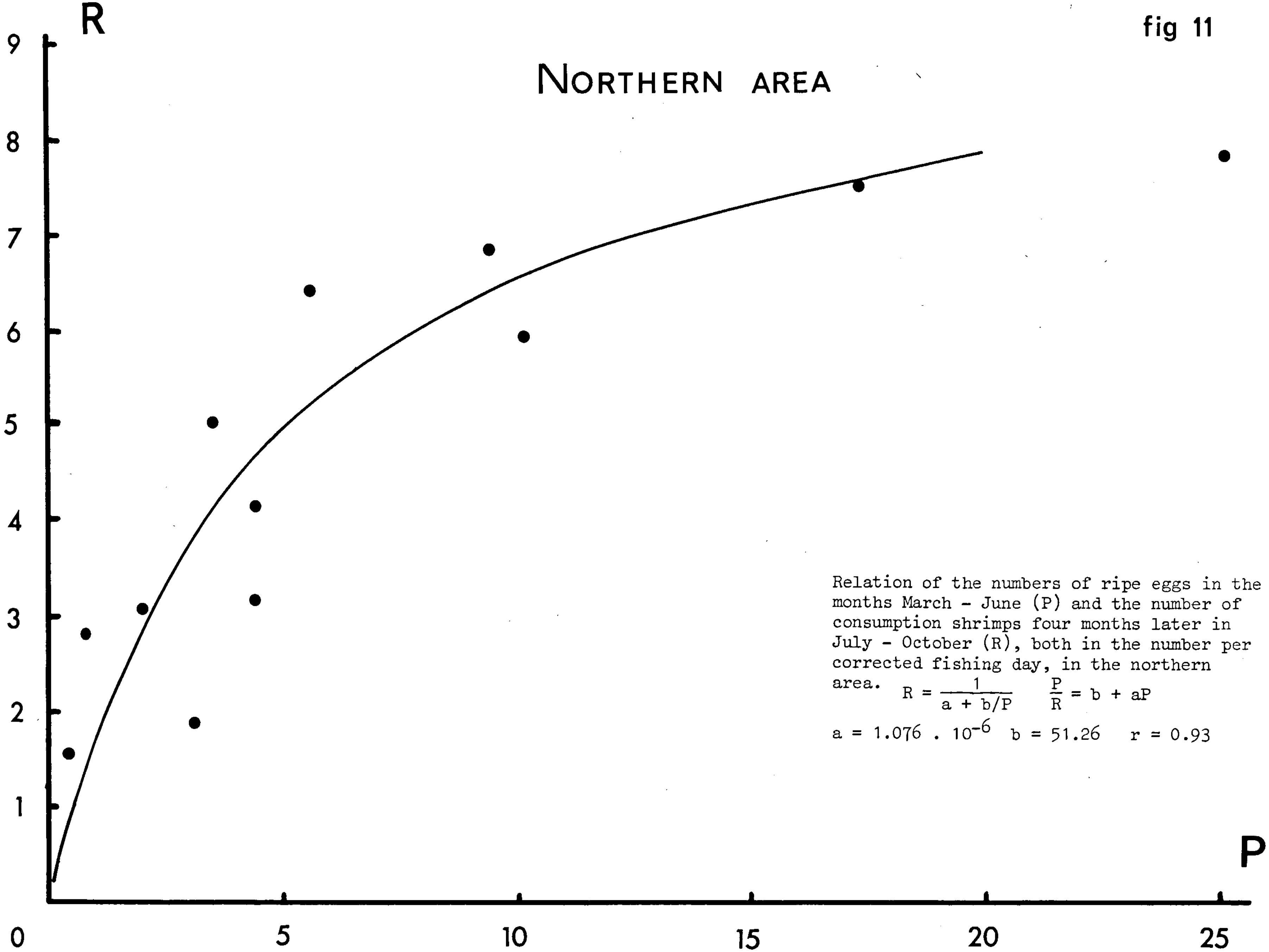


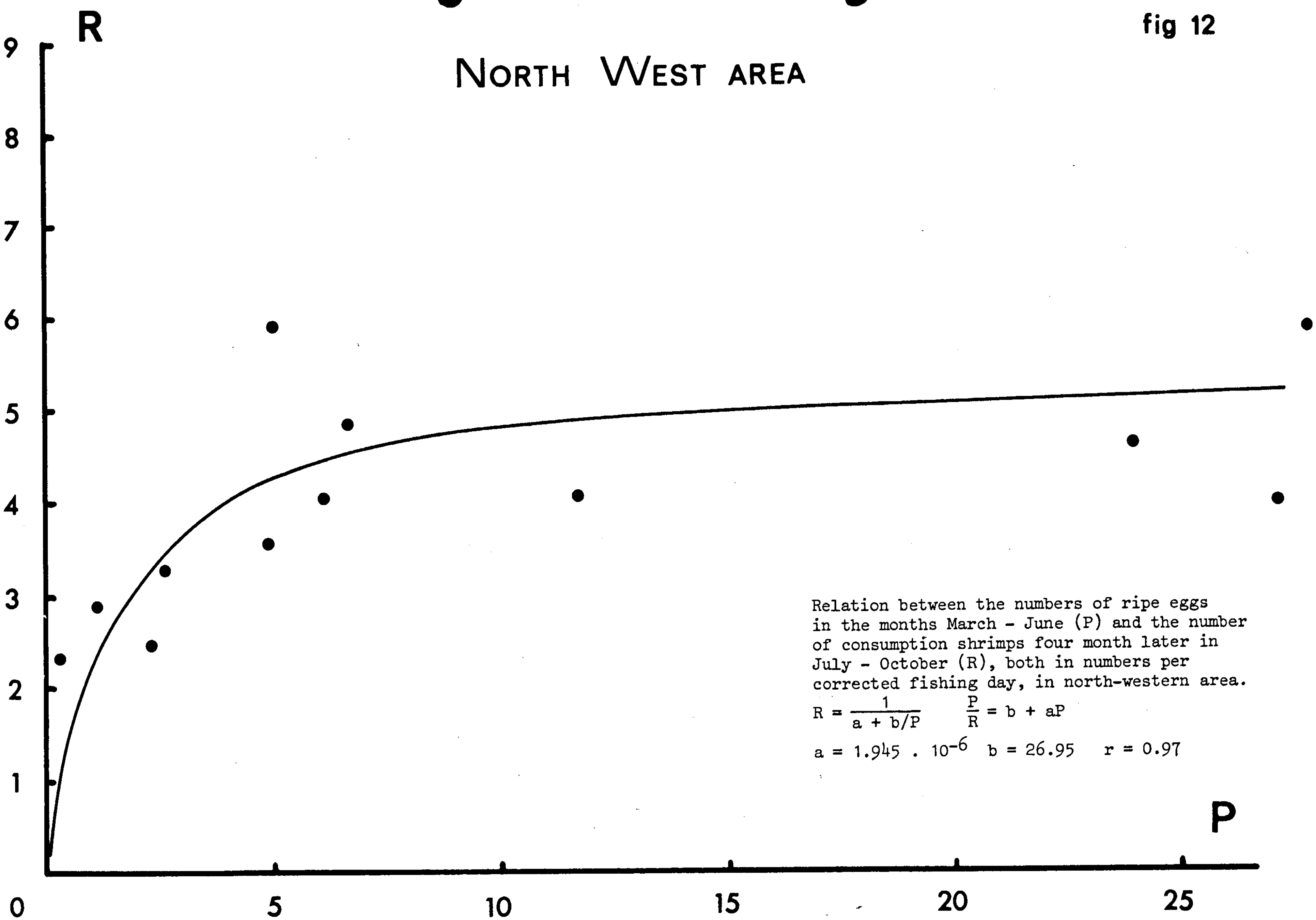
fig 11



Relation of the numbers of ripe eggs in the months March - June (P) and the number of consumption shrimps four months later in July - October (R), both in the number per corrected fishing day, in the northern area. $R = \frac{1}{a + b/P}$ $\frac{P}{R} = b + aP$

