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Feeding and growth in an inshore population of plaice, Pleuronectes Platessa L

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FEEDING AND GROWTH IN AN INSHORE

POPULATION OF PLAICE <u>PLEURONECTES</u> <u>PLATESSA</u> L.

A Thesis

submitted to the University of Wales

by

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in candidature for the degree of

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Abstract

The seasonal variations in diet, feeding chronology, condition and growth of a fishable population of plaice Pleuronectes platessa in two bays off the North Wales coast were investigated. The population, estimated to comprise 478,630 fish ($\pm$ 19%) of ages II - XV, occupied an area of 236.73 Km^2 with an average biomass of 23.36 tonnes (0.11 g/m^2).

Data on diet and feeding chronology were obtained from fish collected by trawling at known intervals (usually every three hours) during a twenty four hour period. The diet of 'small' (15.5 - 19.4 cm) and 'medium' (19.5 - 20.4 cm) fish was similar in each of the months for which data was collected i.e. March, May, August, November and February. The two chief items were the polychaete Pectinaria koreni and the lamellibranch Abra alba. In addition the 'large' fish (30 - 35 cm) also took Nereis spp. and the bivalve Tellina fabula in significant numbers. The diet varied seasonally in all size-groups; it was dominated by polychaetes in the cooler months and by molluscs in the warmer months.

Feeding was considerably synchronised amongst members of the population. Feeding chronology was deduced from variations in average stomach contents with time of day and from the occurrence of food in specific regions of the alimentary canal. In the cooler months - February, March and November - the following phases were recognised: Feeding Peak, Gastric Evacuation, Feeding Pause and Resumption of Feeding. These phases were obscured in May and August probably because higher temperatures led to faster gastric evacuation; this in turn allowed larger meals and increased feeding frequencies, thereby reducing feeding synchrony in the population. Laboratory studies later showed that at a given temperature, the rate of gastric evacuation increases with meal size (gm). [Rate (g/hr) $\propto$ (meal size)$^{0.6}$]. At all temperatures gastric

evacuation time (GET) for a given meal depended on fish size (g). GET was proportional to (fish size)$^{0.42}$ for a meal expressed as % body weight and to (fish size)$^{-0.068}$ for a meal expressed as grams. When all other factors were kept constant GET varied as (temperature)$^{-1.03}$.

An empirical length-weight relationship was used to describe seasonal condition factors ($W = a L^{2.946}$). Peak condition occurred in June and July; condition was intermediate in autumn (deteriorating) and spring (improving) and poor in winter.

The condition of the edge of otoliths was used to determine the limits of the growing season. Improvement in condition preceded seasonal growth in length which started in April and was virtually over by September. Growth was asymptotic in all age-groups and the function $Y = A - B(e^{-kt})$ described the data adequately.

Estimates of daily ration were made from field data on average stomach contents. The population apparently cropped 491.15 tonnes of benthic production annually. Energy budget calculations indicated that in energy terms 32.33% of this intake was used for routine metabolism, 9.62% for growth and 0.97% for reproduction. The remaining 57.08% was lost through egestion, conversion and excretion.

CONTENTS

Introduction

There are two approaches to fisheries biology, frequently merging but generally recognisable. The first approach deals with the basic biology and general biology of fish species. The second approach is a form of demography and deals with the dynamics of fish populations i.e. rates of growth, death etc.

The study of the trophic ecology of fish species has gone through several stages. Much of the work on the feeding of fish populations at the start of the present century was centred around their diet and those factors that affect its composition. Besides providing comprehensive lists of the various items taken by fish species, these studies soon established that several factors affect the diet composition, e.g. age (or more accurately size) and season. By the middle of the present century, attention had largely shifted to rates of ingestion and digestion and the efficiency with which ingested food is converted into fish flesh. Under laboratory conditions maintenance rations were investigated (e.g. Brown, 1946) and conversion efficiencies established (e.g. Hatanaka et al., 1956a, b). Later these relationships between food intake and growth were extrapolated to field situations and used to estimate the rate of food intake in the wild. With the development of techniques for estimating population sizes, attention became focussed on the biomass and production of fish present in a given habitat. Combined with growth and conversion efficiency data, population censuses made it possible to estimate annual production, yield, and the impact of fish populations on the fauna and flora constituting their food supply. It was in this way that several classic production studies became possible (e.g. Ricker and Foerster, 1948 on Oncorhynchus nerka; Gerking, 1962 on Lepomis macrochirus; Mann, 1965 on five cohabiting species in the River Thames U.K.).

It was at this point that studies on marine species fell behind freshwater studies. It is possible that this was partly because population censuses are much less feasible in the marine environment. Also the descriptive models of Graham (1935) and Schaefer(1954) and the analytic model of Beverton and Holt (1957) were proving adequate for the purposes of marine fishery assessments. The demographers were therefore not pressing urgently for more basic biological data. The situation however began to change at the beginning of the present decade. The total annual fish yield from the sea has been increasing by 6% since 1945 and it is generally conceded that this cannot go on indefinitely. Improved methods of fish location and capture are steadily escalating the pressures on exploited stocks. To monitor these stocks more closely, the demographers need the type of basic biological data that is at present available only for some freshwater species. The relationship between stock and recruitment so vital for improving the analytical yield model of Beverton and Holt is still obscure for most exploited species. The metabolic consequences of food quality, routine activity and reproduction remain undetermined. There is still a dearth of information on the interactions between exploited fish populations and their food supplies. Yield equations do not take into account these trophic factors and in the absence of such integration inexplicable events within populations will continue to confound population biologists. A case in point is the estimate by Steele (1965) that total demersal production in the North Sea was 0.57 million tons annually. For the period 1966-1967 however catches from the area reached 1.01 million tons, far in excess of the estimated total production. In attempting to explain this discrepancy Gulland (1970) could only point to a particularly good year class of haddock in 1962, good year classes of cod in 1961, 1962, 1963 and 1964 and what seemed to have been improved growth rates amongst small plaice.

In the late sixties the Ministry of Agriculture, Fisheries and Food, U.K. initiated a programme of detailed ecological studies of O and I group plaice populations (see e.g. Riley, 1964; Corlett, 1966; Macer, 1967; Edwards and Finlayson, 1969; Edwards and Steele, 1970; Lockwood, 1972). From these studies details of the feeding habits, mortality and production of young plaice have emerged. The present work is an attempt to extend investigations of this sort to an inshore fishable population of plaice in the Irish Sea. The plaice Pleuronectes platessa L. is one of several dominant species in the fish population of the two bays studied - the others include the common dab Limanda limanda, pout and whiting spp. and rays, Raia spp. The aim of the investigation will be:-

(i) To investigate the diet and feeding chronology of the population

and to determine how these change with fish size and time of year.

(ii) To conduct laboratory studies on feeding and digestion rate in order

to facilitate interpretation of field data on feeding chronology.

(iii) To investigate the effects of seasonal variations in food density

and temperature on the growth and condition of the plaice.

It is hoped that the study will make it possible to estimate annual food intake, growth, production and conversion efficiencies on both a seasonal and an annual basis. Male and female fish will be treated separately to pinpoint differences, if any, between sexes.

It is hoped that a final annual energy budget can be suggested for each of the dominant age-groups of each sex. Such a budget showing the likely interaction of the population with its food supply should provide an insight into the factors that determine the production and yield of the fishable inshore population.

Chapter 1

The Study Area and its Plaice Population.

The Study Area

The study area (shown in Fig. 1.1) extends from Moelfre Island on the eastern coast of the Isle of Anglesey, across the northern entrance to the Menai Straits and along the coast of North Wales to The Great Orme promontory. The seaward limit was arbitrarily set at a line running due east from Moelfre Island to a point 0.2 kilometres due north of The Great Orme. Thus delimited, the study area comprises two bays, Red Wharf Bay on the Isle of Anglesey and Beaumaris Bay on the Welsh mainland. These two bays are connected by a stretch of water called Table Road. Estimated by planimetry the area covers 23672.5 hectares (= 236.73 km^2). 18.4% of this expanse occurs as intertidal mud and muddy sand flats mainly at the Lavan Sands, Dutchman Bank and Red Wharf Bay. Though these areas obviously do not support permanent plaice populations, their benthos can be rich and when they are trawled at high tide, larger plaice (30-40 cm) almost always form the bulk of the catch. This suggests that the fish make feeding forays with the incoming tide.

The windrose inset in Fig. 1.1 shows the prevailing winds to be south-westerly. The study area is sheltered from these by the island of Anglesey and by the extensive Snowdonia range of mountains inland. In the relative calm resulting from this protection, the mobile impoverished sands which floor most of Liverpool Bay have formed a linear series of sand banks along this section of the Welsh coast. Many of these banks are quite extensive and some may be up to three quarters of a mile long (Rees, Eagle and Walker, 1975; Rees, pers. comm.). Patches of mud occur between these sand banks and they support dense benthic communities. The numbers and diversity of species in these communities can alter dramatically from one year to the next as a result of northerly onshore winter gales from which the two bays are not protected (Rees et al., 1977).

Fig. 2.1   Map of the study area showing

principle features and local

bathymetry.   Stippled areas

are intertidal mud and muddy sand.

Moelfre

Great Orme

5

10

5

10

5

5

5

5

Table Road

Red Wharf Bay

Puffin Is.

2   3

5

3

3

5

Beaumaris Bay

5

dutch man

Menai Straits

3

1

3

2

2

2

1

lavan sands

NORTH

0 3 KNOTS
4 10 "
11 21 "
22 33 "
OVER 34

SOUTH

53° 20′

53°

4° 10′

4° West

3° 50′
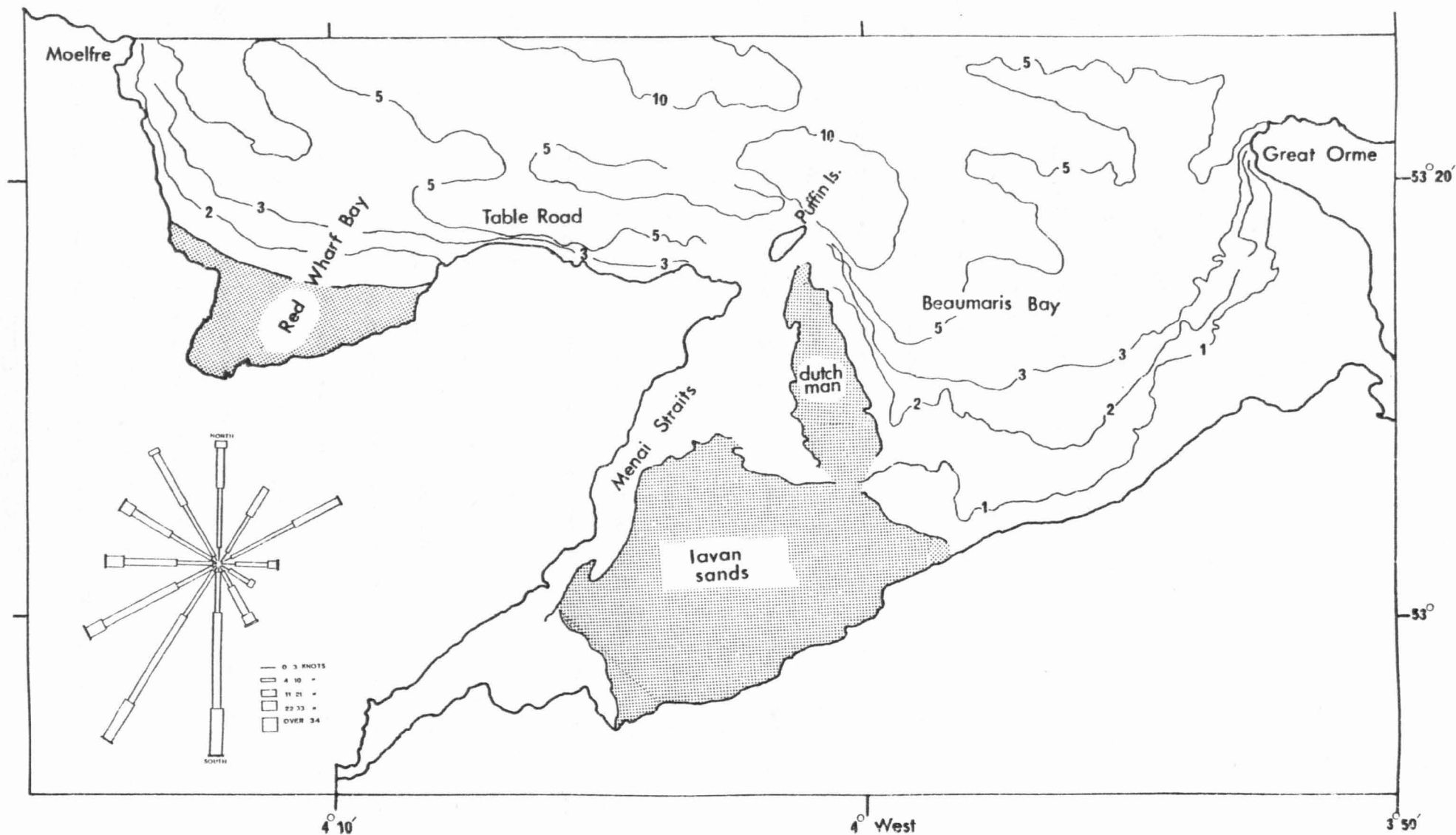
The Plaice Population

Red Wharf and Beaumaris Bays are nurseries for young plaice. With
The Great Orme spawning ground being no more than 10 miles to the north
it is probable that the young O-group plaice are derived from that
region. However, it is doubtful that the adult population is derived
exclusively from these nurseries. Once they are mature, plaice
undertake spawning migrations and the pattern of these movements in
the Irish Sea are complex and incompletely understood (Harden-Jones,
1968). From fish egg surveys, Simpson (1959) has established that
there are four main plaice spawning grounds in the Irish Sea, viz:-
Off the north coast of Cornwall, in Cardigan Bay, off Great Orme, and
between the Isle of Man and the coast of Cumberland. Macer (1972)
found that most mature plaice tagged in The Great Orme spawning ground
during the spawning season returned to the same ground the following
spawning season with only 3.4% recaptured from the adjacent ground off
St. Bees Head. Fish tagged in the St. Bees ground also returned
the next year with only 2.4% of recaptures recorded on the Great Orme
grounds. What is particularly relevant to the present work however,
is the behaviour of mature and immature plaice tagged by Macer in
Red Wharf Bay in November. About 50% of recaptures had travelled
south towards Cardigan Bay, Trevose Head and the Bristol Channel.
Macer concluded that both mature and immature plaice gather in Red
Wharf Bay in November, prior to migrating south, the mature ones to
spawn and the immature ones to recolonise the extreme south of the
geographical range of the species. Some spawning fish tagged in these
southern grounds were later recaptured in the northeast Irish Sea.
However, it was not possible to tell whether these were returned
migrants, or fish indigenous to the south on a feeding migration to
the north.

From the above it follows that the origins of a plaice caught in the study area cannot be ascertained. In the face of such difficulties, a simplistic assumption is made for the purposes of this study, namely that an equilibrium situation exists with the numbers of plaice in the study area remaining stable from year to year. As shown in Fig. 1.2 the composition of the catch does tend to remain unchanged with the modal length lying between 19-22 cm. The catch per hectare in each haul plotted against year (Fig. 1.3) shows no clear trend or sudden marked changes though the distribution within each year is skewed. A comparison of the geometric mean catch between years showed no significant differences at P = 0.05 (Appendix 1.2).

Some vital statistics of the plaice population

Between 1974 and 1977 trawls were made in the study area on board the R.V. Prince Madog at the end of October and the first week in November. The length composition of each catch was recorded and stratified samples were collected. For each fish in the stratified samples the following data was recorded:

(i) Length

(ii) Sex

(iii) Stage of gonad development. The key used was adapted from Wimpenny (1953).

(iv) Otoliths, for age determinations

(a) Population size. The size of the plaice stock in the study area was estimated by the area density method, utilising the data collected from the series of trawls mentioned above. For this purpose, it was necessary to estimate the area covered during each haul. The length of this area is the distance covered during the haul and was obtained from 'Decca Navigation' recordings made during each haul. The width of

Fig. 1.2. The percentage length frequency

of catches from the study area

1974 - 1977.
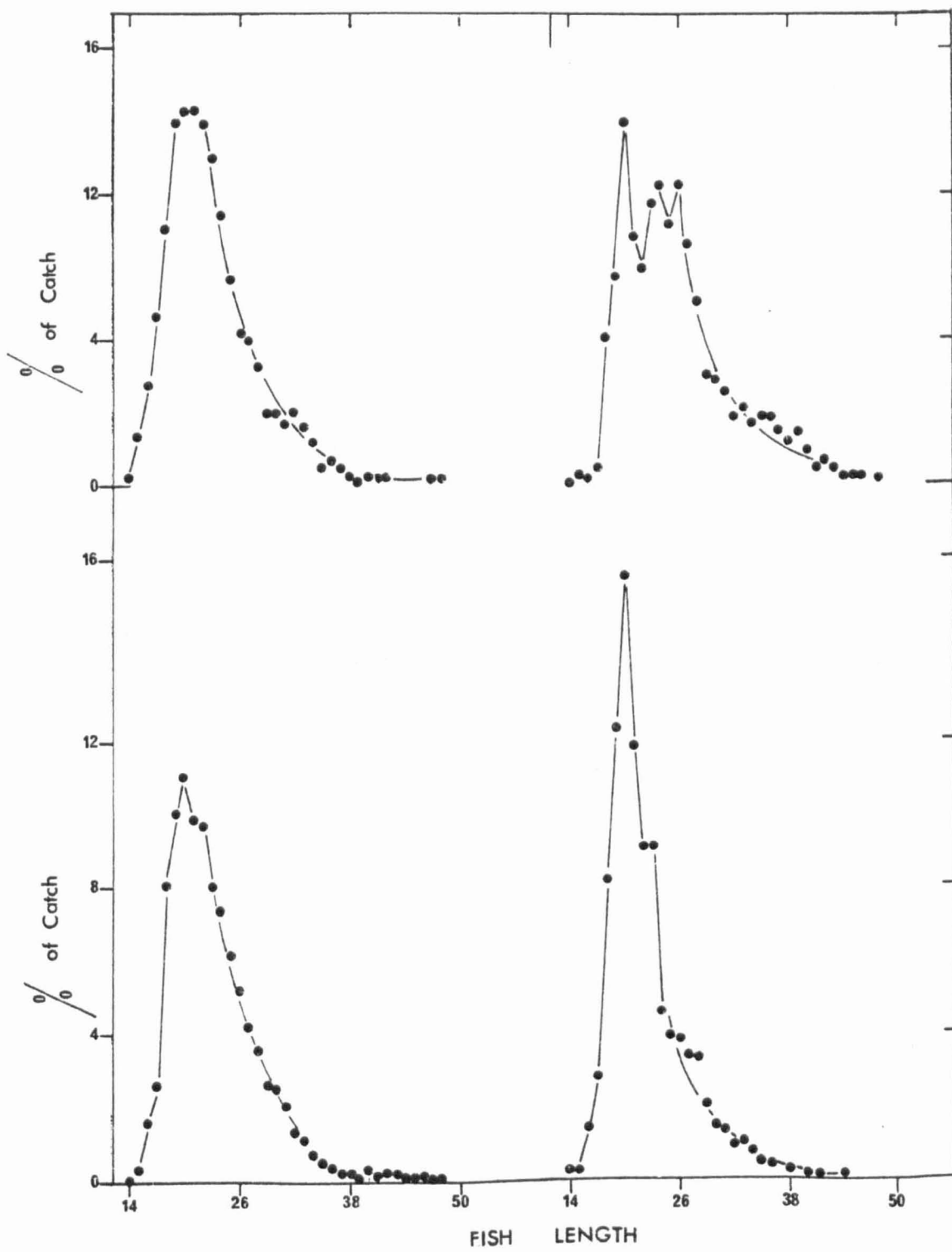
Fig. 1.3. The yearly distribution of catch

size 1974 - 1977.
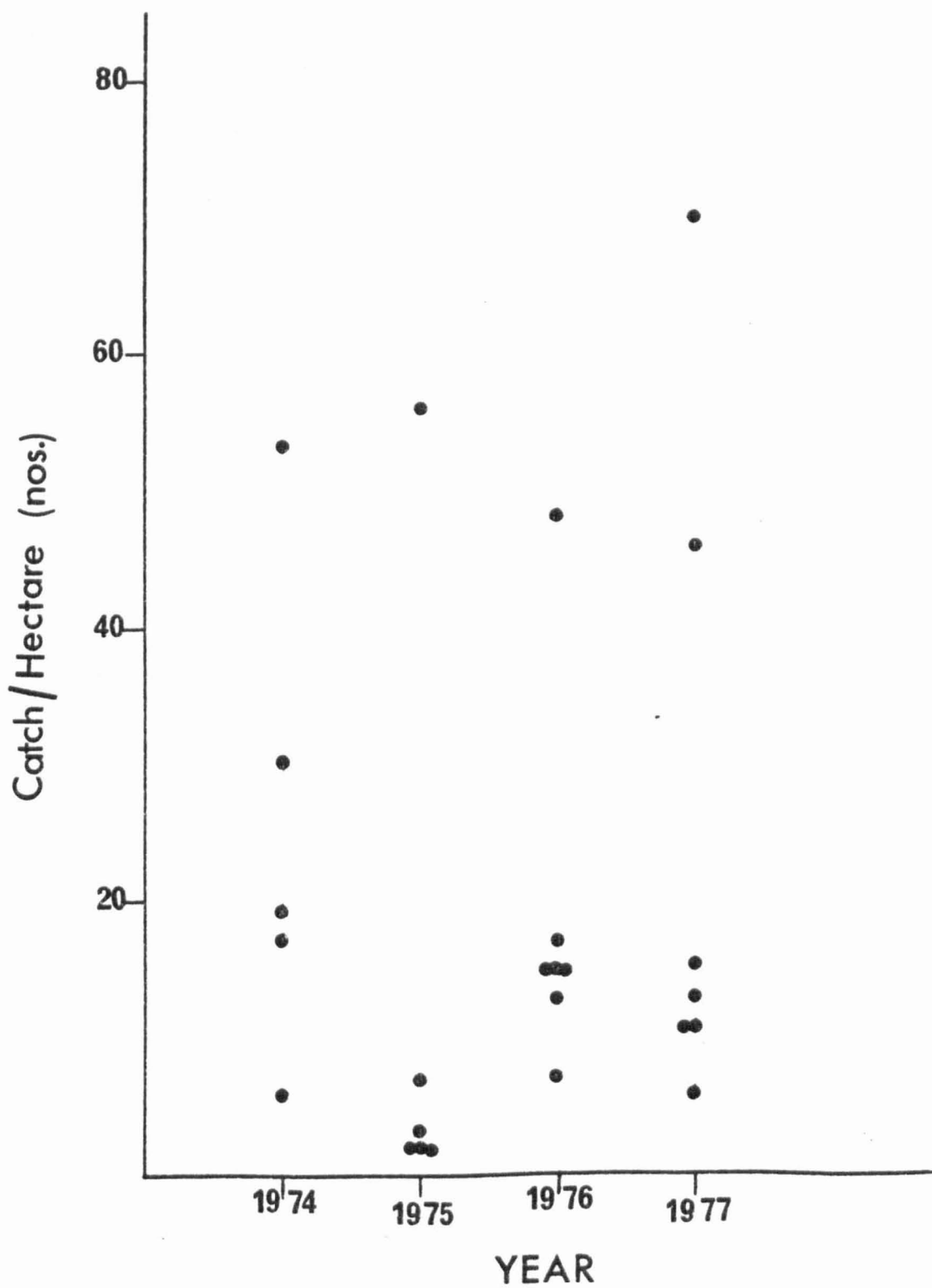
Table 1.a

Technical Data on the Fishing Gear

of the R.V. Prince Madog

Vessel	94' overall length, 182 tons
Doors	40" x 71"
Bridles	7.5 fathoms
Warps	Usually 4 x depth; 5 x depth for depths of 7 fathoms or less. Taken as 40 fathoms in Fig. 1.4.
Foot Rope	12 fathoms
Wing mesh	4"
Cod end mesh	2.9"

Length at 50% retention for plaice - 16.2 cm

(Selection factor for plaice = 1.2) Beverton and Holt (1957)

this area was taken as the distance between the trawl doors during fishing. As this distance could not be measured directly, it was estimated geometrically. The data necessary for this estimation plus other technical data of the fishing gear are given in Table 1.a. The trigonometric considerations involved are shown schematically in Fig. 1.4 and narrated in Appendix 1.3.

The area density method of estimating stock size is based on sample sizes collected from areas of equal size and to this end the catch from each haul has been expressed on a per/hectare basis. Details of the size and composition of each catch are contained in Appendix 1.1 and a synopsis is presented in Table 1.b. The estimated total population size N, is given by the expression

$$N = \frac{A}{a} \sum_{i=1}^{a} N_i \qquad \text{(Everhart, Eipper and Youngs, 1953)}$$

where A is the number of equal units occupied by the stock (hectares in this case), a is the number of equal units sampled, N_i is the number of fish in the ith sample.

As stated in Table 1.a the length of 50% retention was 16.2 cm. This means that almost all I-group fish and the smaller II-group fish are excluded from the estimate that follows.

Using the formula given above, the total stock of plaice was estimated at 478,630 fish. The variance of this estimate is given by the expression

$$V = \frac{A^2 - aA}{a} \left[\frac{a \sum_{i=1}^{a} N_i^2 - \left(\sum_{i=1}^{a} N_i \right)^2}{a(a-1)} \right]$$

$$V = 8.26 \times 10^9$$

Fig. 1.4. Estimating using trigonometry to estimate the distance between the trawl doors during fishing.

(i) DD' = distance between doors.

(ii) AB and A'B' = sides of the ship.

(iii) S and S' = shackler from which the warps leave the ship during trawling.

(iv) SD and S'D' = warps.
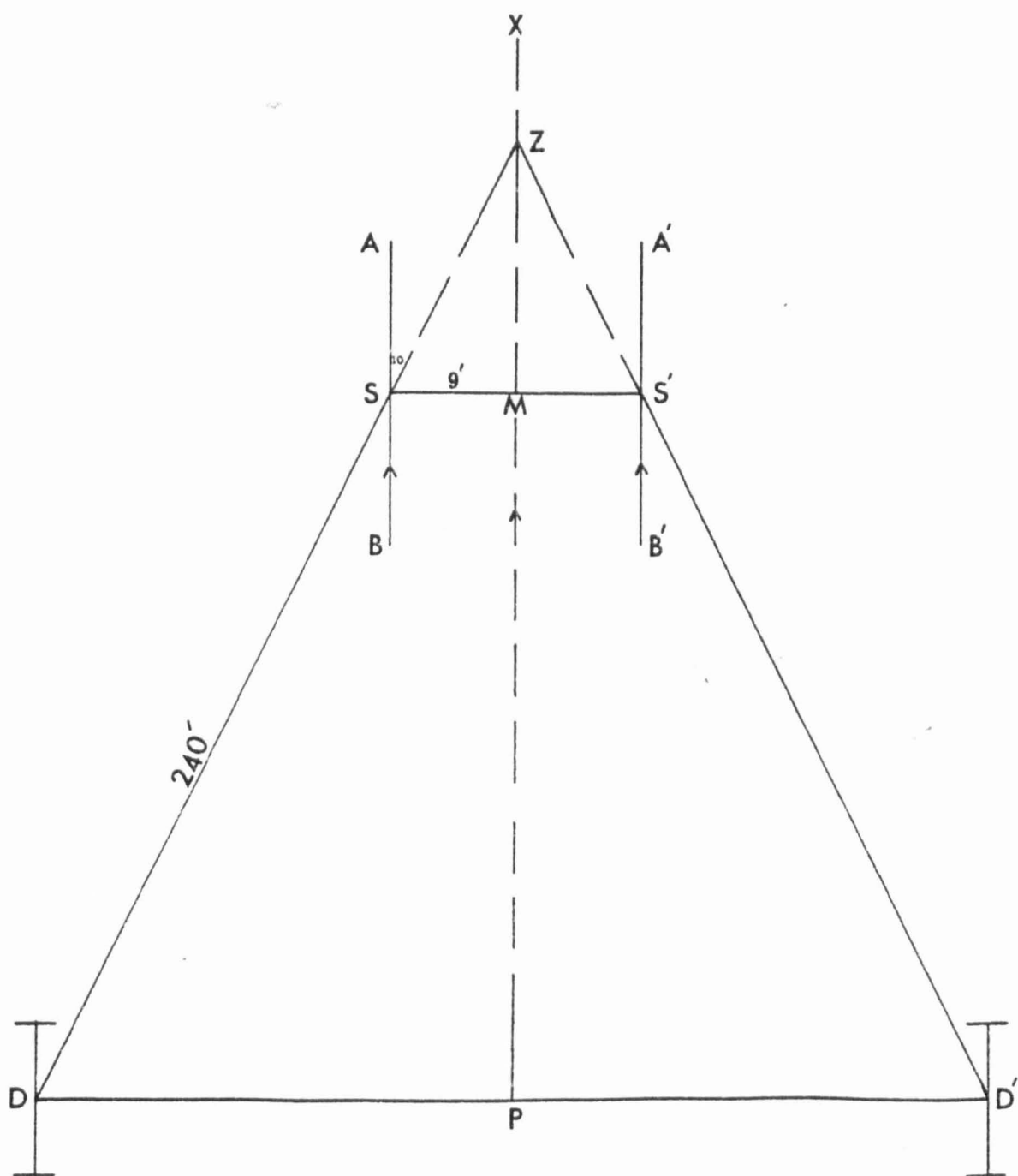
Table 1.b   <u>Summary of Catch Data</u>

Year	Haul	Catch/Hectare (Numbers)
1974	i	53.2
	ii	6.3
	iii	17.1
	iv	29.86
	v	19.60
1975	i	1.88
	ii	1.75
	iii	3.15
	iv	7.34
	v	56.35
	vi	2.17
1976	i	15.56
	ii	13.34
	iii	48.1
	iv	15.1
	v	15.1
	vi	7.2
	vii	17.82
1977	i	46.5
	ii	70.4
	iii	11.9
	iv	13.1
	v	6.2
	vi	15.3
	vii	11.1

The standard error of estimate is

$$v^{\frac{1}{2}} = 90901$$

Stock size = 478630 $\pm$ 90901 ($\pm$ 19%) fish

(b) Sex ratio. The stratified samples mentioned earlier were collected irrespective of sex and the sex ratio of these samples was taken to be representative of the combined catch from which they came. The sex ratio was found to vary with the size of the fish. As shown in Table 1.c male fish are generally more abundant amongst the smaller fish. This ratio is maintained up to length 28 cm after which the females become predominant rather suddenly. From 28 cm on, the male fish become less and less abundant and are not represented at 40 cm.

Table 1.c Sex ratio of Stratified Samples expressed as numbers
of males divided by numbers of females

Fish length (cm)	Numbers examined	Sex ratio
14	4	0.50
15	4	1.50
16	10	1.84
17	19	1.00
18	27	1.43
19	22	1.58
20	28	1.16
21	34	1.22
22	23	2.42
23	28	2.02
24	31	2.27
25	29	2.12
26	29	2.03
27	29	1.86
28	29	1.03
29	33	0.51
30	34	0.41
31	31	0.37
32	36	0.22
33	40	0.15
34	39	0.07
35	34	0.13
36	30	0.06
37	21	0.03
38	35	0.03
39	26	0.07
40	30	-

Total numbers examined = 735 fish

(c) Length at age. With some exceptions (e.g. the capelin, Mallotus vitatus), the females of teleost species tend to grow larger and live longer than the males. For this reason age determinations were made for males and females separately. These determinations were from otoliths extracted from fish of the stratified samples. The otoliths were immersed in xylene and examined under a low power binocular microscope with transmitted light.

Despite its widespread use, the method of ageing plaice by counting the opaque and hyaline bands of their otoliths is still not foolproof. Difficulties arise with older fish as the rings at the periphery tend to become crowded. The occurrence of split and sometimes spurious rings can also make interpretation difficult (see Plate 1). The incidence of 'difficult' otoliths can be a feature of particular populations and Lamont (1967) has suggested without much explanation, that for plaice in some areas along the Scottish coast, 'difficult' otoliths may be a density-dependent phenomenon.

In the present study the chief difficulty encountered was split rings, particularly in age groups IV to VI. In those cases where two otoliths from the same fish differed in detail, they were both rejected. The majority of older otoliths were remarkably easy to read. Where 'crowding' did occur of the outer edge, it proved useful to hold the otolith edge-wise onto the microscope stage and to rotate it slowly in an arc from left to right. In all over 1,500 pairs of otoliths were examined of which less than 5% were rejected.

Despite the abundance of published data on the growth of plaice, very few workers have treated the sexes separately though Beverton (1964) has pointed out that in some ways (e.g. catchability, size at age, longevity) the two sexes behave almost like two different species

Plate 1. Top: A remarkably legible otolith from an

XI$^+$ fish.

Magnification x 6.25.

Bottom: Two otoliths from different fish

showing split (?) and spurious (?) rings.

Magnification x 10.
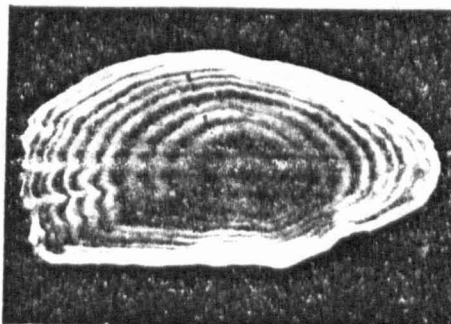
An otolith from an XI$^+$ fish, remarkably
legible with no crowding at the edge.
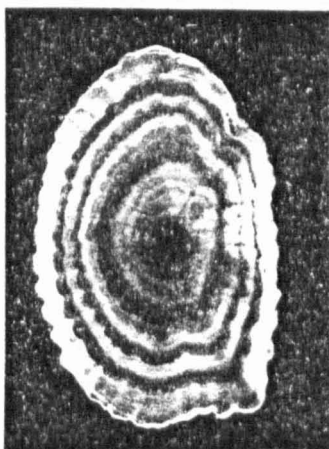
Two otoliths from different fish showing
a series of split (?) and spurious (?)
rings. Age estimates of otoliths of
this sort were regarded as probably
inaccurate and therefore unreliable.

in relation to fishery exploitation. Consideration of the data obtained
in the present work will therefore be mainly confined to comparison
with the data of the ICES Irish Sea Working Group of 1977 - Tables 1d
and 1e. This data was kindly made available by Dr. K.M. Brander of
MAFF Lowestoft.

Table 1.d   Length at Age Data for Female Plaice from the present
              work and from commercial catch samples of Irish Sea
              trawlers of various nationalities

Age Group	Belgian 1970-74	English & Welsh 1964-74	Irish 1962-66	Present Work 1974-77	
0		7.3	11.3		
1		15.3	18.2	19.74	1+1
2		21.0	23.2	25.12	2+1
3	31.1	26.8	31.5	29.57	3+1
4	33.8	31.7	34.0	33.99	
5	37.1	33.6	37.7	36.40	
6	39.3	35.9	39.9	38.65	
7	41.5	38.0	43.6	40.14	
8	43.7	39.1	45.6	41.59	
9	45.3	41.3		42.00	
10	46.8	44.1		42.93	
11	50.5	45.1			
12	50.6	48.3			
13	52.3	47.8			
14	52.5	51.0			
15	51.0	48.6			
16+		53.0			
L_∞		53.79		46.0	
K		0.18		0.25	
t_0		-0.61		-0.20	

              Data for age group 0 - 2 from
              research vessel samples

Table 1.e   Length at age data for male plaice from the present work
             and from commercial catch samples of Irish Sea trawlers
             of various nationalities

Age Group	Belgian 1970-74	English & Welsh 1964-74	Irish 1962-66	Present Work 1974-77	
0		7.3	11.1		
1		15.3	18.3	1++	19.35
2		21.0	22.8	2++	24.16
3	28.8	26.8	28.9	3++	27.48
4	31.4	29.7	31.4	4++	29.17
5	32.4	30.6	33.9	5++	30.34
6	32.8	31.2	35.6	6++	31.05
7	35.8	32.0			32.50
8	36.4	34.8			33.60
9	38.0	34.8			
10+		36.6			
L_∞		37.13			36.3
K		0.35			0.27
t_o		-0.27			-1.97

All These values are for 1 year later Than stated. i.e. 1++ 2++ 3++ etc.

Error.

Data for age group 0 - 2 from
research vessel samples

Tables 1.d and 1.e show that female plaice are larger than their
male counterparts of the same age. The length at age for each sex
varies between samples and it was pointed out in the ICES document
that this is primarily due to differences in the area being fished by
various trawlers. It appears that growth rates differ in the various
areas of the Irish Sea and that they are faster in the south and west
(Brander, 1977). The greater size at age obtained in this work for
ages I and II of both sexes is probably the result of mesh selection
(c.f. Table 1.a p. 7).

Fitting a Growth Equation to the Length at Age Data

The growth equation adopted here is that developed by Von
Bertalanffy (1934)   and used almost without exception in growth

studies of plaice. From this equation the length l, at age t, is given by

$$l_t = L_\infty \left[1 - e^{-K(t - t_0)} \right] \qquad \text{----------------} \quad (i)$$

where L_∞ is an asymptotic length achieved by an average fish if it continued to live and grow indefinitely, K is the rate at which L_∞ is approached, and t_0 is a constant representing a theoretical age at which length is zero.

To fit this expression to a body of data, it is necessary to evaluate the three parameters t_0, K and L_∞. Rough estimates of L_∞ can be obtained by use of the Ford-Walford-Brody method which is a graphical representation developed by Walford (1946) for the equation derived empirically by Ford (1933):-

$$l_{t+1} = L_\infty (1 - K) + Kl_t \qquad \text{------------------} \quad (ii)$$

where K is Ford's growth coefficient and is equal to e^{-K} in the Bertalanffy equation. A plot of l_{t+1} against l_t gives a line which cuts the $45°$ diagonal from the origin at a point which is the asymptotic length, i.e. where $l_t = l_{t+1}$. These plots, carried out separately for males and females are shown in Figs. 1.5M and 1.5F.

The provisional L_∞ value obtained from Fig. 1.5 can be used to estimate K, t_0 and a final value of L_∞ for each sex by taking natural logarithms of (i) and rearranging:-

$$\text{Log}_e (L_\infty - l_t) = \log_e L_\infty + Kt_0 - Kt \qquad \text{------------------} \quad (iii)$$

A graph of $\text{Log}_e (L_\infty - l_t)$ against t should therefore give a straight line of slope -K. This line also provides the value of t_0 since the intercept on the abscissa can be equated to $\log_e L_\infty + Kt_0$. The advantage of plotting $\log_e (L_\infty - l_t)$ against l_t is that it provides

Fig. 1.5 M A: Ford-Walford plot for male plaice.

B: plot of $\log_e (L_\infty - 1_t)$ vs t.

Solid circles are from the trial L_α

and do not give as good a fit as the

open circles derived from the final

L_∞.

Fig. 1.5 F A: Ford-Walford plot for female plaice.

B: plot of $\log_e (L_\infty - l_t)$ vs t.

Solid circles are from the trial L_α

and do not give as good a fit as the

open circles derived from the final

L_∞.
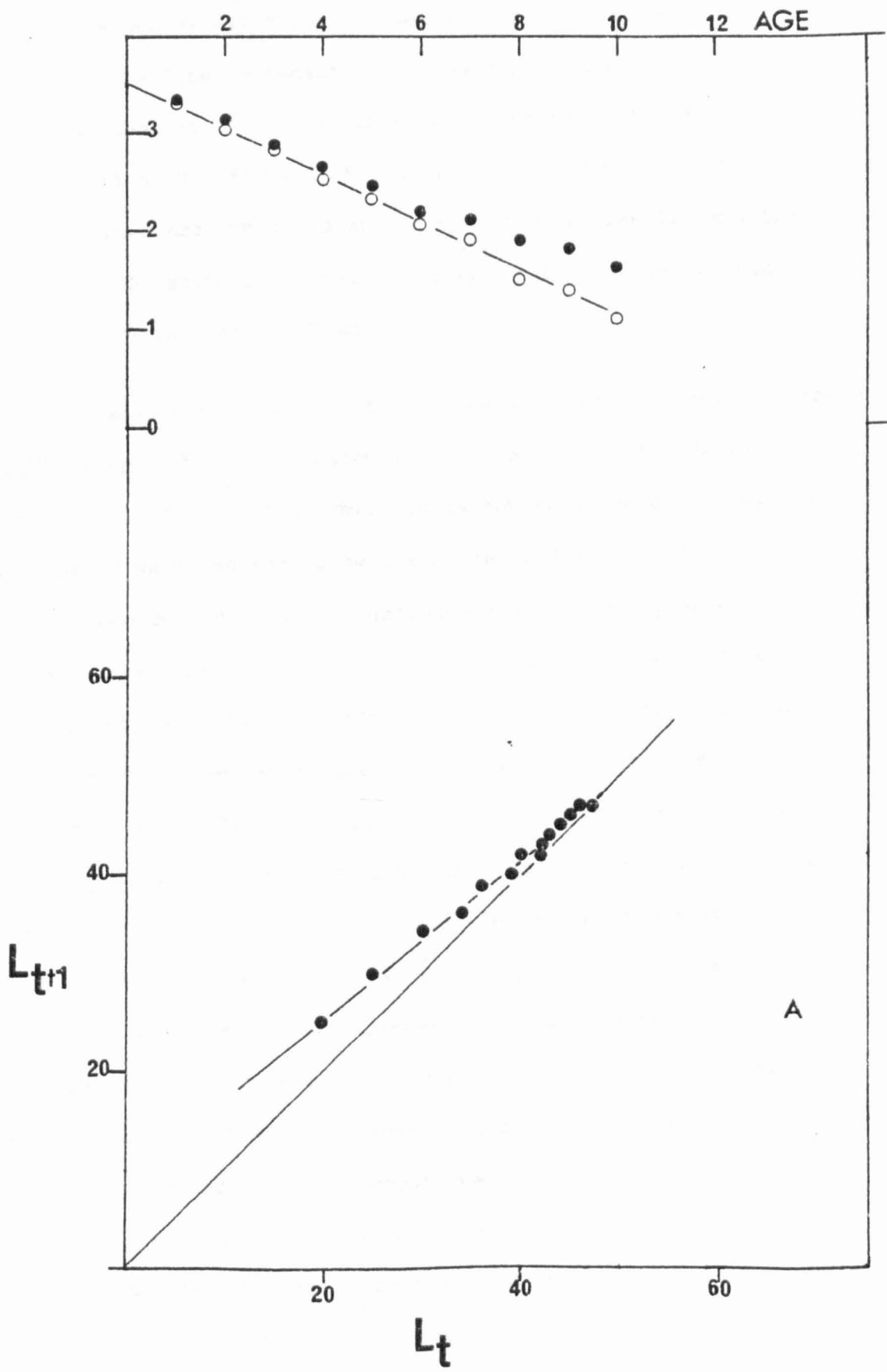
very accurate values of all three parameters. This is because the straightness of the line is sensitive to changes in the value of L_∞, allowing the L_∞ that fits the available data best to be found by graphical iteration (see Figs. 1.5M and 1.5F, and legends). The growth parameters obtained are contained at the bottom of Tables 1.d and 1.e together with ICES estimates. Their goodness of fit to the original data is shown in worksheets 1.1F and 1.1M.

For both sexes, the L_∞ values of the present study are less than those of the ICES group. This discrepancy is much larger in the females (17.69 cm) than in the males (1 cm). It is generally held that plaice move into deeper water as they grow larger (e.g. Heincke, 1913). In view of this, and considering the shallowness of the study area, the differences between the male values should perhaps have been higher. There are differences, however, between the ecology of the Irish Sea and that of the North Sea where the depth phenomenon was first observed. Much of the Irish Sea is floored with mobile impoverished sands (Rees et al., 1977) and the rich banks found in the deeper areas of the North Sea are absent. In the Irish Sea the benthos-rich areas occur much closer inshore where local topography provides enough shelter from prevailing winds and tidal currents to allow formation of the muddy sediments that can support rich benthic communities. As a result, it is possible that Irish Sea plaice remain in shallow coastal areas to a greater size than their North Sea counterparts. Indeed Bowers and Lee (1971) describe Laxey Bay on the Isle of Man as a feeding ground for plaice from which large mature individuals set out each year on spawning migrations. The same is probably true of Red Wharf and Beaumaris Bays.