$a = 1.076 \cdot 10^{-6}$ $b = 51.26$ $r = 0.93$

fig 12

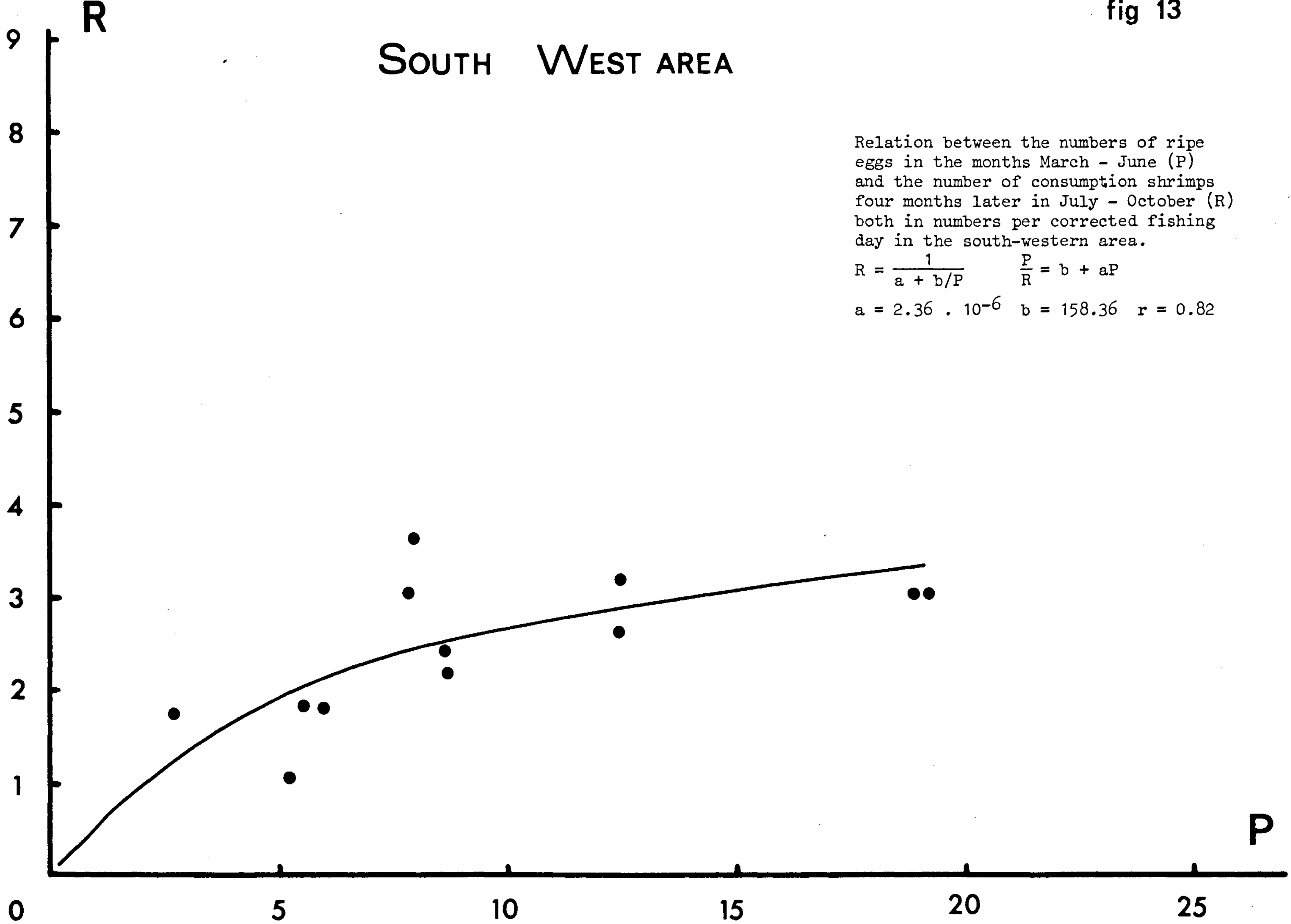


Relation between the numbers of ripe eggs in the months March - June (P) and the number of consumption shrimps four month later in July - October (R), both in numbers per corrected fishing day, in north-western area.