Worksheet 1.1 F   Length at age data for female Plaice and the computations involved in determining the theoretical curves of length and weight at age

Age t (years)	No. of Fish	Observed Length l_t (cm)	Using Trial $L_\infty = 48$ $L_\infty - l_t$ (cm)	$Log_e(L_\infty - l_t)$	Using Final $L_\infty = 46$ $L_\infty - l_t$ (cm)	$Log_e(L_\infty - l_t)$	$t - t_o$ (years)	$K(t - t_o)$	$1 - e^{-K(t - t_o)}$	Calculated Length (cm)	Calculated weight $W_t = 0.0093 L_t^{3.11}$ (gms)
							1.2	0.30	0.259	11.91	20.63
1	164	19.74	28.26	3.34	26.26	3.27	2.2	0.55	0.423	19.46	95.00
2	205	25.12	22.38	3.13	20.28	3.04	3.2	0.80	0.551	25.33	215.67
3	155	29.57	18.43	2.91	16.43	2.80	4.2	1.05	0.650	29.90	361.26
4	111	33.99	14.01	2.64	12.01	2.49	5.2	1.30	0.728	33.46	512.58
5	96	36.40	11.60	2.45	9.60	2.26	6.2	1.55	0.788	36.24	656.99
6	63	38.65	9.35	2.24	7.35	2.00	7.2	1.80	0.835	38.40	786.60
7	37	40.14	7.86	2.06	5.86	1.77	8.2	2.05	0.871	40.08	898.65
8	32	41.59	6.41	1.86	4.41	1.48	9.2	2.30	0.900	41.39	993.18
9	23	42.00	6.0	1.79	4.00	1.39	10.2	2.55	0.922	42.41	1071.30
10	15	42.93	5.07	1.62	3.07	1.12	11.2	2.80	0.939	43.20	1134.59
11	7	43.85	4.				12.2	3.05	0.953	43.82	1186.00
12	7	45.00					13.2	3.33	0.964	44.35	1231.18
13	6	45.67					14.2	3.55	0.971	44.68	1259.90
14	3	46.67					15.2	3.80	0.978	44.97	1285.50
15	1	47.00					16.2	4.05	0.983	45.20	1306.06

$$t_o = -1.2 \text{ years}$$
$$K = 0.25$$

Worksheet 1.1 M   Length at age data for male Plaice and the computations involved in determining the theoretical curve of length, and weight, at age

Age t (years)	No. of Fish	Observed Length (cm)	Using Trial $L_\infty=35.3$		Using Final $L_\infty=36.3$		$t-t_o$ (years)	$K(t-t_o)$	$1-e^{-K(t-t_o)}$	Calculated Length (cm)	Calculated Weight $Wt = 0.0241_t{}^{2.8}$ (gms)
			$L_\infty-l_t$ (cm)	$Log_e(L_\infty-l_t)$	$L_\infty-l_t$ (cm)	$Log_e(L_\infty-l_t)$					
							1.97	0.53	0.411	14.93	46.51
1	173	19.35	15.95	2.77	16.95	2.83	2.97	0.80	0.551	19.99	105.31
2	200	24.16	11.14	2.41	12.14	2.50	3.97	1.07	0.657	23.85	172.65
3	131	27.48	7.82	2.06	8.82	2.18	4.97	1.34	0.738	26.80	239.33
4	48	29.17	6.13	1.81	7.13	1.96	5.97	1.61	0.800	29.04	299.64
5	29	30.34	4.96	1.60	5.96	1.79	6.97	1.88	0.847	30.76	352.03
6	18	31.05	4.25	1.45	5.25	1.66	7.97	2.15	0.884	32.07	395.63
7	8	32.50	2.80	1.03	3.80	1.34	8.97	2.42	0.911	33.07	431.15
8	5	33.60	1.70	0.53	2.70	0.99	9.97	2.69	0.932	33.84	459.85
9	4	32.30					10.97	2.96	0.948	34.42	482.26
10	2	35.00					11.97	3.23	0.960	34.86	499.72

$t_o = -1.97$

$K = 0.27$

(d) <u>Mortality Rates</u>. The instantaneous coefficient of total mortality of males and females were estimated separately using a simple catch curve. As the same vessel and gear was used throughout, the area fished unchanged, and each haul lasted about 1 hour, the total catch for 1974-1977 was used for these curves. In effort units this could be expressed as catch per 25 Madog hours (a total of 25 hauls were taken). Plots of the natural logarithm of numbers at age against age are given in Figs. 1.6M and 1.6F.

Though a straight line has been fitted to Fig. 1.6M and F, they are both really curves. A concave catch curve may be the result of one or more of a number of factors. An increase in fishing effort recent enough to allow the older age-groups to reflect the earlier mortality rate will result in a catch curve with a descending line that gets progressively flatter as the older age-groups are approached. A second possibility is an immigration of large fish into the fished area with or without emigration of younger individuals. Earlier in this chapter it was pointed out that larger plaice in the Irish Sea may move into shallow areas on feeding forays. It is also worthwhile to recall the findings of Macer (1972) on the movements of tagged plaice in the Irish Sea: there was immigration of large plaice into the study area in preparation for a southward spawning migration. This occurred in November which is the time of year when the samples for the present work were collected. A third possibility arises from the demonstration by Cushing (1975) that natural mortality of plaice decreases with age. He points out, however, that this may only be noticeable when the population is either unexploited or very lightly fished so that enough survivors get to the older ages for the phenomenon to become apparent. Of the

Fig. 1.6 M   Catch curve for male plaice.

$\log_e N_t$ vs   t

Dashed line shows the decline in

mortality with age. The solid line is

a least squares line. Age 0 and I were

regarded as still in the pre-

recruitment phase and were excluded

from the regression.

$Z = 0.98$

$Z = 62 \cdot 5 \%$ per annum
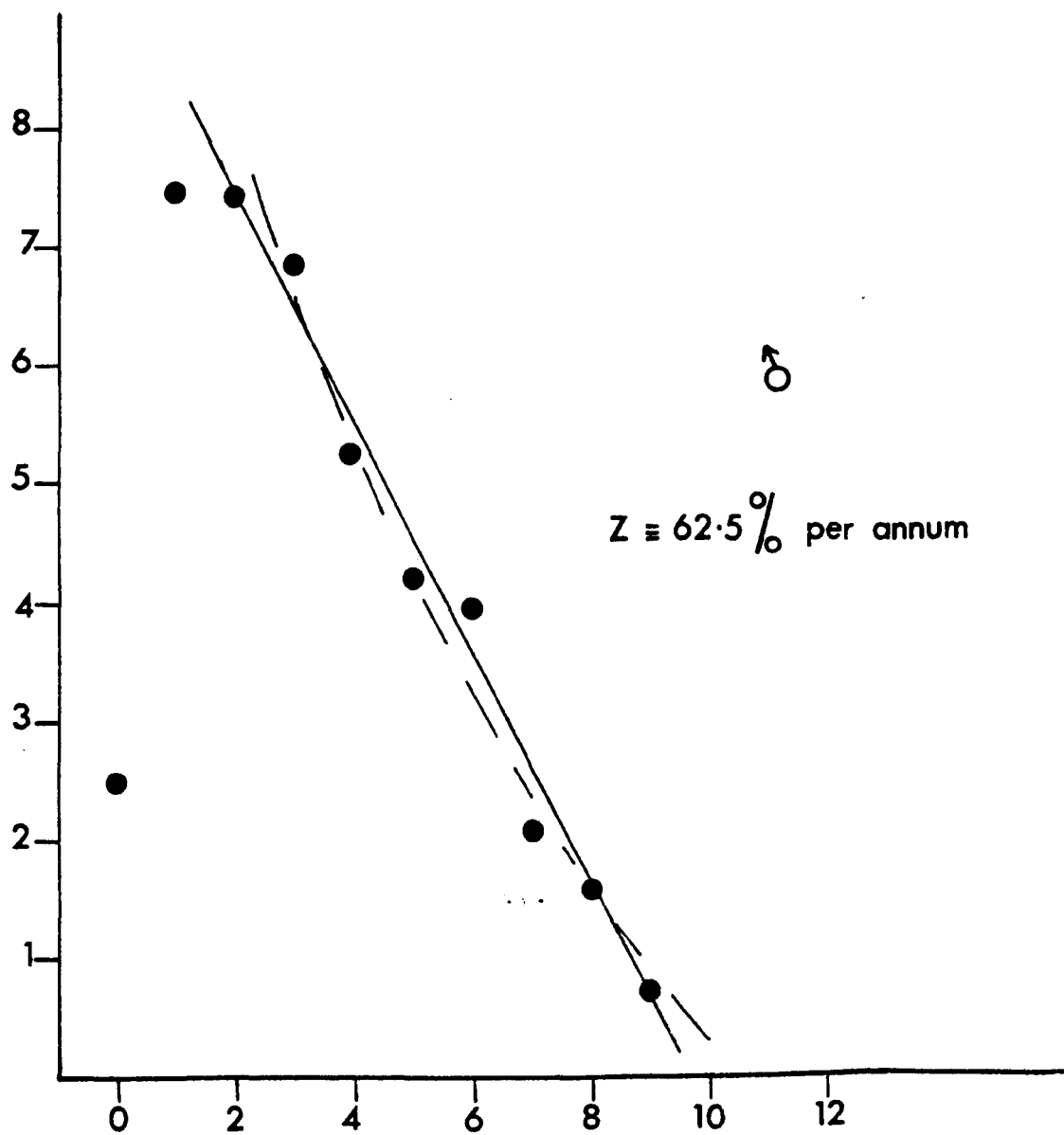
Fig. 1.6 F Catch curve for female plaice

$\log_e N_t$ vs t

Dashed line shows the decline in

mortality with age. The solid

line is a least squares line. Age

0 and I were regarded as still in

the pre-recruitment phase and were

excluded from the regression.

$Z = 0.65$

$Z = 47.9 \%$ per annum
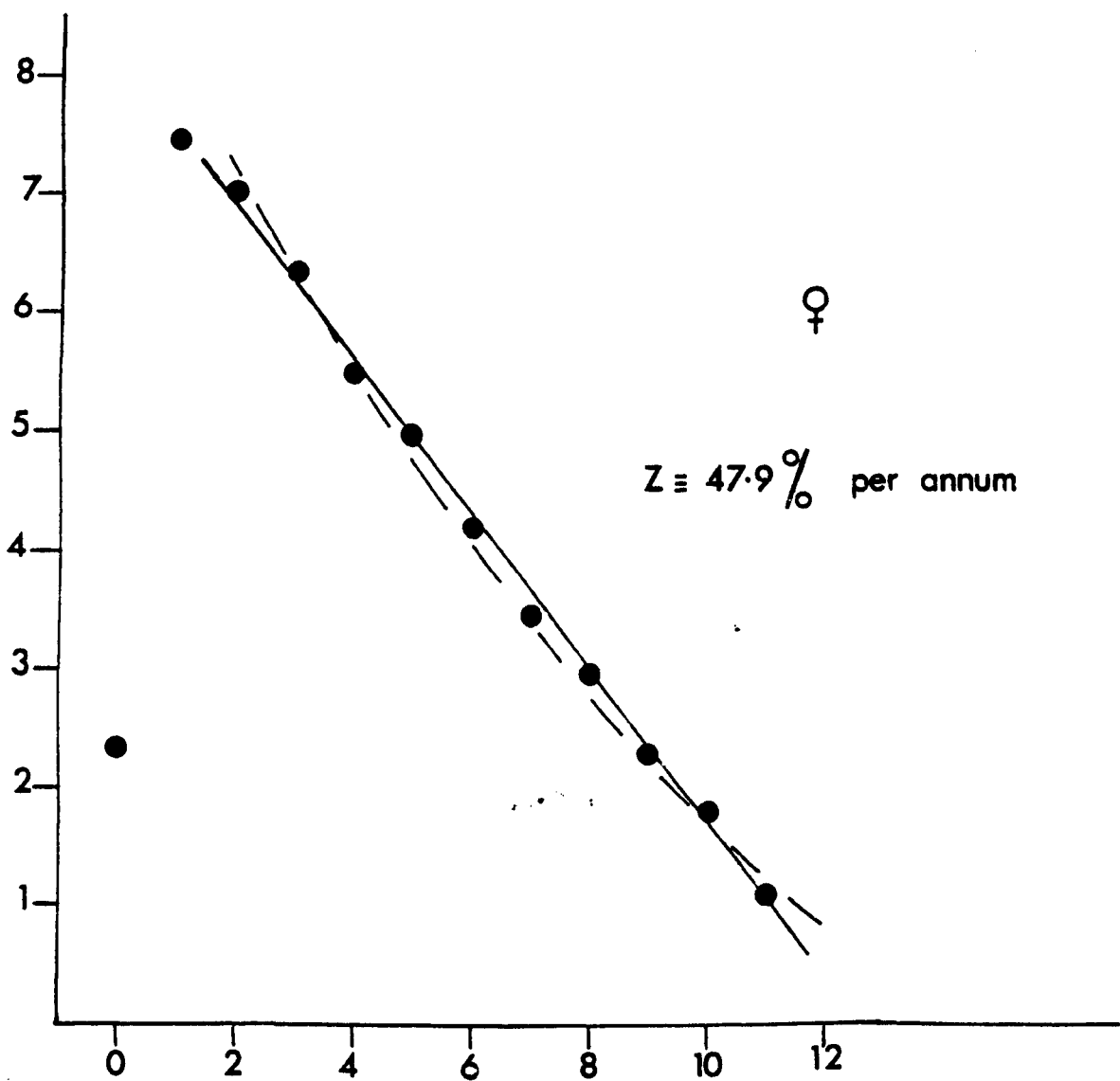
other two possibilities, the more likely is the annual immigration of
larger fish into the study area.

The calculated slopes of Figs. 1.6M and F show male mortality to be
much higher than female mortality. These slopes have been compared
statistically and found to be significantly different at $P_{0.05}$
(Appendix 1.5). The greater mortality amongst males is curious when
it is recalled that they have a smaller size at age and therefore must
enter the exploited phase later. Perhaps this is offset by their greater
catchability (Beverton, 1964) and greater natural mortality (Beverton
and Holt, 1957).

(e) <u>Age and Length at Maturity</u>. Data for this aspect of the study also
came from observations made on the specimens of the stratified samples.
Figs. 1.7M and F show the percentage of fish mature at 1 cm intervals
for males and females. For both sexes the data approximate a sigmoid
curve. The length at which 50% of the fish become mature, LM_{50}, has
been calculated using the LD_{50} procedure (Bliss, 1935a and b) as applied
by Fleming (1960) to maturity of cod off Labrador and Newfoundland.
(This method was originally devised to assess the effects of varying
doses of poisons on test animals).

The first step in this process is to transform the % mature at each
length to a probit value. A probit is the distance from the mean of a
normal curve to a given point, divided by the standard deviation with 5
added to make all the numbers positive. Therefore the mean of a normal
curve has a probit of 5. Conversion of percentage to probits is done
by means of Table IX of Fisher and Yates (1948). These probits are
regarded as empirical probits. When plotted against the relevant length
they give a provisional line from which new predicted probits can be

Fig. 1.7 M Maturity data for male plaice.

The sigmoid curve was fitted by

eye and shows the percentage

mature at each length. The top

plot is an empirical probit

transformation of the sigmoid

curve (see text p. 19).
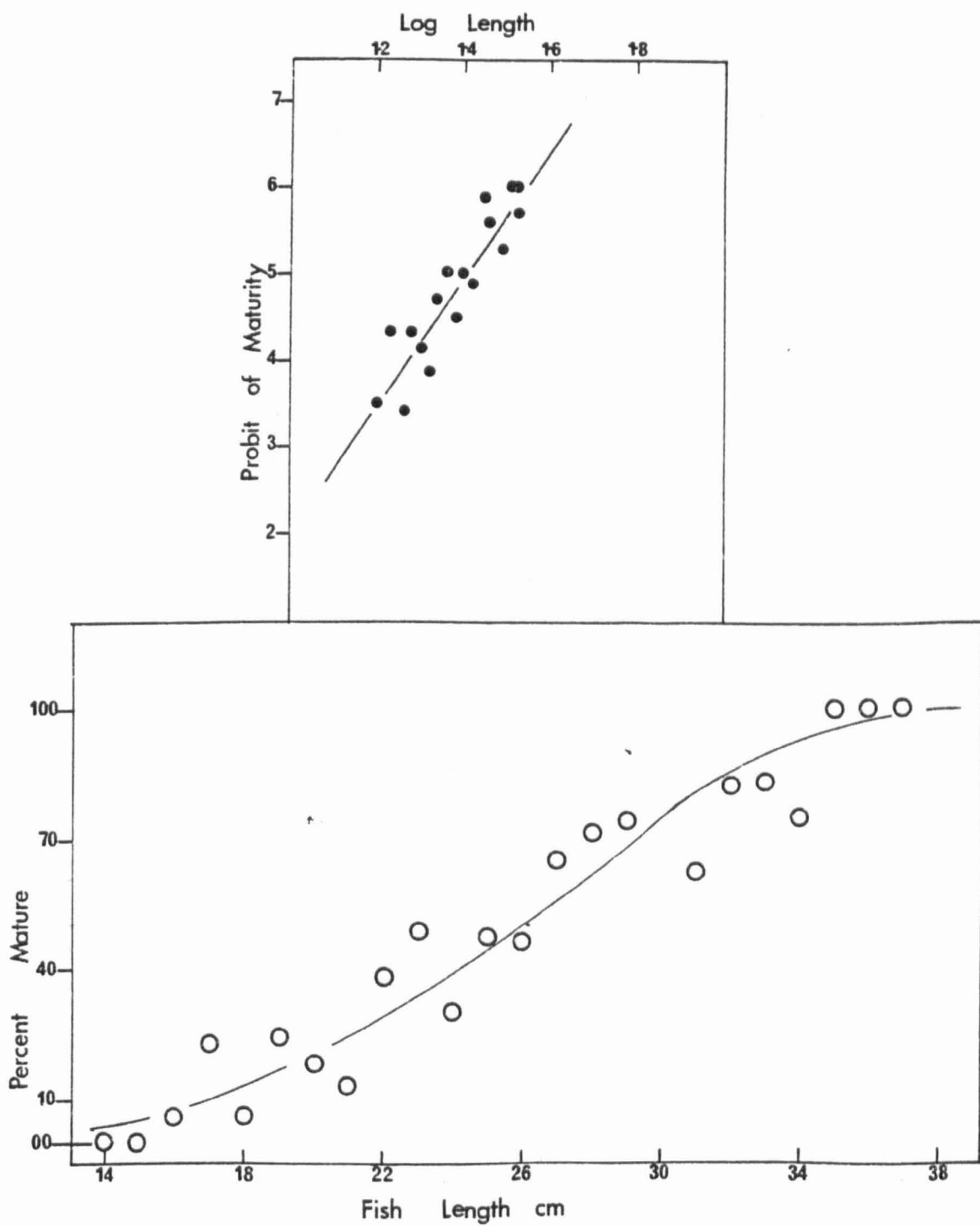
Fig. 1.7 F Maturity data for female plaice.

The sigmoid curve was fitted by

eye and shows the percentage

mature at each length. The top

plot is an empirical probit transformation

of the sigmoid curve (see p. 19   ).
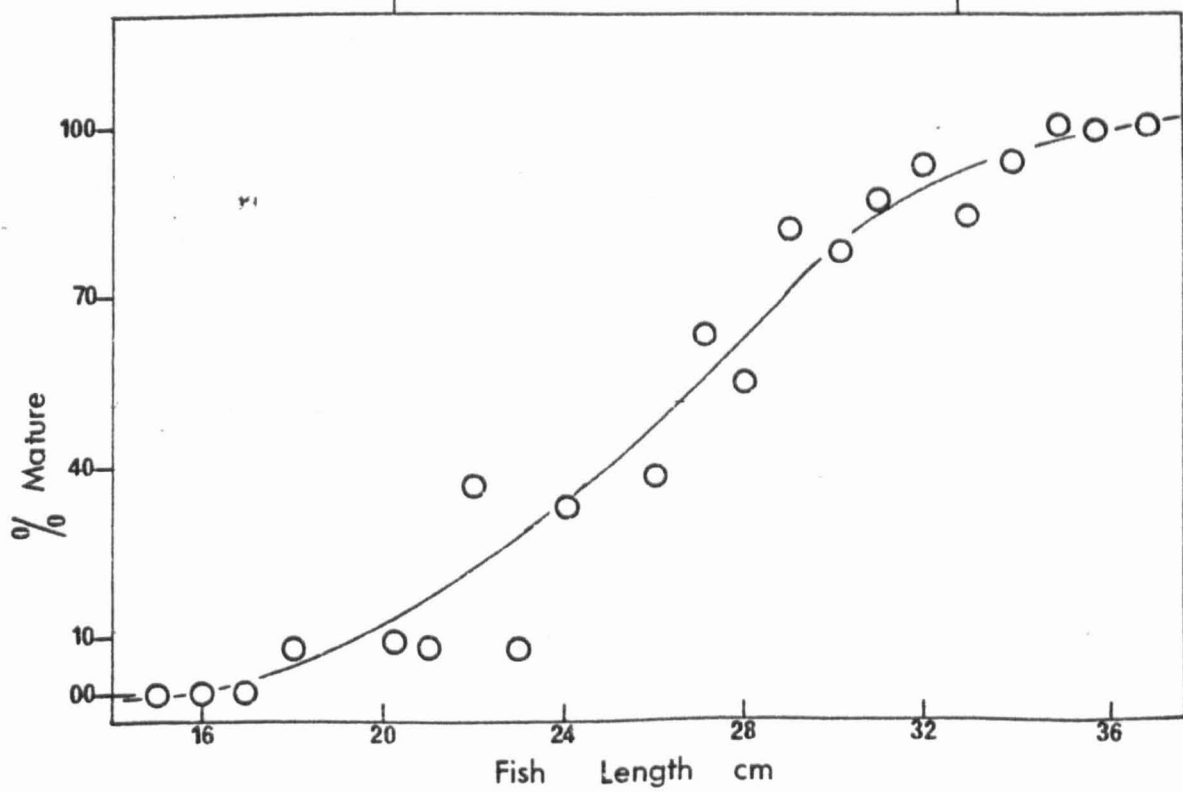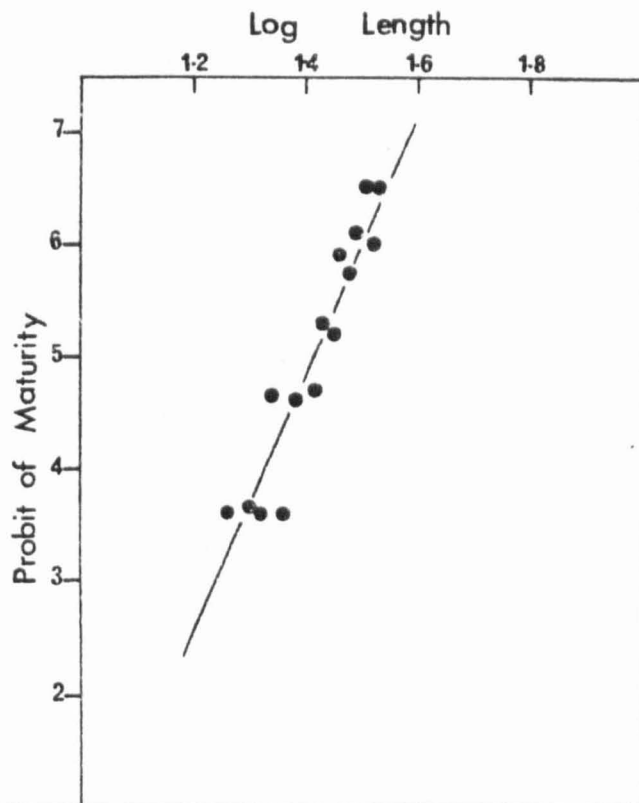
Worksheet 1.2 Computation for fitting a line to data on the development of sexual maturity with length in female Plaice

			Data for Provisional Line			Computation of Weighted Line				Intermediate Products	
Length	Log Length X	No. of Fish N	Percent Mature P	Percent Immature Q	Empirical Probit	Expected Probit	Weighting Coefficient C	Weight W = C x N	Working Probit y	WX	WY
17	1.23	15	0.00	100.00		2.81	0.09179	1.377	2.41	1.69	3.32
18	1.26	12	8.33	91.67	3.62	3.17	0.17994	2.159	3.80	2.72	8.20
19	1.28	9	0.00	100.00		3.41	0.23753	2.138	2.91		6.22
20	1.30	11	9.09	90.91	3.65	3.65	0.33589	3.695	3.67	4.80	13.56
21	1.32	24	8.33	91.67	3.89	3.89	0.40474	9.714	3.66	12.84	35.55
22	1.34	11	36.36	63.64	4.13	4.13	0.47144	5.186	4.78	6.96	24.79
23	1.35	13	7.69	92.31	4.37	4.37	0.55788	7.252	3.81	9.88	27.63
24	1.38	12	33.33	66.67	4.60	4.60	0.60052	7.206	4.57	9.95	32.93
25	1.40	7	0.0	100.00		4.84	0.62742	4.392	6.25	6.15	27.45
26	1.42	8	37.50	62.50	5.08	5.08	0.63431	5.075	4.69	7.18	23.80
27	1.43	8	62.50	37.50	5.20	5.20	0.62742	5.019	5.32	7.18	26.70
28	1.45	16	56.25	43.75	5.44	5.44	0.60052	9.608	5.15	13.90	49.48
29	1.46	11	81.82	18.18	5.56	5.56	0.55788	6.137	5.88	8.98	36.09
30	1.48	22	77.27	22.73	5.76	5.76	0.50260	11.057	5.90	16.33	65.24
31	1.49	23	86.96	13.04	5.92	5.92	0.47144	10.843	6.10	16.17	66.14
32	1.51	30	93.33	6.67	6.15	6.15	0.37031	11.109	6.45	16.72	71.65
33	1.52	33	84.84	15.16	6.39	6.39	0.30199	9.966	5.93	15.13	'59.10
34	1.53	30	93.33	6.67	6.42	6.42	0.30199	9.060	6.49	13.88	58.80
35	1.54	25	100.00	0.00		6.51	0.26907	6.727	7.06	10.36	47.49

$$\Sigma W = 127.72$$
$$\Sigma WX = 183.56$$
$$\bar{x} = \Sigma WX/\Sigma W = 1.44$$
$$\Sigma WY = 684.14$$
$$\bar{y} = \Sigma WY/\Sigma W = 5.36$$
$$\Sigma WX^2 = 264.84$$
$$\Sigma WXY = 993.84$$
$$\Sigma WY^2 = 3821.57$$
$$A = \Sigma WX^2 - \bar{x}\Sigma WX = 0.5136$$
$$B = \Sigma WXY - \bar{x}\Sigma WY = 8.6784$$
$$C = \Sigma WY^2 - \bar{y}\Sigma WY = 154.5796$$
$$\text{Slope} = m = B/A = 16.897$$

Age at 50% Maturity = Length $AM_{50} = \bar{x} + \dfrac{(5.0 - \bar{y})}{m} = 1.419 = 26.2$ cm

Variance = $V = \dfrac{1}{m^2}\left[\dfrac{1}{\Sigma W} + \dfrac{(M_{50} - \bar{x})^2}{A}\right] = 3 \times 10^{-5}$

Standard Error = $\sqrt{V} = 5.5 \times 10^{-3} = \underline{1.01 \text{ cm}}$

X^2 for goodness of fit of weighted line = $X^2 = C - mB = 7.94$

d.f. = 11 - 2 = 9

Standard Error of $m = \sqrt{\dfrac{X^2}{nA}} = 1.966$

Equation of weighted line: $Y_c = \bar{y} + m(x - \bar{x}) = \underline{16.897x - 18.972}$

obtained for each length. These expected probits are then used in the computation of a new line.

A working probit y is obtained from each expected probit as follows: when the expected probit is less than 5 the working probit y is given by the minimum working probit plus the correction factor. The correction factor equals the proportion of mature fish (P) x Range. When the expected probit is 5.0 or greater the working probit is given by the maximum working probit minus the correction factor. The correction factor here is the proportion of immature fish Q x Range. Values of maximum and minimum working probits and their range are contained in Table XI, Fisher and Yates (1948).

In using the working probits y to compute the new line, weighting coefficients can be found for each expected probit value (Table XI, Fisher and Yates, 1948). These weighting coefficients (c) multiplied by the number of fish examined at each length provide a relative weight (w) which can be assigned to each point on the line. Worksheet 1.2 gives a worked-out example for the data on female plaice.

The chi square test is used to test the goodness of fit of the computed line at a level of $P_{0.05}$ (Fleming, 1960). The significance of this statistic depends on the number of degrees of freedom allowed. Of the total allowed, one degree is lost in establishing the slope of the line and another in establishing its position (Bliss, 1935a). Small expected values have been combined at either end when calculating the total number of degrees of freedom allowed for each distribution.

Tables 1.f and 1.g give a summary of the results obtained from the probit analysis of length and age at maturity data for both sexes. P_c values at 10 and below and at 90 and above have been combined at either end in assigning the total number of degrees of freedom

Table 1.f   The expected numbers of mature male and female fish at each age, from computed lines

	Age	\multicolumn{3}{c}{Original Data}		\multicolumn{4}{c}{Data from computed line}	
		No. of Fish	No. of Matures	Percent Mature		Probit Y_c	Percent Mature P_c	No. of Matures	Degrees of Freedom	
FEMALES	1	50	0	0.00		3.91	13.70	6.85	1	
	2	94	37	39.36		4.70	38.20	35.91	1	Weighted line $Y_c = 0.795x + 3.11$
	3	98	74	75.51		5.50	69.00	67.62	1	
	4	67	61	91.04		6.29	90.10	60.37		$AM_{50} = 2.38 \pm 0.096$ years
	5	55	55	100.00		7.09	98.16	53.99		
	6	48	47	97.92		7.88	99.80	47.90	1	$x^2 = 9.03$
	7	30	30	100.00		8.68	100.00	30.00		d.f. $= 4 - 2 = 2$ (x^2 for $P_{0.05} = 5.99$)
MALES	1	90	18	20.00		4.27	23.2	20.08	1	Weighted line $Y_c = 0.503x + 3.763$
	2	113	49	43.36		4.77	40.9	46.22	1	
	3	60	39	65.00		5.27	60.7	36.42	1	$AM_{50} = 2.46 \pm 0.16$ years
	4	18	13	72.22		5.78	78.1	14.06	1	
	5	7	6	85.71		6.28	89.9	6.29	1	$x^2 - 2.69$
	6	15	14	93.33		6.78	96.2	14.43		
	7	2	2	100.00		7.28	98.9	1.98	1	d.f. $= 6 - 2 = 4$ x^2 for $P_{0.05} - 9.488$

Table 1.g F — The expected number of mature fish at each length from the computed line (Females)

Length	No. of Fish	No. of Matures	Percent Mature	Probit Y_c	Percent Mature P_c	No. of Matures E_c	Degrees of Freedom n
	Original Data			Data from Computed Line			
17	15	0	0.00	1.82	0.1	0.02	
18	12	1	8.33	2.24	0.3	0.04	
19	9	0	0.00	2.64	0.9	0.08	1
20	11	1	9.09	3.01	2.3	0.25	
21	24	2	8.33	3.37	5.1	1.22	
22	11	4	36.36	3.71	9.9	1.09	
23	13	1	7.69	4.04	16.8	2.18	1
24	12	4	33.33	4.35	25.7	3.08	1
25	7	0	0.00	4.65	36.3	2.54	1
26	8	3	37.50	4.94	47.4	3.79	1
27	8	5	62.50	5.21	58.4	4.70	1
28	16	9	56.25	5.48	68.4	10.90	1
29	11	9	81.82	5.74	77.0	8.50	1
30	22	17	77.27	5.99	83.8	18.44	1
31	23	20	86.96	6.23	89.0	20.47	1
32	30	28	93.33	6.46	92.8	27.84	
33	33	28	84.84	6.69	95.4	31.48	1
34	30	28	93.33	6.91	97.1	29.13	
35	25	25	100.00	7.12	98.3	24.16	

Weighted Line = Y_c = 16.897x - 18.972

LM_{50} = 26.2 ± 1.01 cm

x^2 = 7.94

d.f. = n-2 = 11 - 2 = 9; x^2 for P_{05} = 19.688

Table 1.g M — The expected number of mature fish at each length from the computed line (Males)

Length	No. of Fish	No. of Matures	Percent Mature	Probit Y_c	Percent Mature P_c	No. of Matures	Degrees of Freedom
	Original Data			Data from Computed Line			
15	15	0	0.00	3.90	13.4	2.01	1
16	16	1	6.25	4.03	16.5	2.64	1
17	13	3	23.08	4.16	20.0	2.60	1
18	17	1	5.68	4.27	23.3	3.96	1
19	17	4	23.53	4.39	27.0	7.43	1
20	11	2	18.18	4.49	30.7	3.37	1
21	16	2	12.50	4.60	34.3	5.49	1
22	24	9	37.50	4.69	37.9	9.10	1
23	21	10	47.62	4.79	41.5	8.72	1
24	27	8	29.63	4.88	45.0	12.15	1
25	19	9	47.37	4.96	48.3	9.18	1
26	33		45.45	5.04	51.7	17.06	1
27	26	17	65.39	5.12	54.8	14.25	1
28	25	18	72.00	5.20	57.8	14.45	1
29	19	14	73.68	5.27	60.0	11.51	1
30	9	9	0.00	5.34	63.3	5.70	1
31	8	6	62.50	5.41	65.5	5.24	1
32	6	5	83.33	5.48	68.3	4.10	1
33	6	5	83.33	5.54	70.5	4.23	1
34	4	3	75.00	5.61	72.6	2.90	1
35	7	7	100.00	5.66	74.6	5.22	1

Weighted Line = Y_c = 4.807x - 1.76

LM_{50} = 25.51 ± 1.04 cm

x^2 = 22.22

d.f. = n-2 = 21 - 2 = 19. x^2 for $P_{0.05}$ = 30.14

allowed in each case.

Like the length at age data, these results show a marked difference between males and females. Though the LM_{50} values are within a centimetre of each other, male fish become mature at a smaller size than female fish. The computed lines show 20% of males mature at 17 cm while only 0.1% of females are mature at this length. The fact that the LM_{50} values are so close means that when the females start to mature in significant proportions (around 23 cm) these proportions increase much faster with size than in the males. Compared statistically the slope of the fitted lines show a significant difference at $P_{0.05}$.

The same features are shown by the age data. At age 1 the fitted line gives 23.2% of males as mature, almost twice the proportion of females at the same age. The AM_{50} values are comparable and again their steeper slope allows the females to catch up with the males at the 50% point.

The interesting outcome of these differences in slope and intercept between males and females is that while a young or small male fish is more likely to be mature than a female fish of comparable age and size, it is also easier to find an older and larger immature fish amongst the males than amongst the females (see the values of Tables 1.f to 1.g).

CHAPTER 2

Diet and Feeding Chronology of the Plaice

Population.

MATERIALS AND METHODS

Data on diurnal changes in stomach contents were obtained from fish collected by trawling at known intervals (usually every three hours) during a twenty-four hour period.   Such trawls were carried out in March, May, August and November 1976, and in February 1977.   The trawls were randomly distributed over the study area and each catch was sorted into the following size-groups:

$$15 \quad - \quad 19.4 \text{ cm} \quad \text{(smalls)}$$

$$19.5 \quad - \quad 2\mathbf{5}.4 \text{ cm} \quad \text{(mediums)}$$

$$30 \quad - \quad 35 \text{ cm} \quad \text{(large)}$$

The following data was recorded for each size-group:

(i)   Total numbers of stomachs sampled - a maximum of twenty whenever the size of the catch allowed.

(ii)   The number of empty stomachs in (i).

Stomach contents were frozen on board and taken back to the laboratory for further analysis according to the following scheme:

Laboratory Analysis of Stomach Contents

Frozen stomach contents
|
Volume
(Displacement of 10% formalin)
|
Diet composition*
|
Dry weight
(Dried in oven to constant weight at 60°C)
|
Subsamples

Ash weight
(12 hours in muffle furnace at 600°C)

Caloric content**
(Combusted in bomb calorimeter at 20 atm. O_2)
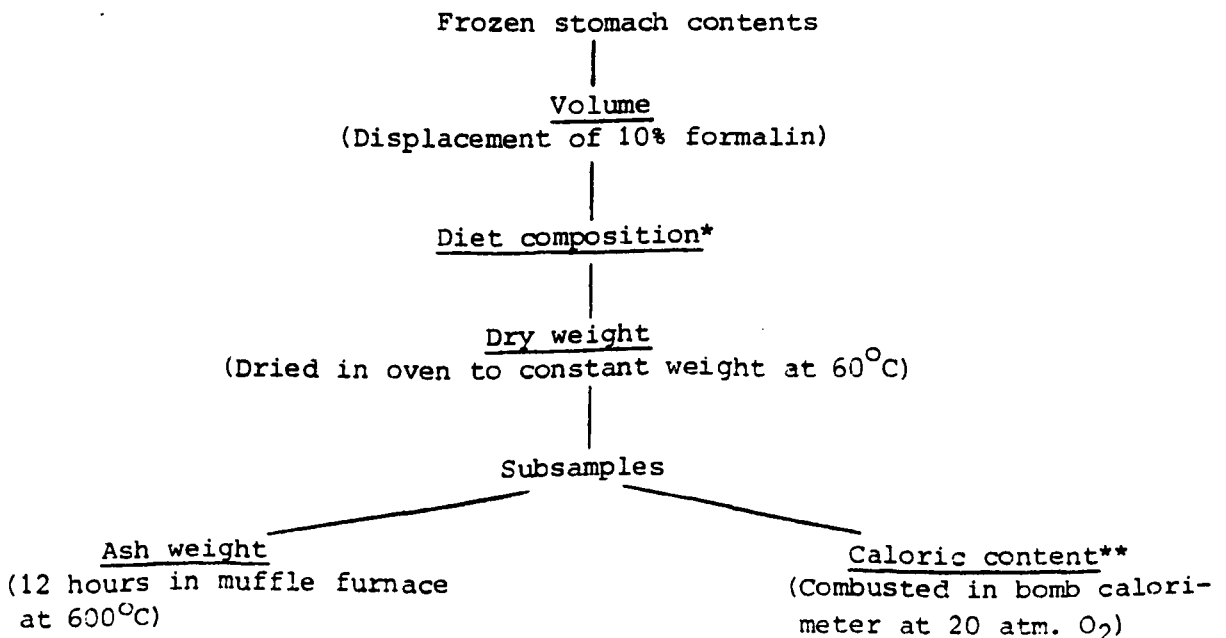
* The composition of each subsample was established by counting the numbers of each prey species present. These numbers were later converted to wet and dry weights (including shells) by use of a numbers/weight relationship obtained for the more important prey species from benthic samples.

** The bomb calorimeter used was a Gallenkamp Ballistic Bomb Calorimeter calibrated periodically with benzoic acid (1 gm benzoic acid $\equiv$ 6319 calories).

Preliminary analysis of the data collected in March 1976 revealed that recording only the percentage of empty stomachs at various times of day did not provide sufficient data for a detailed and comprehensive description of daily feeding chronology. As a result, an extended scheme was adopted which recorded the percentage of fish containing food in specific regions of the alimentary canal. The following categories were used:

S.O : Fish with food in the stomach only

S.I : Fish with food in both stomach and intestines

I.O : Fish with food in the intestines only

E : Completely empty fish

Volume measurements were discontinued after it became obvious that they offered no advantage over weight measurements.

The sampling programme was altered as new aspects of the investigation became obvious. In August and November 1976 for example, it was decided to collect intestine contents to aid the planned estimation of daily food intake. In all, a total of 2,121 fish were examined.

RESULTS

(a) <u>Diet</u>   Table 2.a lists every prey species encountered in the stomach contents of fish of all size-groups during the entire study period. Appendix 2.1 gives the numbers of each species in each sample. The diversity of the list in Table 2.a is misleading as over half the species involved were taken very rarely. Indeed, the asterisks indicate those species whose total numbers for all size-groups combined was less than 10 for the duration of the study. In contrast, the two most important species <u>Abra alba</u> (Lamellibranchiata) and <u>Pectinaria koreni</u> (Polychaeta) usually occurred in much greater numbers (> 30) in each sample.

Table 2.a   <u>List of Prey Items taken by Plaice of the Three Size-Groups
Studied</u>

Bivalves	<u>Abra alba</u>	
	<u>Ensis ensis</u>	
	<u>Cultellus pellucidus</u>	
	<u>Tellina fabula</u>	Other bivalves
	<u>Montacuta ferruginosa</u>	
	<u>Nucula turgida</u>	
	<u>Mysella bidentata</u>	
Polychaetes	<u>Pectinaria koreni</u>	
	<u>Nereis</u> spp.	
	<u>Nephthys</u> spp.	
	<u>Lanice conchilega</u>	Other polychaetes
	<u>Notomastus latericeus</u>	
	<u>Phyllodoce</u> spp.	
Miscellaneous	*<u>Ampelisca</u>	Crustacea
	*<u>Crangon crangon</u>	"
	*<u>Philine aperta</u>	Gastropoda
	*<u>Amphiura filiformis</u>	Echinodermata
	*<u>Achronidae branchiata</u>	"

Fig. 2.1a shows the composition of the diet of the 'smalls' in both numbers and wet weight at various times of year. P. koreni dominated the diet in February. Other polychaetes, mainly Nereis spp. and Lanice conchilega, were next in importance. Very few bivalves were taken and the number of A. alba for the entire 24-hour period was less than 10. In May there was a distinct reversal. A. alba formed over 80% of the diet in both numbers and wet weight, and all other species were secondary to this bivalve. In August the dominance of A. alba was very much reduced. There was a considerable contribution from P. koreni and, in both numbers and weight, the diet seemed evenly divided between bivalves and polychaetes. In November A. alba exceeded P. koreni in numbers whilst the reverse was true in terms of weight. The explanation of this may lie in the timing of the breeding season of these two species. P. koreni spawns in summer and settlement takes place in June. The average weight per individual in a Pectinaria cohort thus varies from 0.04 gms in July to 0.257 gms in March with a November value of 0.259 gms (Nickolaidou, 1977). Abra alba has its main spawning season at the end of autumn. As a result most of the Abra taken by the plaice in November were spat with an average weight per individual of 0.09 gms; this value rose to 0.259 gms by the following spring. The situation in November then, is that there were large numbers of very small Abra, and relatively fewer, but larger specimens of Pectinaria.

The trends described above for the small size-group apply very well to the 'mediums' (Fig. 2.1b). In the case of the large fish however, several differences exist. Fig. 2.1c shows that no single prey species ever formed more than 60% of the diet either by weight or by numbers. Whereas the small and medium fish concentrated very heavily on P. koreni in February, this species was only marginally outstanding in the diet of

Fig. 2.1.   The species composition of the diet

of plaice in the study area in

different months.