$R = \frac{1}{a + b/P}$ $\frac{P}{R} = b + aP$

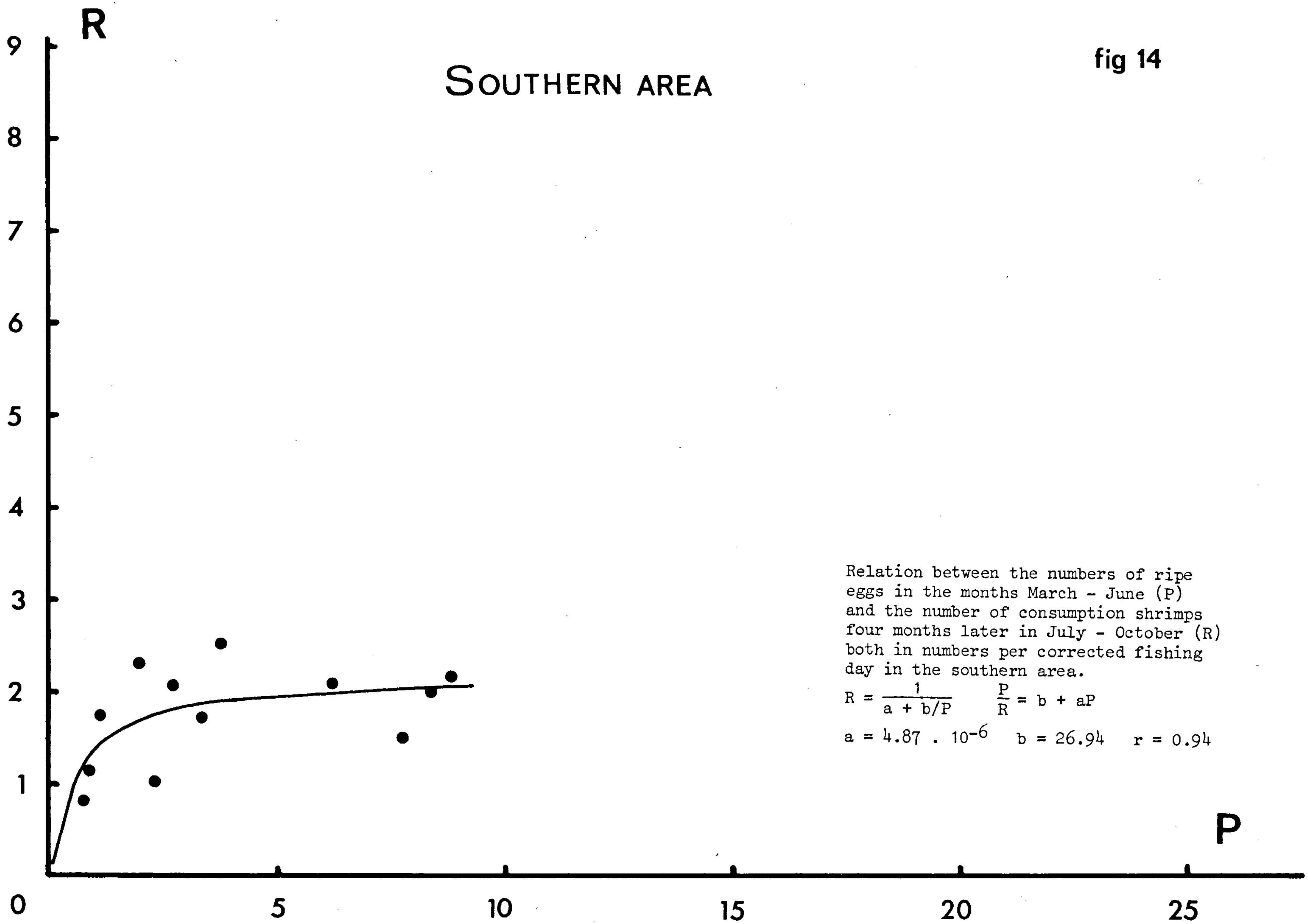
$a = 1.945 \cdot 10^{-6}$ $b = 26.95$ $r = 0.97$

fig 13



SOUTH WEST AREA
R
P
9
8
7
6
5
4
3
2
1
0
5
10
15
20
25
Relation between the numbers of ripe eggs in the months March - June (P) and the number of consumption shrimps four months later in July - October (R) both in numbers per corrected fishing day in the south-western area.
$R = \frac{1}{a + b/P}$ $\frac{P}{R} = b + aP$
$a = 2.36 \cdot 10^{-6}$ $b = 158.36$ $r = 0.82$

fig 14



Relation between the numbers of ripe eggs in the months March - June (P) and the number of consumption shrimps four months later in July - October (R) both in numbers per corrected fishing day in the southern area.

$R = \frac{1}{a + b/P}$ $\frac{P}{R} = b + aP$

$a = 4.87 \cdot 10^{-6}$ $b = 26.94$ $r = 0.94$