Open blocks = % by numbers

Solid blocks - % by weight

a: size group 15.5 - 19.4 cm

b: size group 19.5 - 25.4 cm

c: size group 30.0 - 35.0 cm
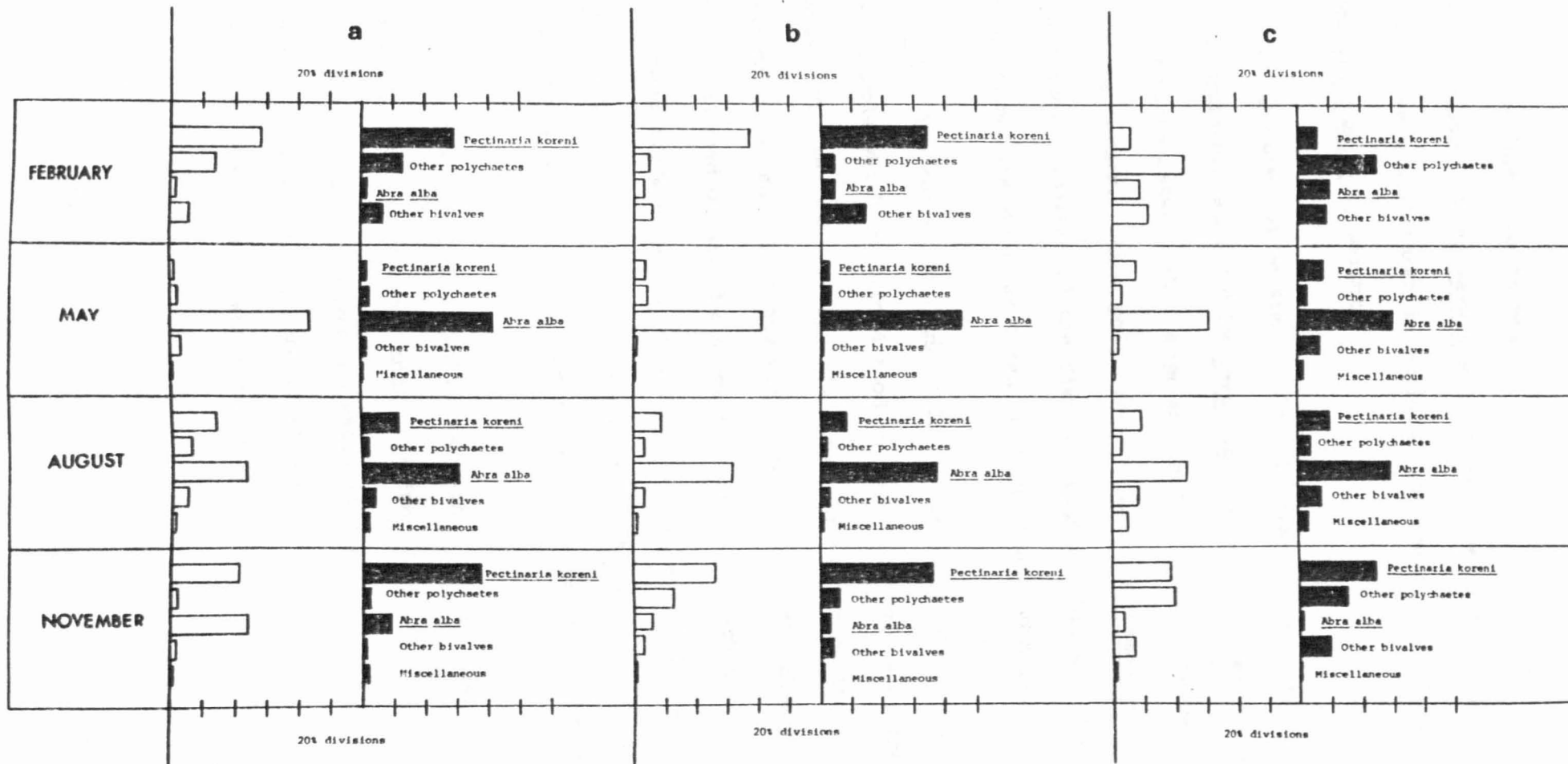
the large size-group at that time of year. The dominant items were the 'other polychaetes' amongst which Nereis spp. formed over 23% of the diet by weight. Bivalves were also taken in appreciable quantities: 21.4% Abra and 17% Tellina fabula by weight.

In May the diet appeared to be similar in all size-groups except that the extent of the dominance achieved by Abra alba was not so great in the large fish. Differences between the large and smaller groups reappeared in November. In the former, 'other polychaetes', mainly Notomastus latericeus formed over a quarter of the diet by weight. This was the only occasion on which this worm was taken in significant numbers.

(b) Feeding Chronology   The series of Figs. 2.2a - 2.2e shows the fraction of fish in each sample which contained food in specific regions of the alimentary canal. The series 2.2i to 2.2v shows the variation in average dry weight of stomach contents with time of day. The closed circles are averages based on all the stomachs sampled in each size-group at each haul. These averages will, in what follows, be referred to as total averages. Assuming less than 100% synchronisation in the feeding of each size-group, total averages will derive from fish of the following categories:

(i)   Fish that are feeding, and contain food either in the stomach only (S.O), or in both stomach and intestine (S.I).

(ii)   Fish that have stopped feeding and while evacuating the stomach, contain food in both stomach and intestines (S.I).

(iii) Fish that have completed gastric evacuation but still contain food in the intestine (I.O).

(iv)   Fish that have completed both gastric and intestinal evacuation and are completely empty (E).

Fig. 2.2.   Feeding Chronology.

   Top - 'smalls'; middle - 'mediums';

   bottom - 'large'.

Fig. 2.2a-e. The fraction of fish in each sample

   with food in specific areas of the

   alimentary canal.

   ☐ Totally empty

   ▤ with food in the intestines

      only (I.O)

   ▦ with food in both stomach

      and intestines (S.I)

   ■ with food in the stomach only (S.O)

Fig. 2.2(i-v) The variation in average stomach contents

   with time of day.

   Open circles - feeding averages

   Solid circles - total averages

   ↑ high tide   ↓ low tide

   Dark bars indicate hours of darkness

Fig. 2.2 (i) and 2.2 (a)

Feeding chronology in March.
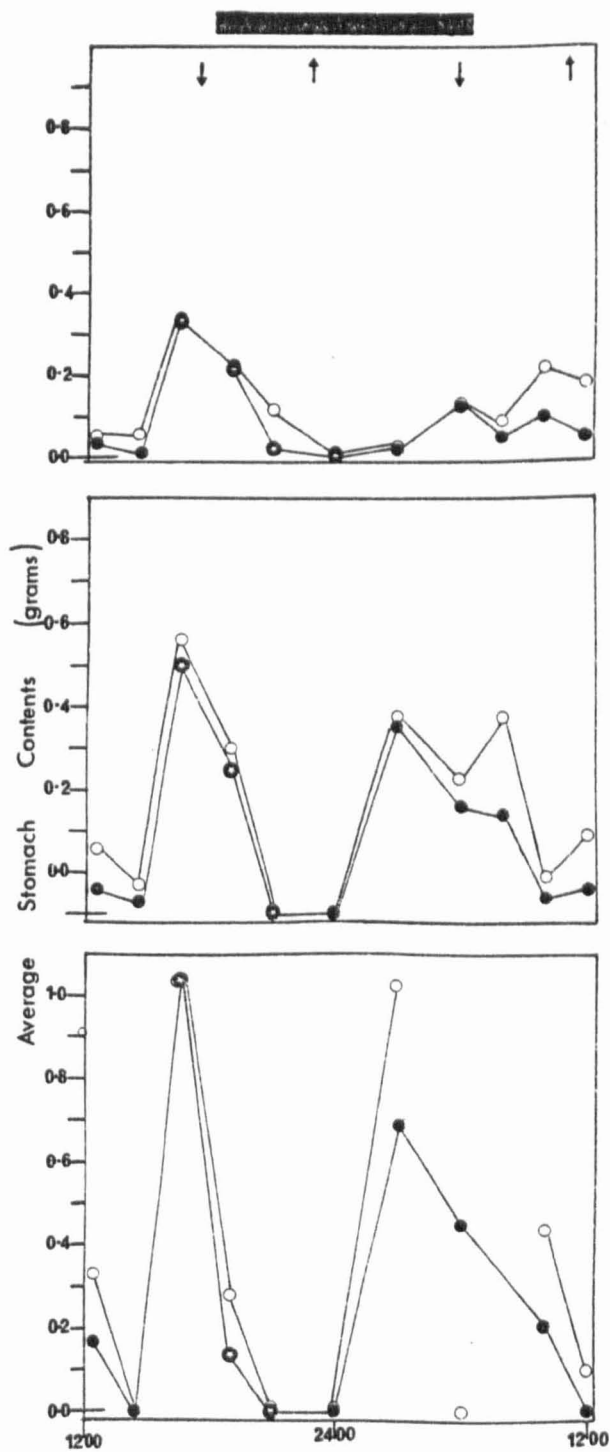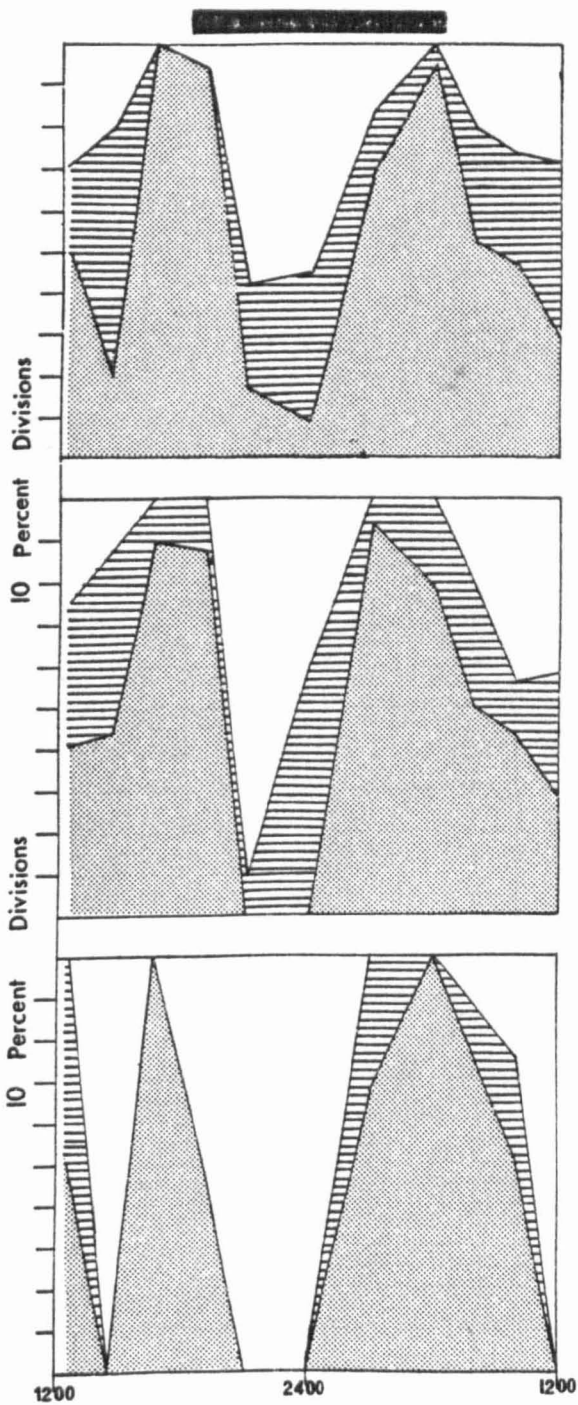
Time of Day (hours)

Fig. 2.2 (ii)   and 2.2 (b)

Feeding Chronology in May.
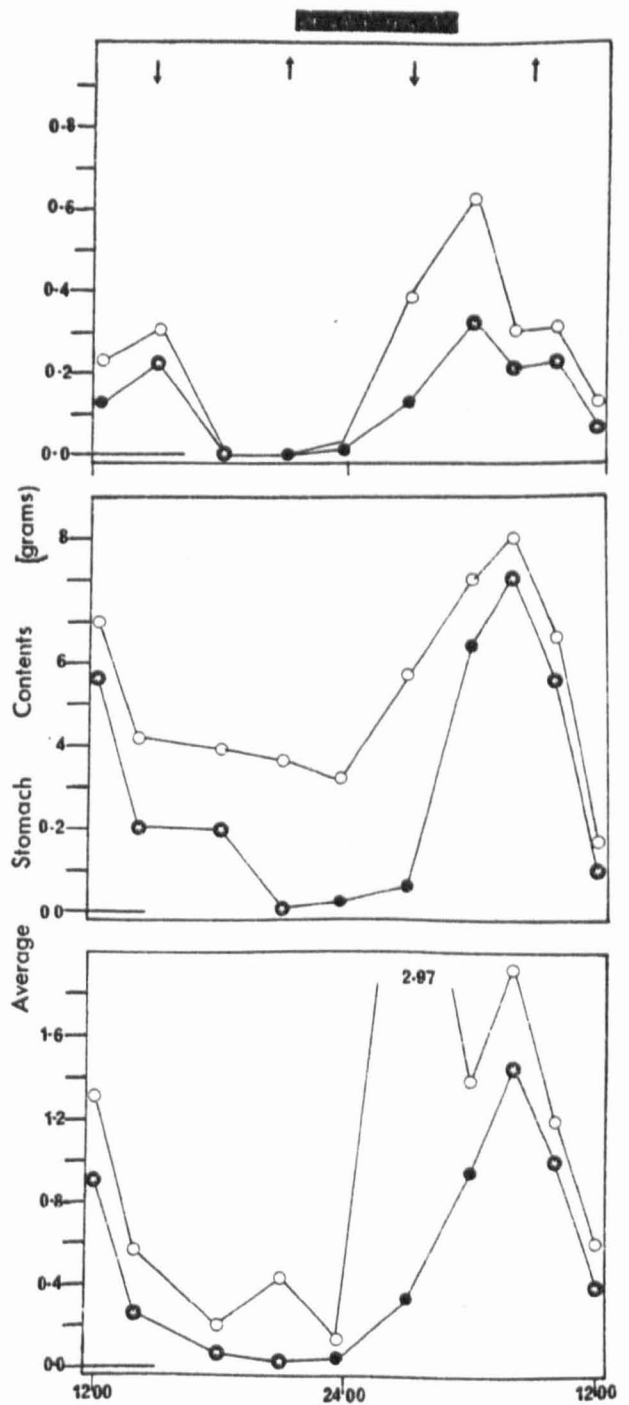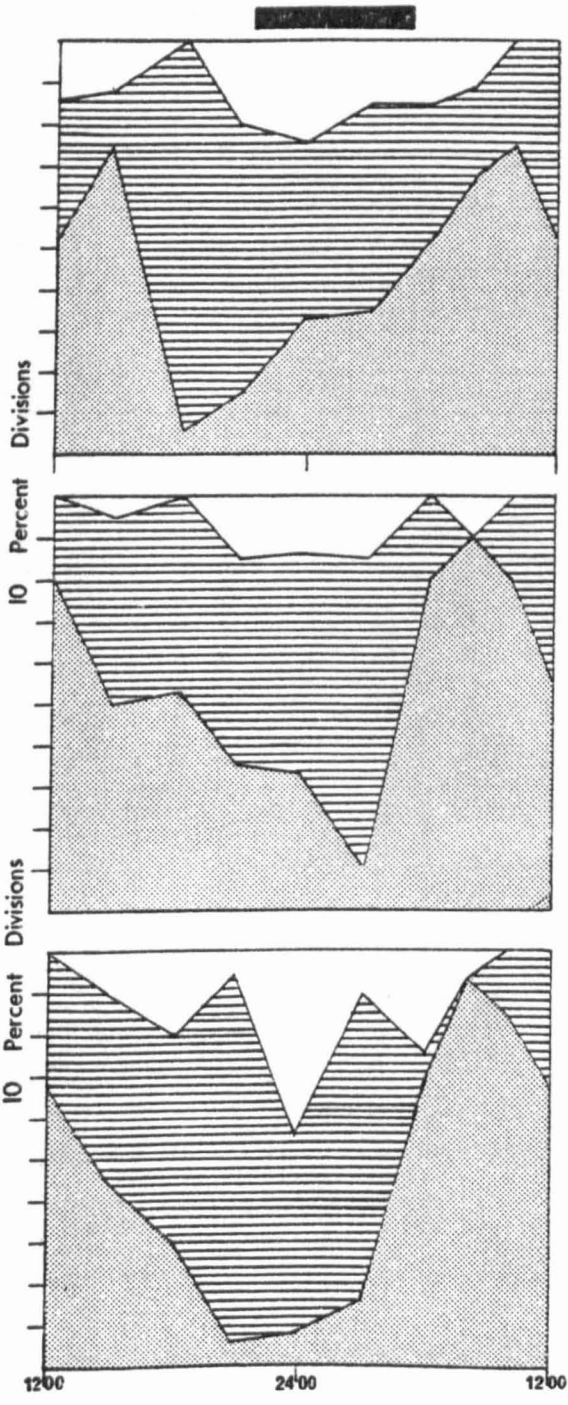
Time of Day (hours)

Figs. 2.2 (iii) and 2.2 (c)

Feeding Chronology in August.

Average Stomach Contents (grams)

10 Percent Divisions

10 Percent Divisions
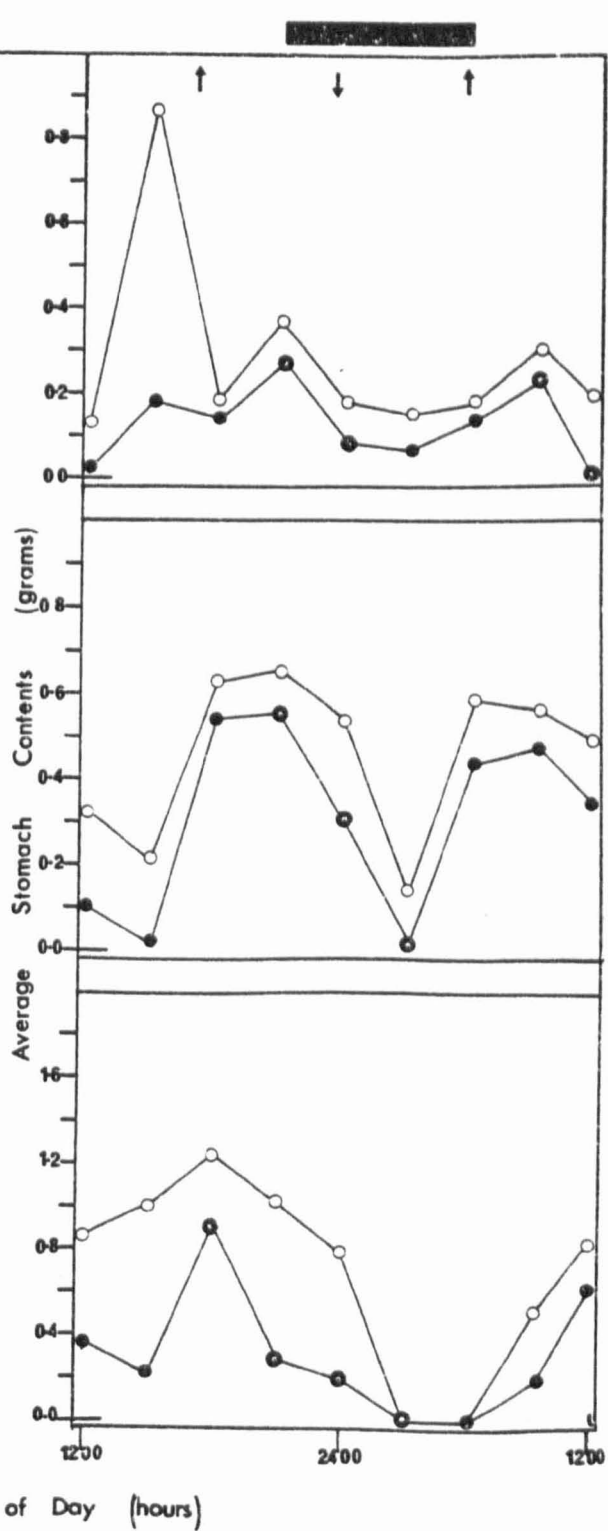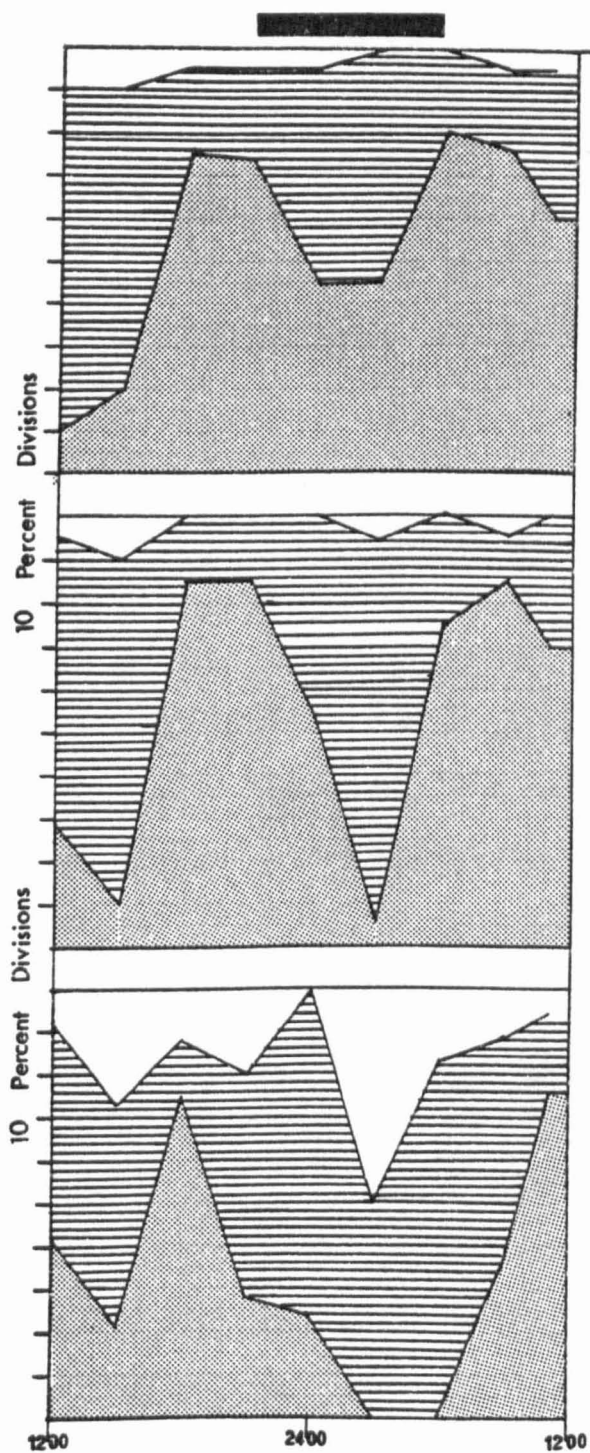
Time of Day (hours)

Figs. 2.2 (iv)   and 2.2 (d)

Feeding Chronology in November.
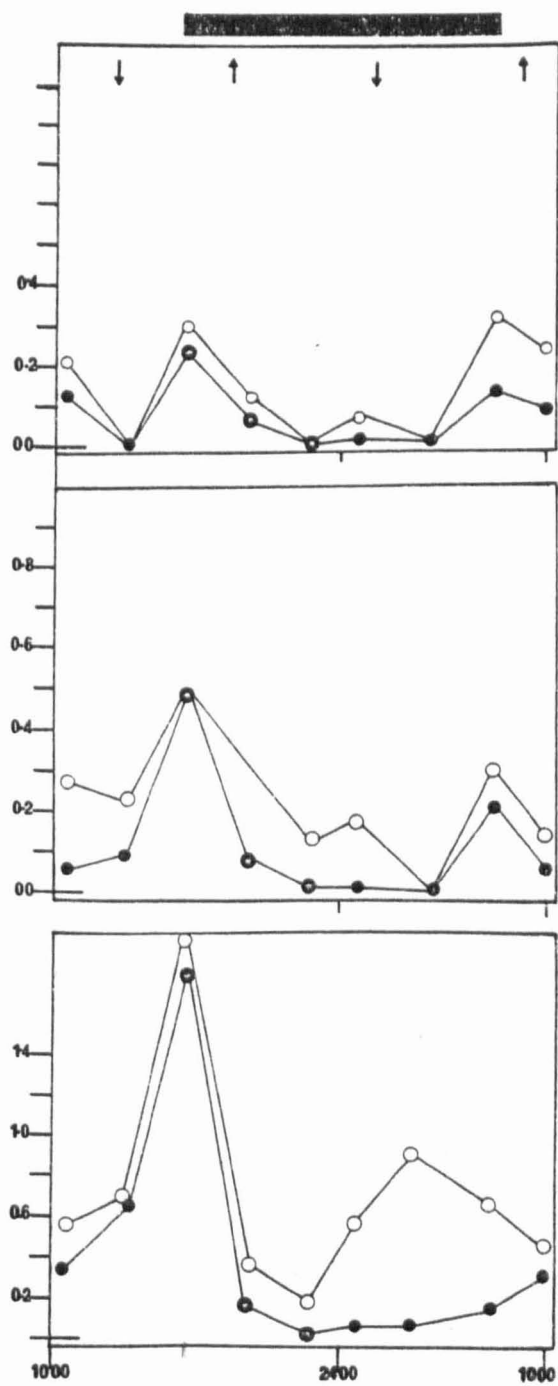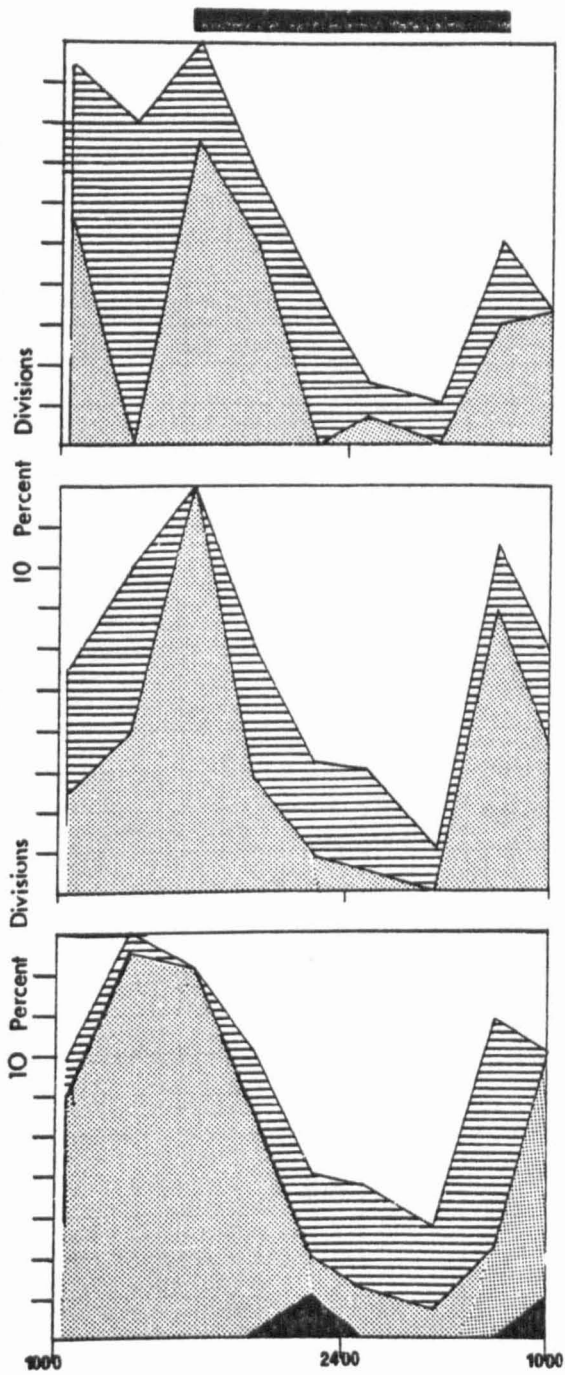
Time of Day (hours)

Figs. 2.2 (v)   and 2.2 (e)

Feeding Chronology in February.

10 Percent Divisions

Average Stomach Contents (grams)
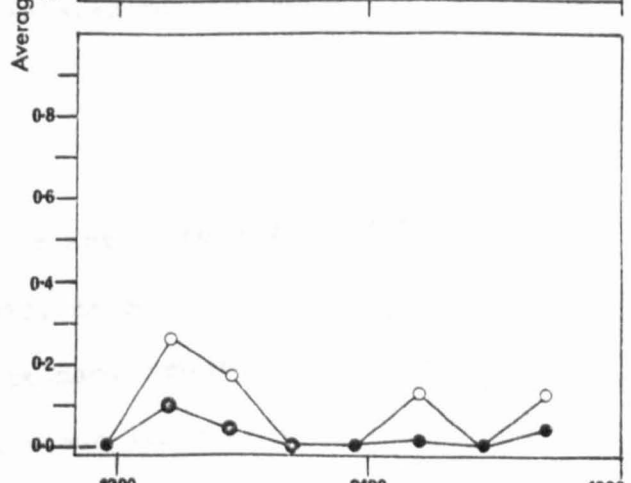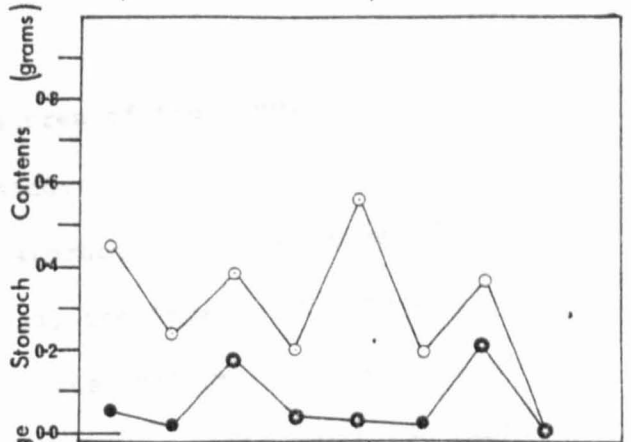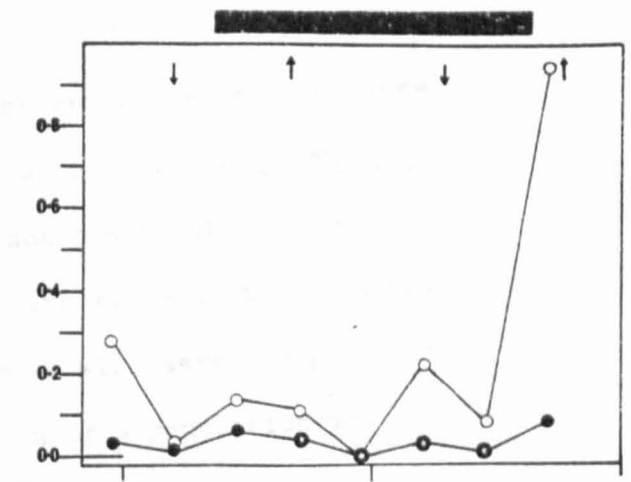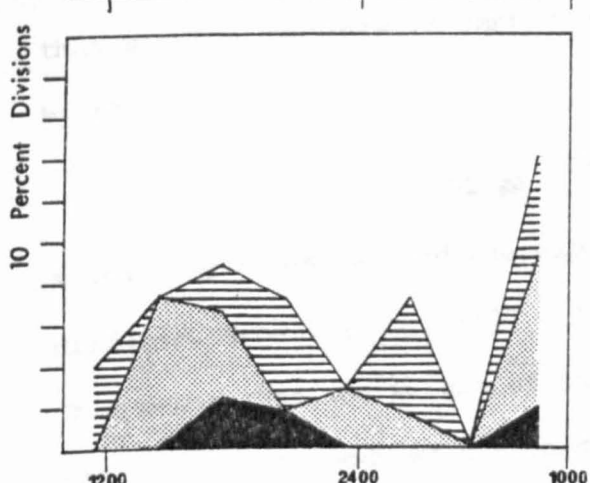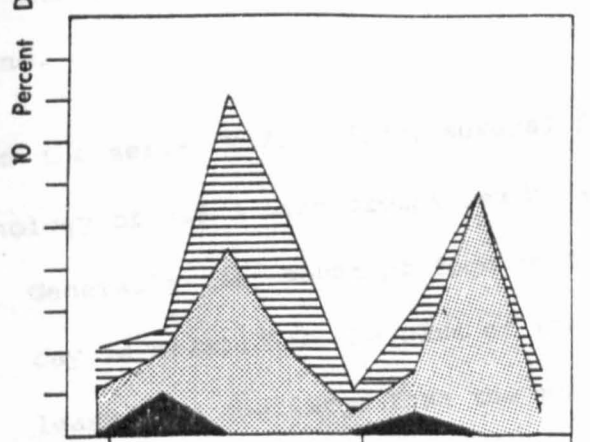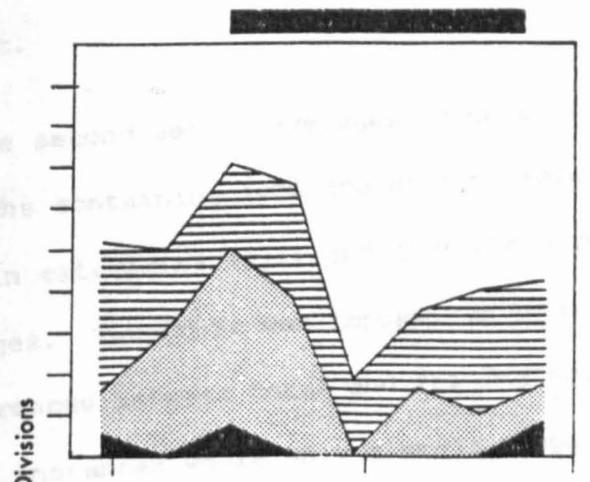
Time of Day (hours)

Total averages therefore treat each size-group population as a single 'corporate' fish and variations between individuals are not taken into account.

The second set of averages (open circles) are based only on those stomachs containing food and will be referred to as <u>feeding averages</u>. Fish in categories (iii) and (iv) above do not contribute to these averages. Though it was impossible to separate (i) and (ii) further, differences between total and feeding averages will serve to pinpoint those instances where only a small proportion of a population may be feeding.

From the series 2.2i - 2.2v, several features of the feeding chronology of all 3 size-groups can be listed:

(i)   Generally the amount of food in the stomach at a given time of day is related to the size of the fish, the 'smalls' having the least, and the large fish the most. Data collected in June showed that stomach contents (Y gms) were related to fish weight (W gms), by the equation

$$Y = 0.002 \ W^{1.26}$$

A standard t-test showed the exponent not to be significantly different from 1 $\left(t_{0.05}(2)27 = 2.052, \text{ calculated } t = 0.673 \right)$. This means that the weight of the stomach contents is the same fraction of the body weight in different sized fish. The absolute amount (gms) will however increase with the weight of the fish.

(ii)   Feeding activity does not appear to be entrained to the state of the tide.

(iii)   Feeding seems generally restricted to daylight hours. The important exceptions to this, i.e. March and May, will be discussed later (see p. 34).

When the two series are considered together, details of the feeding chronology appear to vary with time of year. In November, (Figs. 2.2d and 2.2iv) it is possible to define distinct phases in the feeding chronology of all 3 size-group populations:

Feeding Peak: This occurred at about 16.30 hrs. Over 80% of each population contained food in the stomach and intestines. Total and feeding averages were at a peak value.

Gastric Evacuation: This lasted 6 hours between 16.30 and 22.30. During this period, there was a fall in the fraction of S.I and an attendant rise in the incidence of I.O and of E. At 22.30, all three populations had over 70% of the stomachs empty. These changes were accompanied by a steady fall in both averages of stomach contents.

Feeding Pause: 22.30 - 04.30 hrs. There was little change during this period. The percentage of empty fish increased slightly and total averages remained at a minimum. Feeding averages showed an unsustained rise between 22.30 and 02.10, suggesting that a few fish had taken some food at this time.

Resumption of Feeding: Between 04.30 and 07.30 hrs. there was a sharp rise in S.I (from zero to 70% in the mediums), a slight rise in I.O, and an increase in the average dry weight of stomach contents.

The four phases described above are recognisable with slight modifications in February and March (Figs. 2.2a and 2.2i; 2.2e and 2.2v). In February, a large proportion of each population appeared not to be feeding, and the feeding averages indicate that even those that were feeding ingested relatively small amounts. February also showed the highest incidence of fish in the S.O condition. From personal observations

made during this study, and from surveys carried out in the study area between 1970 and 1977 by undergraduate classes from this laboratory, most plaice digestive tracts are completely empty from December to January. This suggests a winter fast and February may mark the earliest resumption of feeding.

The trends in May and August appear to be substantially different from those already described. S.0 fish were totally absent, feeding pauses did not occur, and very few completely empty fish were encountered throughout each sampling period.

DISCUSSION

(a) Diet: Almost all earlier reports agree with the results of the present

study that plaice are polychaete-mollusc feeders (Smith, 1889-1891;

Blegvad, 1916, 1925, 1928, 1930; Steven, 1930; Hartley, 1940; Jones,

1952; De Groot, 1964; Vaas, 1970). There are reports in the literature

that the plaice is best suited to deal with polychaetes and molluscs

both by the morphology of its mouth and associated structures (De Groot,

1964) and its foraging posture (Jones, 1952). In those cases where

polychaetes or molluscs have been replaced in the diet with either

crustaceans or echinoderms, this has often been shown to be the result of

a scarcity of the two preferred classes in the benthos (Blegvad, 1916;

Jones, 1952).

The change in diet with size of plaice observed in this study is

also not unique. A similar phenomenon has been reported for several

species of flatfish (see Blegvad, 1932 on Pleuronectes (= Platichthys)

flesus in the Baltic; Hartley, 1940 on Limanda limanda in Plymouth Sound,

U.K.; Rae, 1956 on Microstomus kitt in the North Sea; Braber and De Groot (1973)

on Scophthalmus rhombus in the southern North Sea). The reports dealing

with this subject on the plaice have not always concurred in detail. In

the North Sea, Todd (1915) found an increase in the importance of molluscs

in the diet as the fish grew larger. Polychaetes also rose in importance

but declined in the two largest groups (> 30 cm). Exactly the same

trends have been reported by Ritchie (1937) working in Scottish waters.

However, in the Norwegian fjord studied by Lande (1973), there was no

correlation between size of plaice and relative importance of either

polychaetes or molluscs in the diet. In the present study the changes

observed are a general increase in the diversity of prey items taken by

fish larger than 30 cm. Such items as Crangon crangon, Amphiura filiformis

and _Achronidae_ _branchiata_ were taken only by the large size-group. It may be expected that larger fish with correspondingly larger mouth parts will be able to exploit a more catholic diet than smaller individuals.

In contrast to the subject of change in diet composition with size, there is fair agreement in the literature that when plaice alter their diet with time of year, molluscs are usually preponderant in late spring and summer, whilst polychaetes predominate in autumn and winter (see Todd, 1915; Lande, 1973). In some cases, such a change in the principle item of the diet occurs in response to changes in availability (see e.g. Seshappa and Bhimachar,(1955)on the Malabar sole _Cynoglossus_ _hemifasciatus_). In the plaice, no such connection has been shown to exist. Todd (1915) suggested that as the trend from molluscs to polychaetes occurs around the plaice breeding season, it could be a way of avoiding damage to swollen gonads from the jagged ends of shells. This does not explain why the phenomenon is common to both mature and immature fish. In the present case the change does not seem to have been the result of an alteration in the relative abundance of _Pectinaria_ and _Abra_ in the benthos (Table 2._d_ , p.36).

(b) _Feeding Chronology_ : From studies of feeding activity both in the field and under laboratory conditions, there is a consensus in the literature that plaice are mainly visual feeders (Wilson, 1893; Bateson, 1889; De Groot, 1967). On the basis of this it is generally inferred (probably mistakenly) that plaice feed only during the day (e.g. Edwards and Steele, 1968). The results of the present study indicate that feeding can occur in the dark. This is shown clearly in the average stomach contents (especially the feeding averages) in Figs. 2.2a - 2.2e. Hempel (1964) observed night feeding in large plaice (> 25 cm) in the deeper waters off Helgoland, but failed to emphasise its significance. Lockwood (1972)

also detected night feeding in O-group plaice along the east coast of England but surmised that this was only made possible by ~~exceptionally~~ bright moonlight. In an experimental situation, Blaxter (1968) demonstrated that newly metamorphosed young plaice can feed in the dark. Both Wilson (1893) and De Groot (1969) have shown, also experimentally, that plaice can supplement their vision with the olfactory sense when locating prey. The relative size of the olfactory lobes in this species also indicates that this sense is of some importance in routine life (Evans, 1937). In view of the foregoing, it may be unrealistic to contend without strong evidence, that the species feeds only by day.

The feeding pattern during the day is unresolved. There have been reports of gradual filling of the stomach during the day (De Groot, 1971; Lockwood, 1972), a dawn and a dusk peak of feeding activity (Bregnballe, 1961), and maxima of feeding entrained to the period shortly after high tide (Kuipers, 1973; Thijssen et al., 1974). This controversy is due in part to inadequate sampling procedures: Bregnballe's feeding chronology for example, was based on data collected over two months. This was bound to mask the effects of other fluctuating environmental features besides the day/night cycle (e.g. benthos abundance, tides). The results of the present study fail to show any obvious relationship between feeding activity and the state of the tides. The feeding pattern during each twenty-four hour period appeared to vary between size-groups in some cases, and between seasons for each size-group.

The more important points emerging for discussion from the results on feeding chronology are the differences between the summer months (May and August), and the autumn / early spring months (November, February and March). These differences include the proportion of each size-group population with food in their stomachs during each twenty-four hour sampling period, the quantitiy of such stomach contents, and

Table 2.b

Monthly Variation in Temperature

Month	Temperature ^{o}C
March	6.09
May	12.34
August	16.34
November	9.88
February.	6.06

Data collected at Menai Bridge 1977

Table 2.c

Variation in Duration of Daily Underwater Irradiance
at Moelfre (from Topliss, 1977)

Month	Duration of Daily Irradiance (hrs)
March April	10.9
May June	14.2
July	13.1
August September	11.7
October November	6.2
December	6.0

Data collected from an inshore site in 1974

Table 2.d

Monthly Variation in the Denisty of the Principle
Food Organisms in Red Wharf Bay (from A. Nott, pers.
comm.)

Month	Density (Nos./m^2)	
	P. koreni	A. alba
January	11.3	7.3
February	1.7	1.3
March	2.9	1.3
April	0	1.7
June	6,690.5	161.7
July	5,922.5	20.4
August	4,890.3	36.7
November	...	...

Data collected in 1976 and 1977

the temporal relationship between gastrointestinal emptying and the intake of fresh food. In the spring/summer months, the proportion of feeding fish seemed higher, average stomach contents were also higher than in winter/spring and there were no pauses for gastric evacuation between feeding bouts.

In predatory demersal fish such as the plaice, the rate of feeding probably depends on the distance between prey items (i.e. their abundance and patchiness) and the speed at which this distance can be covered. Being poikilotherms, the swimming speed will be affected by the ambient temperature. Temperature is also likely to affect appetite and the rate of gastric evacuation through its effects on gastric motility and enzyme activity (see e.g. reviews by Kapoor et al., 1975 and Fänge and Grove, 1978). Total food intake within each twenty-four hour period may also be affected by the duration of daily bottom irradiance as the eyes are the primary (though not the only) organs of food location. Tables 2b, 2c and 2d show the monthly variation in temperature, duration of daily bottom irradiance and variation in the density of primary food organisms in Red Wharf Bay. These tables suggest that feeding conditions are ideal in summer, and deteriorate towards autumn, winter and early spring.

The above considerations imply that the feeding pauses observed in November, February and March occurred not because a certain hunger threshold was required to stimulate resumption of feeding, but as a result of a combination of lowered swimming speeds and an impoverished benthos. The restriction of the S.O condition to these cooler months can only tentatively be explained on these grounds. It is possible that in the cooler months the stomach functions much as it does in most carnivorous species: ingested food is retained in this region for some degree of

physical and chemical breakdown before it is transferred into the intestines.   In late spring and summer increased feeding frequency, larger meals and higher temperatures may stimulate the gastrointestinal tract to the extent that this retention period is drastically shortened and food is transferred into the anterior regions of the intestines almost immediately after ingestion.   Support for this theory comes from the following:

(i)   Edwards (1971) has produced X-ray photographs of a piece of Arenicola marina being evacuated from the stomach of plaice.   His plates showed that there was very little physical disruption before evacuation commenced.

(ii)   In his study of daily food intake in a II-group population of plaice in the Wadden Sea, Kuipers (1975) observed that on resumption of feeding at high tide food was passed almost immediately into the intestines.   He concluded that the anterior intestine has a 'gastric' role which enabled the plaice to store enough food during a short feeding period to meet their requirements.

(iii) Amongst flatfish (Heterostomata), there is a gradual reduction of the relative size of the stomach from fish feeders (mainly Psettotidae, Bothidae and some Pleuronectidae) through the crustacean feeders (Pleuronectidae and Cynoglossidae) to polychaete-mollusc feeders (Pleuro-nectidae and Soleidae).   At the same time, the intestines form a greater proportion of the total length of the alimentary tract. From the present study the oesophagus and stomach accounted for only 16.5% of the total length of the alimentary canal.   This is very much lower than the 40-50% quoted for bothids by De Groot (1969).   On the basis of the foregoing, it is tempting to suggest that as the inorganic content of the diet increases, the need for a

stomach gradually recedes and a long complicated intestinal loop results. In at least two Pacific pleuronectids which feed on polychaetes and molluscs, (Ammotretis rostrata and Rhombosolea tapirina) the stomach has disappeared altogether (Grove, pers. comm.).

Chapter 3

Laboratory studies on gastric evacuation.

PREFACE

In the last section gastric evacuation emerged as one of the more important processes controlling the pattern of food intake in the wild. Certain assumptions were made on how this process could be affected by those environmental factors which alter between seasons to result in differences in the daily ration taken at different times of the year. This section will be specifically concerned with quantifying the effects of some of these factors on the rate and speed of gastric evacuation. The number of studies of this kind already reported in the literature is immense. However, not all of them were undertaken to facilitate the interpretation of field data and only one (Edwards, 1971) has dealt with the species under investigation here. Still, it will be worthwhile to preface the present study with a brief review of this extensive literature in order to provide a background and an introduction to the experimental techniques and precautions involved in studies of this kind.

Gastric evacuation rates have been measured in a variety of ways. Most methods involve giving the experimental animals a meal of known size and estimating the amount remaining in the stomach after various time intervals. Meal sizes have been expressed in such units as volume (Hunt, 1960; Seaburg and Moyle, 1964), wet weight (Magnusson, 1969; Jones, 1974), dry weight (Shrable et al., 1969; Tyler, 1970), dry digestible organic matter (Windell, 1966; Kitchell and Windell, 1968), and caloric content (Gerald, 1973).

The method of presenting the test meal to the experimental animals has also varied. The simplest method has been to allow the experimental animals to feed voluntarily. This is not always possible in practice

as in many cases the animals do not sufficiently adapt to the experimental situation for voluntary feeding to occur. In the majority of cases therefore, (e.g. Windell, 1966; Steigenberger and Larkin, 1974), the animals have been force-fed. Force-feeding involves handling and the resultant stress may significantly depress gastric evacuation rates (see Swenson and Smith, 1973; Jones, 1974). Still, this method remains virtually the only means of getting relatively large numbers of fish to each consume a meal of pre-determined size at a particular time.

With the test meal consumed, the next step is to monitor the rate at which it leaves the alimentary canal. This requires that the test meal be distinguishable from other items in the stomach. To meet this condition, fish are usually deprived of food prior to the start of the experiment to ensure that the alimentary canal is empty (Cameron and Kostoris, 1973; Peters and Hoss, 1974). There are reports that such pre-experimental starvation (Ishiwata, 1969; Tyler, 1970; Brett, 1971) may depress the rate of gastric evacuation. In an extensive review of the literature, Fänge and Grove (1978) state that gastric evacuation rates of previously deprived fish are usually 50-60% less than those measured in actively feeding fish. To circumvent this difficulty some workers have made the experimental meal distinguishable from items of a previous meal by the use of dyes (Laurence, 1971) or a change to recognisable items (Blaxter, 1963).

Methods which monitor the progress of a meal along the alimentary canal vary in the level of detail they yield. Tagging the meal with a poorly assimilated radioisotope and performing whole body counts (e.g. [144]Cerium, Peters and Hoss, 1974) gives only estimates of the total time required to clear the whole of the alimentary canal. When the test animals are transparent

larvae, direct visual examination of the progress of the meal may be possible (Rosenthal and Hempel, 1970). Molnár and Tölg (1962 et seq) have developed a method of in vivo X-ray examination which requires only that the test meal contains a contrast medium. Edwards (1971, 1973) and Jobling et al. (1977) added barium sulphate to their flatfish meal to provide a contrast medium. Such visual examination provides information on how long it takes the experimental meal to be transferred along specific sections of the alimentary canal; quantitative data on the amount of food leaving the stomach per unit time cannot be obtained in this way. To date such data has only been obtained by recovery of the residuum from the stomach at a chosen time after ingestion. Methods of recovery have included the use of an emetic (Markus, 1932), a stomach pump (Seaburg, 1956) and perhaps most commonly, the serial slaughter of sub-samples of the experimental group of fish.

Reports so far indicate that after ingestion there may be a delay before the gastric evacuation of a meal commences. The extent of this delay is affected by temperature and food type (Jones, 1974), and absorption of fluid may result in an increase in the wet weight of the test meal (Steigenberger and Larkin, 1974). Once evacuation commences, the amount of residuum in the stomach decreases with time. For some species, the shape of the curve describing this decline is rectilinear: Lepisosteus (Hunt, 1960), Katsuwonus (Magnusson, 1969), Gadus and related species (Daan, 1973; Jones, 1974). An exponential decline has been reported for young Gadus (Tyler, 1970), Oncorhynchus (Brett and Higgs, 1970), Salmo trutta (Elliot, 1972) and others.

When an evacuation curve is a straight line, the implication is that the rate at which the meal leaves the stomach (gms/hr) is independent

of the bulk of food in the stomach once evacuation has started. An exponential curve on the other hand, suggests that the rate of evacuation is proportional to the instantaneous bulk of food in the stomach. Mathematically this can be expressed as

$$W_t = W_o e^{-b(t-a)}$$

where

W_t is the stomach contents at time t after ingestion

W_o is the size of the meal given

a   is the delay before evacuation commences

b   is the instantaneous rate of evacuation

In man (Hopkins, 1966), a linear relationship exists between the square root of the volume of the residuum and time. Hunt and Knox (1968) have also reported this for other mammals and suggested that the stomach may function as a constant frequency pump whose stroke volume increases with radial distension. There are indications that this may apply to some fish species: in Sebastes inermis the stomach diameter increases linearly with meal size (Karya et al., 1969); Jobling (pers. comm.) has shown for O-group Pleuronectes platessa that a linear evacuation curve is obtained when the square root of the residuum (dry weight) is plotted against time.

The speed of gastric evacuation measured either as gms/hr or as time taken to evacuate a given percentage of a meal is now generally accepted to be affected by 4 main factors, viz:

i) Temperature The influence of temperature on the speed of gastric evacuation in fish is in keeping with the susceptibility of poikilotherm physiology to changes in the ambient temperature. This susceptibility

Table 3.a   Some Published Data on the effect of (I) Temperature and (II) Meal size on
             Gastric Evacuation Time

Species	Fish Size	Temp. ^{O}C	Time for 100% evacuation (hrs)	Food and amount	Author
Ictalurus punctatus	380 g	10	24	3 gm pellets	Shrable et al. 1969
		16	24		
		22	7-10		
		27	3- 4		
Pleuronectes platessa	280-320 g	1	36	Arenicola	Edwards 1971
		5	25	1.3 - 1.5 g	
		9	16		
		14	12		
		20	10		
Salmo trutta	90 g	5.2	49	Gammarus	Elliot 1972
		7.6	37	1% body wt.	
		9.8	29		
		12.0	22		
		15.0	16		

Species	Fish size	Meal size % body wt.	Time for 100% evacuation (hrs)	Temperature and food	Author
Micropterus salmoides	91 g	4	20	$25^{O}C$, emerald shiner Notropis atherinoides	Beamish 1972
		6	24		
		8	27		
Limanda limanda	80 g	1	18	$12^{O}C$, Artificial flatfish diet with $BaSO_4$	Gwyther 1978
		2	24		
		3	32		

is usually expressed in alterations in the rate and intensity of physiological processes (e.g. basal metabolism) to achieve a new steady state. Temperature can thus affect gastric evacuation rates via its effects on the underlying physiological processes, e.g. rate of enzyme secretion, molecular kinetics of enzyme hydrolysis, gastro-intestinal motility and rate of intestinal absorption. Achievement of a new steady state for such processes is gradual and experiments which measure performance at different temperatures must allow time for acclimation to occur. When acclimation is incomplete performance at a new temperature will differ from the acclimated rate. Gwyther (1978) has noted that not all workers have been sufficiently thorough in this respect and the instance of Nicholls (1933) was cited - killifish Fundulus heteroclitus were acclimated to 15-19°C and then tested over the much wider range of 6-30°C.

Whatever the shortcomings of individual studies, the literature does indicate (Table 3.a(i)) that the speed of gastric evacuation increases with temperature, though the trend may be reversed at temperatures near the physiological limit of the species being investigated (Tyler, 1970). A plot of evacuation time against temperature can give a straight line with either semi-log (Jones, 1974) or log-log units (Molnár and Tölg, 1967). This is not always the case and when the data shows marked deviations from a straight line with these units, Fänge and Grove suggest that a Krogh's Curve (Krogh, 1914) with a Q_{10} of ca. 2.6 (after Backiel, 1971) may be more appropriate.

ii) Meal size The general opinion in the literature is that large meals take longer to evacuate. Table 3a(ii) illustrates this effect. Digestion is a surface area phenomenon and it may be reasonable to suppose that the rate of digestion will be proportional to the surface

area of the bolus. Thus

$$\frac{dW}{dt} = -f(area) = -f(L^2) = -f(W^{2/3}) \quad \text{------------ (a)}$$

where L gives the linear dimensions of the bolus and W its weight or volume. From the above relationship a plot of log evacuation rate (g/hr) against log meal size should have a slope of 0.67. It also follows that a larger meal will have a faster rate of evacuation (g/hr) than a small meal. If equation (a) is integrated then the time to complete digestion (t_λ) of a given meal (W) is given by

$$t_\lambda = f(W^{0.33}) \quad \text{------------ (b)}$$

Thus though a large meal will be digested at a faster rate (g/hr), the total time required for complete digestion is also greater than for a small meal.

These considerations, expounded in the literature by Fänge and Grove (1978), receive some support from the available evidence. Beamish (1972) has found for Micropterus that a fourfold increase in meal size will only double the gastric evacuation time. Jobling et al.(1977) have similarly reported for Limanda limanda that increasing the meal size from 1% to 5% body weight led to only a fourfold increase in the time to clear the stomach. In both cases gastric evacuation rate and gastric evacuation time altered with meal size in the manner predicted by the model. Fänge and Grove (1978) have analysed data from several sources and found that the exponent describing the change in digestion rate (g/hr) with wet weight of meal lies between 0.5 (Jobling et al., 1977, Limanda) and 1.0 (Windell, 1966, Lepomis). Digestion and gastric evacuation are the outcome of several processes acting in concert and

these variations about the 0.67 value predicted by the model may
represent distortions of the surface area phenomenon by these processes.
For instance, enzyme concentration may increase with meal size (Smit,
1967) to raise the evacuation rate above that predicted by the model.

iii) Fish size It has been reported for several species that larger
fish evacuate a given weight of meal (g) faster than smaller individuals
e.g. Gadus and related species (Jones, 1974), Stizostedion (Swenson and
Smith, 1973), Limanda limanda (Jobling et al., 1977). In the latter
report the authors pointed out that stomach volume in Limanda is
related to fish size and suggested that it would be more appropriate
to compare evacuation times for meals of equal stimulus by feeding fish
to a given percentage of their body weight. In those cases where this
has been done (Pandian, 1967 and Gerald, 1973) small fish evacuated a
given meal (as % b.w.) in a shorter time than large fish. This lends
additional support to the surface area model, as a given % body weight
means a small meal (gms) in small fish and a comparatively large meal
(gms) in large fish.

iv) Type of food Results from several studies show that gastric
evacuation rates can be markedly affected by the digestibility of the
food ingested. Differences in digestibility of prey items taken in the
wild are usually the outcome of differences in the thickness of exo-
skeletal structures. Thus Elliot (1972) found that brown trout Salmo
trutta completed 90% evacuation of gammarids in 22 hours at 12°C whilst
Protonemura required 26 hours and Hydropsyche 30 hours. The same trend
has been reported for gadoids by Jones (1974) where after an initial
delay, evacuation rates for different items at 12°C were as follows:

Nereis/Nephthys   0.31 g/hr

Pollachius muscle   0.26 g/hr

Crangon   0.19 g/hr

From the foregoing survey it is obvious that the study of gastric

evacuation in fish can be fraught with practical difficulties. Some

familiarity with the literature is required of the experimenter if

flaws in technique which may invalidate the results are not to occur.

Perhaps more important, the conditions of each experiment need to be

defined in terms of a considerable number of factors before results

can be evaluated with any certainty. Amongst these are the four main

factors just outlined plus such others as feeding history, method of

presenting the test meal and type of food. The present study was

undertaken to facilitate the interpretation of the field data presented

in section II. The aim was to establish quantitative relationships

between the speed of gastric evacuation (measured as gastric evacuation

time, GET) and certain factors which fluctuate between seasons in the

field. These factors were temperature, meal size as a measure of

benthic density, and inorganic content of the diet. The last factor was

included as a means of determining the effect of the change to an almost

exclusive bivalve diet in future, reported in section II. Such a change

would have resulted in an increase in the inorganic content of the diet

since A. alba is 75% ash, Pectinaria 55% ash and Nereis/Nephthys 15% ash.

Table 3.c.

Composition of the Flatfish Meal, "50% White Fish
Meal Protein"   (Values are g/Kg)

White fish meal	714
Vitamin mix	28
Mineral mix	5
Dextrin	100
Cod liver oil	54
α-cel	49
Edifus binder	50

Prepared by the NERC Unit, Institute of Marine
Biochemistry, Aberdeen

Materials and Methods

The test animals used in the experiments to be described were trawled from the study area as they were needed. In the laboratory they were kept in 20 gallon fibreglass tanks containing recirculating seawater. Temperature was maintained to within $\pm 0.5^{\circ}C$. The animals were allowed a fortnight to adapt to laboratory conditions before being used in experiments. Besides routine cleaning of the tanks, the fish were left completely undisturbed during the first five days of this period. Thereafter each fish was weighed, tagged and then force-fed once to satiation on alternate days. If the holding tanks are shallow and the incident light too bright, plaice will only feed voluntarily in the laboratory after prolonged training. Because of this, the animals were force-fed for all experiments and the maintenance meals given during the adaptation period also served to accustom them to handling.

Test meals were based on an artificial powdered flatfish diet (Table 3.c). After mixing with 25% w.w. barium sulphate, water was added in the ratio of 1 part mixture to 3 parts water to give a paste with the following weight relationships:

1 ml = 1.01 gms wet = 0.242 gms dry.

Experimental meals were administered 48 hours after the last maintenance meal as preliminary observations showed that the digestive tract was empty by then. The evacuation of the meal from the stomach was followed by periodic X-ray examination using a portable Chirax unit (Model PR I 10/III). Care was taken to disturb the fish as little as possible during experiments. With practice it became possible to make conservative estimates of the time required by individual fish to complete evacuation after their first X-ray examination. This obviated

the need for examinations at regular intervals thus reducing the risk of additional stress on the test animals.

Total time to evacuate the stomach (GET) was investigated with respect to the following conditions:

(i)   Fish size

(ii)   Temperature

(iii) Meal size

(iv)   Meal composition

It was not possible nor indeed necessary to do a complete factorial design and the following format was adopted:

Experiments were conducted at each of 3 temperatures (9.5, 12.5, 15.5°C), chosen for their similarity to field temperatures (see Table 2.b, p.36). At each of these temperatures fish of varying sizes (50-350 gms) were given meals corresponding to 0.5%, 1% and 2% body weight in three separate experiments. Meals larger than 2% body weight appeared to exceed the stomach capacity in some cases. As the volume of the stomach is proportional to fish weight in plaice, it was considered that weight-specific meals would present an equal 'stimulus' to fish of different sizes. In addition two experiments were conducted to determine the effects of meal composition on GET. In these experiments the test paste was altered to 75% and 50% barium sulphate respectively.

The shape of the gastric evacuation curve was investigated by serial slaughter. Two size-groups of fish of average weight, 94 gms (range 80-110 gms) and 190 gms (range 170-220 gms) were fed a meal of 1% body weight and killed at various intervals afterwards. The contents of each stomach was rinsed into a crucible and dried to constant weight at 60°C.

Plate 2.   X-ray photographs of the position of a 1%

meal (25% $BaSO_4$) in the alimentary canal

of a 30 cm fish at various intervals after

force-feeding. Temperature = $12.5^{\circ}C$.

1·5 Hours

5 Hours
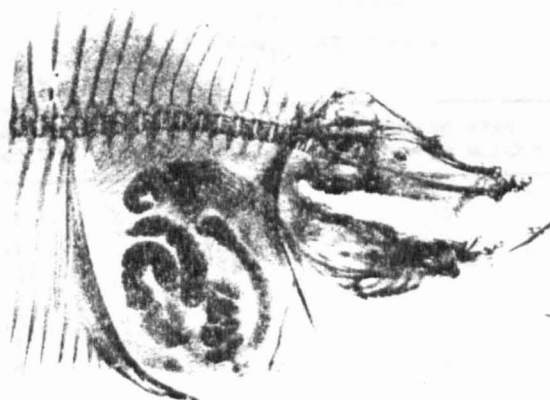
9 Hours
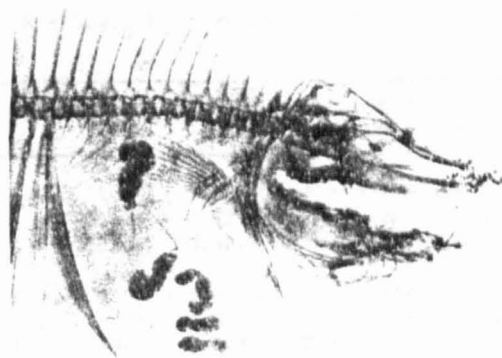
13 Hours
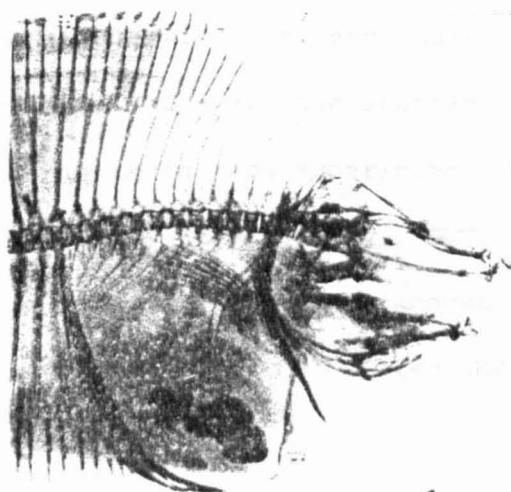
19 Hours
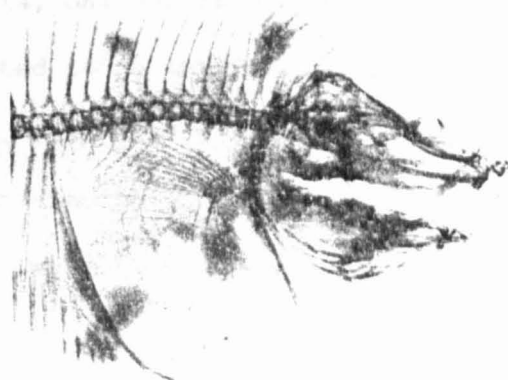
23·5 Hours

RESULTS

The results of the experiment on gastric evacuation time are shown
in Fig. 3.1. The equation for the lines in this figure are contained
in Table. 3b. There is considerable scatter about some of the lines
and Steigenberger and Larkin (1974) have suggested that this may mean
that the conditions of the experiment were not adequately controlled.
Peters and Hoss (1974) have also shown that fish of similar size can
give consistently different evacuation times when fed meals of

Table 3.b.   The Relationship between Gastric Evacuation Time (GET) and Fish Weight under
Specified Conditions

$Y = Log_{10}$ GET. (hours) $X = Log_{10}$ Fish weight (gms)

Temperature $^{\circ}C$	Sample Size	Ration Size % body weight	Regression Equation	Calculated Fit with Common slope
9.5	15	0.5	Y = 0.3802X + 0.2304	Y = 0.4227X + 0.1470
9.5	19	1.0	Y = 0.3526X + 0.4270	Y = 0.4227X + 0.2860
9.5	13	2.0	Y = 0.3322X + 0.5819	Y = 0.4227X + 0.4045
12.5	14	0.5	Y = 0.5679X - 0.3763	Y = 0.4227X - 0.0523
12.5	12	1.0	Y = 0.4557X + 0.032	Y = 0.4227X + 0.1069
12.5	12	2.0	Y = 0.5346X + 0.0342	Y = 0.4227X + 0.2738
15.5	19	0.5	Y = 0.3532X + 0.0284	Y = 0.4227X - 0.1151
15.5	18	1.0	Y = 0.4399X + 0.0554	Y = 0.4227X + 0.0992
15.5	12	2.0	Y = 0.4245X + 0.1681	Y = 0.4227X + 0.1774

identical size. In the present case at least some of this variability
must be the result of stress caused by handling during periodic X-ray
examinations. Despite the scatter of points, GET varies quite clearly
with fish size in each experiment. Subjected to an analysis of
covariance, the slope of log_{10} GET on log_{10} fish size was found to be
not significantly different amongst all experiments (Worksheet 3.1).
From the common slope calculated GET varies with fish size raised to
the power 0.42.

The lines in Fig. 3.1 have been replotted in Fig. 3.2 using the
common slope. From this second series of lines and the intercept
values in Table 3.b it will be noticed that the elevation of the line

Fig. 3.1. The relationship between $\log_{10}$ GET (h)
and $\log_{10}$ fish ~~size~~ weight (g) under specified

conditions. Each point represents

1 fish.
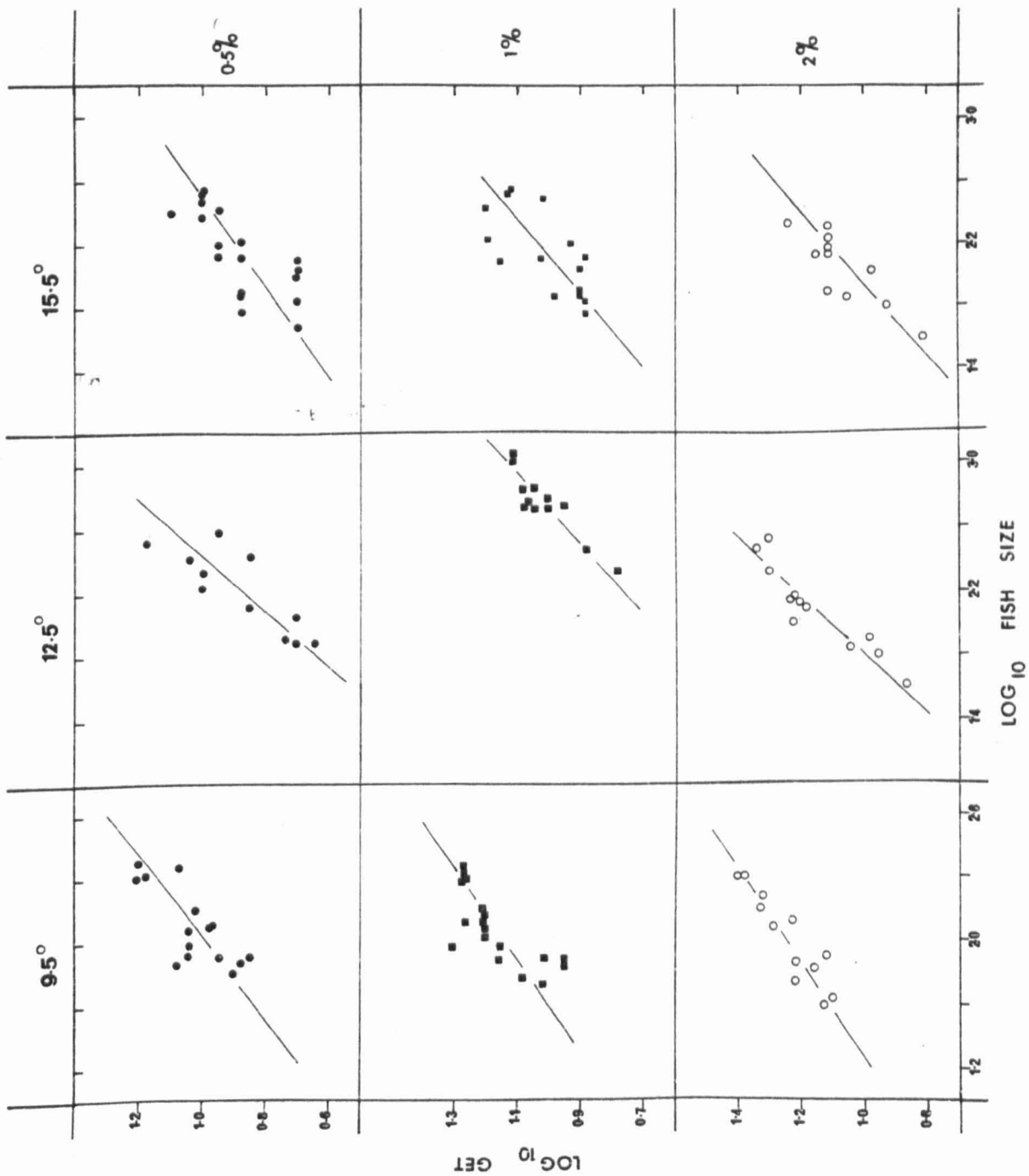
Fig. 3.2.   Utilising the common slope from

Worksheet 3.1 to replot the data

in Fig. 3.1.
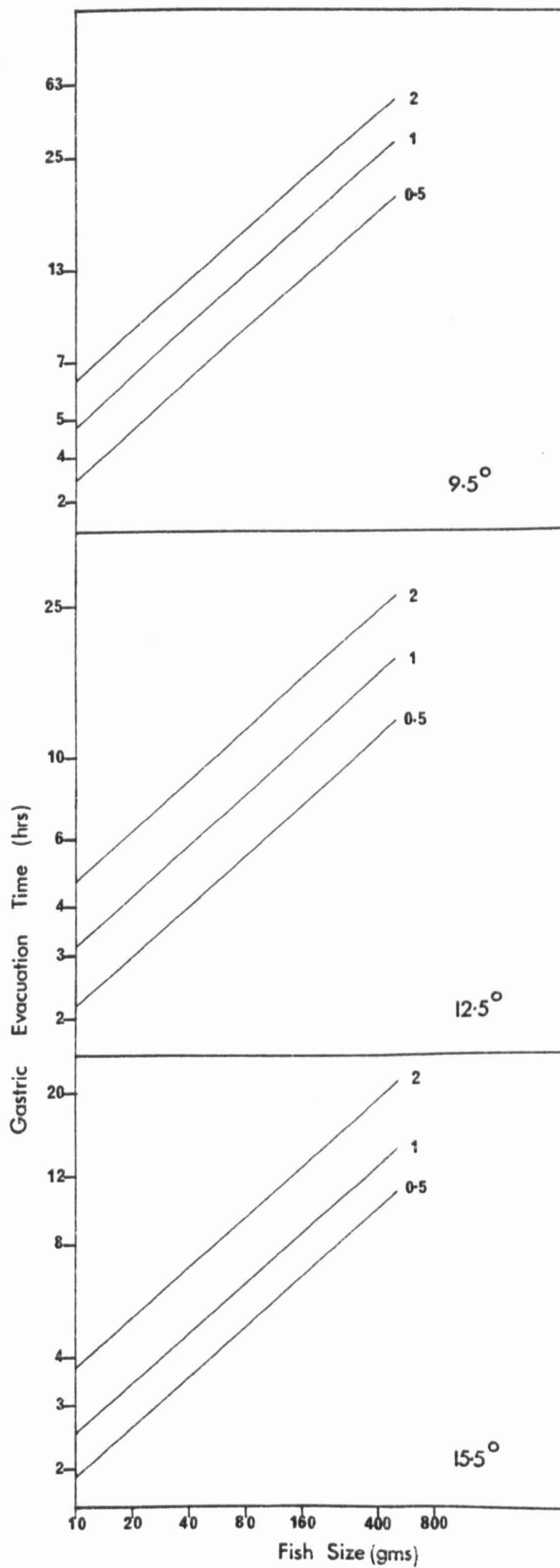
Worksheet 3.1 Calculations for Testing for Significant Differences between Slopes and Elevations of the Simple Linear Regression Lines (Log$_{10}$ GET vs Log$_{10}$ Fish Weight) obtained under specified conditions

Temperature ^{o}C	Meal size % body wt.	Σx^2	Σxy	Σy^2	Residual SS	Residual DF
9.5	0.5	0.7660	0.2913	0.1753	0.0645	13
"	1.0	0.9265	0.3267	0.3817	0.2665	17
"	2.0	0.900	0.2999	0.1141	0.0142	11
12.5	0.5	0.8547	0.4854	0.3522	0.0765	12
"	1.0	0.4709	0.2146	0.1088	0.0110	10
"	2.0	0.8447	0.4516	0.2765	0.0351	10
15.5	0.5	1.0893	0.3847	0.2942	0.1583	17
"	1.0	1.0716	0.4714	0.3146	0.1072	16
"	2.0	0.7100	0.3014	0.1557	0.0278	10
Pooled Regression				2.1731	0.7611	116
Common Regression		7.6337	3.2270	2.1731	0.8090	
Total Regression		7.9784	2.5079	4.8377	4.0494	132

(i) To test for differences between slopes: $H_0 : \beta_1 = \beta_2 = \beta_3$, H_A : All 9 β's are not equal

$$F = \frac{0.8090 - 0.7611}{9 - 1} \div \frac{0.7611}{116} = 0.913$$

Since $F_{0.05}$ (1), 8, 116 = 2.02, do not reject H_0

Common slope = 0.4227

(ii) To test for differences between elevations : $H_0 : \alpha_1 = \alpha_2 = \alpha_3$, H_A : All 9 α's are not equal

$$F = \frac{4.0494 - 0.8090}{9 - 1} \div \frac{0.8090}{116} = 58.03$$

Since $F_{0.05}$ (1), 8, 116 = 2.02, reject H_0

Worksheet 3.2 Testing for Significant Differences between the Elevations of the Simple Linear Regression (Log$_{10}$ GET vs Log$_{10}$ Fish Weight) obtained under specified conditions

Condition Temperature ^{o}C	Between meal sizes % b. wt.	Critical q $\alpha = 0.05$	Calculated q	Whether significant
9.5	0.5 vs 1.0	2.89	31.93	YES
	1.0 vs 2.0	2.89	4.40	"
12.5	0.5 vs 1.0	4.46	9.30	"
	1.0 vs 2.0	4.46	12.28	"
15.5	0.5 vs 1.0	2.89	10.26	"
	1.0 vs 2.0	2.92	4.07	"

Condition Meal size % body wt.	Between temperatures ^{o}C			
0.5	9.5 vs 12.5	2.92	22.56	YES
	12.5 vs 15.5	2.89	11.04	"
1.0	9.5 vs 12.5	2.89	15.77	"
	12.5 vs 15.5	2.92	5.31	"
2.0	9.5 vs 12.5	2.95	11.42	"
	12.5 vs 15.5	2.95	18.96	"

Condition 12.5^{o}C, 1% body wt.	Between meal composition % BaSO$_4$			
	25 vs 50	3.01	2.05	NO
	50 vs 75	2.99	0.836	"
	25 vs 75	2.97	-3.378	YES

N.B. The summations Σx^2, Σxy, Σy^2 are sums of squares.

relating $\log_{10}$ GET to $\log_{10}$ fish size increases with meal size at each temperature. The elevation also decreases with a rise in temperature at each meal size. These differences are statistically significant (Worksheet 3.1) and more detailed tests were carried out to determine between which lines the significant differences occurred. The test used was a modification of the Newman-Keuls Test (Zar, 1974) for which the test statistic q, is given by:

$$q = \frac{\bar{Y}_A - \bar{Y}_B - b_c \, (\bar{X}_A - \bar{X}_B)}{SE}$$

where

$$b_c = \frac{(\Sigma xy)_A + (\Sigma xy)_B}{(\Sigma x^2)_A + (\Sigma x^2)_B}$$

$$SE = \sqrt{\frac{(S^2 y \cdot x)_p}{2} + \frac{1}{n_A} + \frac{1}{n_B} + \frac{(\bar{X}_A - \bar{X}_B)^2}{(\Sigma x^2)_A + (\Sigma x^2)_B}}$$

and the suffices A and B refer to the two regressions being compared (Worksheet 3.2). The worksheet shows that at each temperature GET is significantly shorter the smaller the meal. In addition, for each meal, GET is significantly reduced by a rise in temperature. Before these alterations in GET could be quantified it was necessary to determine whether the extent of each (i.e. that caused by changes in temperature and that caused by changes in meal size) was affected by the specified conditions of the experiment.

To do this the fish used in each experiment were grouped into 3 size classes: 60-100 gms, 120-160 gms and 220-260 gms. Worksheet 3.3a shows that neither fish size nor temperature affects the rate at which GET alters with meal size and the common slope calculated is 0.21. The effect of temperature on GET is similarly unaffected by the

Worksheet 3.3a   <u>Testing for Differences in the Slope of the Simple Linear Regression (Log_{10} GET vs Log_{10} Meal Size) obtained for 3 size groups of fish each tested at 3 temperatures</u>

Fish Size (gms)	Regression Temperature (^{O}C)	Σx^2	Σxy	Σy^2	Residual SS	DF
60-100	9.5	4.735	1.007	0.265	0.051	15
"	12.5	3.875	0.777	0.172	0.016	6
"	15.5	4.229	0.838	0.272	0.106	10
120-160	9.5	3.909	0.685	0.170	0.050	9
"	12.5	3.682	0.821	0.198	0.015	9
"	15.5	3.909	0.923	0.288	0.070	9
220-260	9.5	2.719	0.427	0.084	0.017	6
"	12.5	2.714	0.646	0.177	0.023	5
"	15.5	0.375	0.226	0.150	0.014	4
Pooled					0.362	73
Common		30.147	6.350	1.776	0.439	

$F_{0.05}$ 6, 73 = 2.07   Calculated F = 1.941 (not significant)

<u>Common slope = 0.211</u>

Worksheet 3.3b   <u>Testing for differences in the slope of the Simple Linear Regression (Log_{10} GET vs Log_{10} Temperature) obtained for 3 size groups of fish each tested at 3 meal sizes</u>

Fish size (gm)	Regression Meal size (% b. wt.)	Σx^2	Σxy	Σy^2	Residual SS	DF
60-100	0.5	0.135	−0.195	0.411	0.129	14
"	1.0	0.115	−0.092	0.173	0.100	9
"	2.0	0.068	−0.07	0.100	0.030	7
100-160	0.5	0.101	−0.124	0.246	0.094	10
"	1.0	0.101	−0.122	0.195	0.048	13
"	2.0	0.079	−0.059	0.052	0.008	9
220-260		0.055	−0.063	0.123	0.051	5
"		0.068	−0.014	0.017	0.014	5
"		0.031	−0.037	0.048	0.004	2
Pooled					0.478	74
Common		0.753	0.776	1.365	0.566	

$F_{0.05}$, 8, 74 = 2.06   Calculated F = 1.70 (not significant)

<u>Common slope = −1.03</u>

Worksheet 3.3c

MEANS:

N = 134
M = 4
K = 3

1	2.1163
2	1.0892
3	0.0916
4	1.0283

SUMS OF SQUARES AND CROSS PRODUCTS ABOUT MEANS:

	1	2	3	4
1	7.9737	0.3271	6.9023	2.4994
2	0.3271	1.0874	0.1767	−1.0752
3	6.9023	0.1767	13.4518	5.9399
4	2.4994	−1.0752	5.9399	4.6586

CORRELATION COEFFICIENTS:

	1	2	3	4
1	1.0000	0.1111	0.6665	0.4101
2	0.1111	1.0000	0.0462	−0.4777
3	0.6665	0.0462	1.0000	0.7503
4	0.4101	−0.4777	0.7503	1.0000

VARIABLE	REG. CO.	S.E. OF R.C.	T-VALUE
1	−0.06784	0.03724	−1.82157
2	−1.04801	0.07527	−13.92302
3	0.49014	0.02853	17.18119
CONST	2.26855	0.10647	21.30732

MULTIPLE CORRELN.   0.91128

STANDARD ERROR OF ESTIMATE   0.07795

F-VALUE   212.22062

SUM OF SQUARES ATTRIBUTABLE TO REGRESSION   3.86864

SUM OF SQUARES OF DEVIATION FROM REGRESSION   0.78994

Variables: $1 = X_1 = Log_{10}$ Fish Weight (gms)

$2 = X_2 = Log_{10}$ Temperature (^{O}C)

$3 = X_3 = Log_{10}$ Meal size (gms)

$4 = Y = Log_{10}$ GET (hours)

Equation: $\underline{Y = 2.269 - 0.068X_1 - 1.048X_2 + 0.490X_3}$

specified meal size or fish size and GET alters with temperature raised to the power -1.03 (Worksheet 3.3b).

The common slope obtained in Worksheet 3.3a is of limited use. As the meal sizes are expressed in % body weight, this exponent does not describe the change in GET with change in absolute mass (or volume) of food given. To obtain a more relevant exponent, it was necessary to return to the raw data and transform the meal given to each fish from % body weight units to grams. A graph of $\log_{10}$ GET against $\log_{10}$ meal size was then prepared for each of the three size groups of fish used in Worksheet 3.3a and b. Fig. 3.3 gives the series of lines obtained for GET data at 15.5°C. These lines are almost parallel and the differences between slopes not being significant amongst all size-groups at all temperatures (Worksheet 3.3d p57) a common slope was obtained with a value of 0.516. A significant point to note from Fig. 3.3 is that for a given meal size (gms) the GET is shorter the larger the fish; this trend is opposite to that obtained when meal sizes are expressed to % body weight (see Fig. 3.2).

In Worksheet 3.3c all the gastric evacuation data have been pooled and analysed by computer to give the multiple regression equation:

$$Y = 2.269 - 0.068X_1 - 1.048X_2 + 0.490X_3$$

It will be noticed that the exponent describing the change in log GET (Y) with log animal size (X_1) is negative, so that when all other factors are kept constant and meal size is expressed in grams, GET will be shorter the larger the fish. The correlation coefficients in Worksheet 3.3c indicate that meal size is the most potent factor affecting GET whilst fish size produces the least effect.

Fig. 3.3.   The relationship between $\log_{10}$

evacuation ~~rate~~ *time* and $\log_{10}$ meal size

at 15.5°C.

Squares and dashed line 、 60-100 gm fish

Circles and solid line   200-260 gm fish
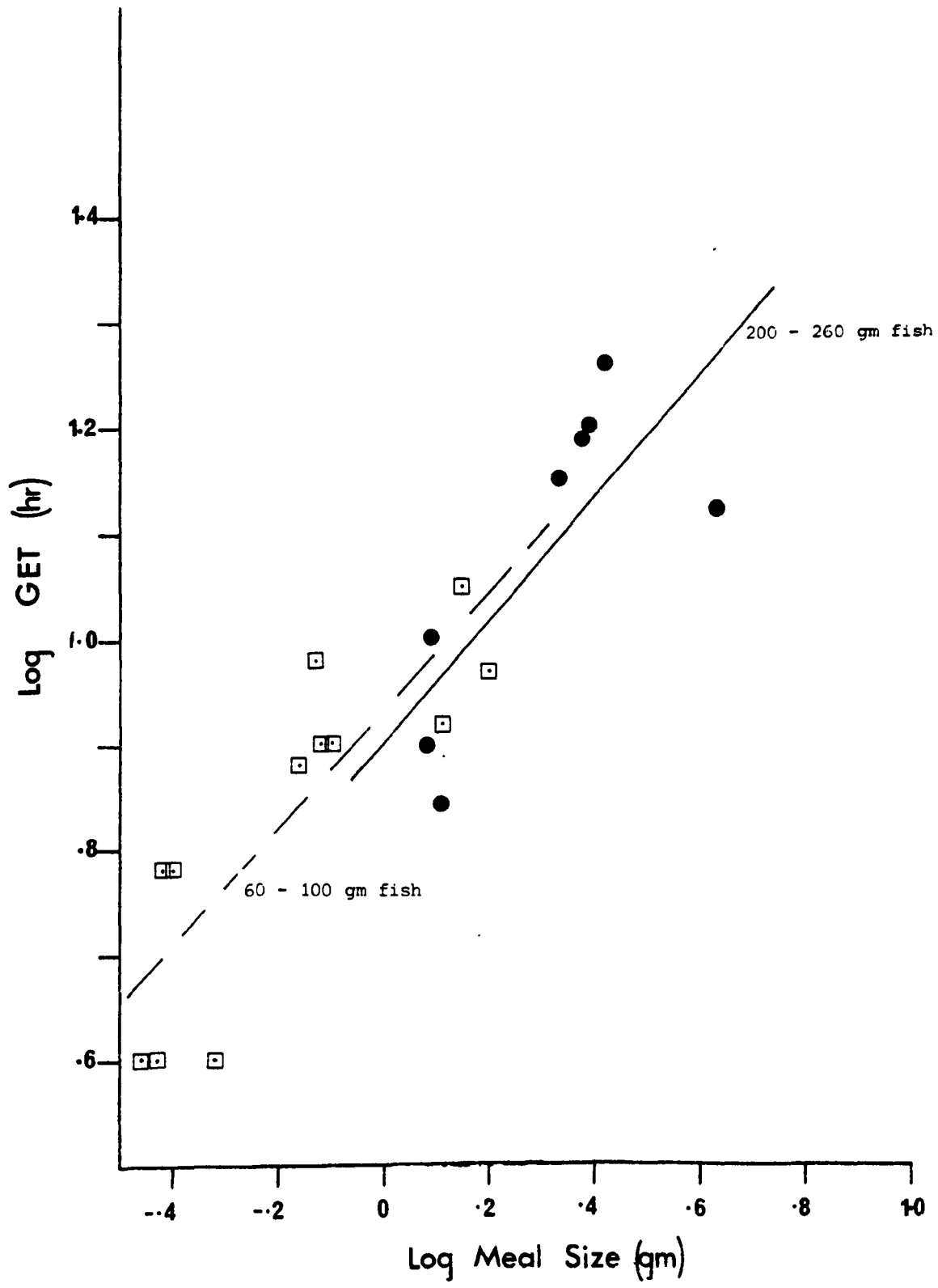
Worksheets 3.3d. Testing for differences in the slopes of the simple linear regressions relating $\log_{10}$ GET (Y) to $\log_{10}$ meal size (X) obtained under specified conditions

Regression					Residuals	
Fish weight (gms)	Temperature (°C)	Σx^2	Σxy	Σy^2	SS	DF
60-100	9.5	0.836	0.353	0.666	0.517	15
"	12.5	0.578	0.306	0.172	0.01	6
"	15.5	0.610	0.344	0.271	0.077	10
120-160	9.5	0.813	0.374	0.232	0.060	11
"	12.5	0.566	0.330	0.199	0.007	10
"	15.5	0.679	0.40	0.293	0.057	9
200-260	9.5	0.426	0.170	0.076	0.010	6
"	12.5	0.265	0.146	0.111	0.031	3
"	15.5	0.264	0.156	0.156	0.064	
300-360	15.5	0.333	0.196	0.138	0.023	5
Pooled					0.856	81
Common		5.380	2.775	2.314	0.883	

To test H_O: $B_1 = B_2 \ldots\ldots\ldots B_{10}$ H_A: all 10 B's are not equal.

F   Since $F_{0.05(1)}$ $9,81 = 1.99$ Do not reject H_O.

Common slope = 0.516

Establishing the shape of the Gastric Evacuation Curve: The data
obtained from the serial slaughter experiments are shown untransformed
in Fig. 3.6. The scatter of points confirm that fish of similar size
do have different evacuation rates. To determine the best description
of the decline of stomach contents with time the data were transformed
to give several regression models as shown in Worksheet 3.4. Each

Worksheet 3.4 Comparisons of Regressions performed on gastric evacuation data obtained from plaice force-fed
1% body weight of a paste meal and sacrificed at intervals
Top series: 20-22 cm fish   Bottom series: 26-28 cm fish   Y = dry weight of residuum

Regression type	Total SS	Regression SS	DF	MS	Deviation SS	DF	MS	F Value
Linear with untransformed Y	632.77	269.53	1	269.53	354.24	15	23.62	11.41*
Linear with $\sqrt{Y}$	21.36	14.15	1	14.15	7.21	15	0.48	29.48*
Semilog	3.16	2.042	1	2.042	1.11	15	0.07	29.14*
Log-log	3.16	1.907	1	1.907	1.25	15	0.08	23.84*
Exponential	15.66	8.76	1	8.76	6.91	15	0.46	19.04*
Linear with untransformed Y	4088.96	2158.29	1	2158.29	1930.68	26	74.26	29.06*
Linear with $\sqrt{Y}$	77.47	45.36	1	45.36	32.12	26	1.24	36.58*
Semilog	6.88	4.10	1	4.10	2.79	26	0.11	37.27*
Log-log	6.88	4.21	1	4.21	2.68	26	0.10	42.10*
Exponential	36.93	21.76	1	21.76	15.17	26	0.58	37.52*

* Significant at $P \leqslant 0.05$

model used gave a significant regression with both sets of data but
there were considerable variations between the F-values. The F-values
for the larger fish were generally higher than those for the smaller
fish. This may be the result of greater variability amongst the Y
values of the smaller fish caused by proportionally larger losses in
the recovery of the much smaller residues. The status of the models
alter between the two size-groups, e.g. the linear plot of $\sqrt{Y}$ gives
the highest F-value with the smaller fish but ranks only fourth with
the larger size-group. The overall fit appears to be provided by the
linear $\sqrt{Y}$ and the semi-log plots. Of the two the former is more
acceptable since as outlined in the preface to this chapter, it may

Fig. 3.6. The decline in amount of stomach
           contents with time. Each point
           represents 1 fish.

           Top   20-22 cm fish
           Bottom   26-28 cm fish

Dry weight of residue (grams)

Hours after ingestion
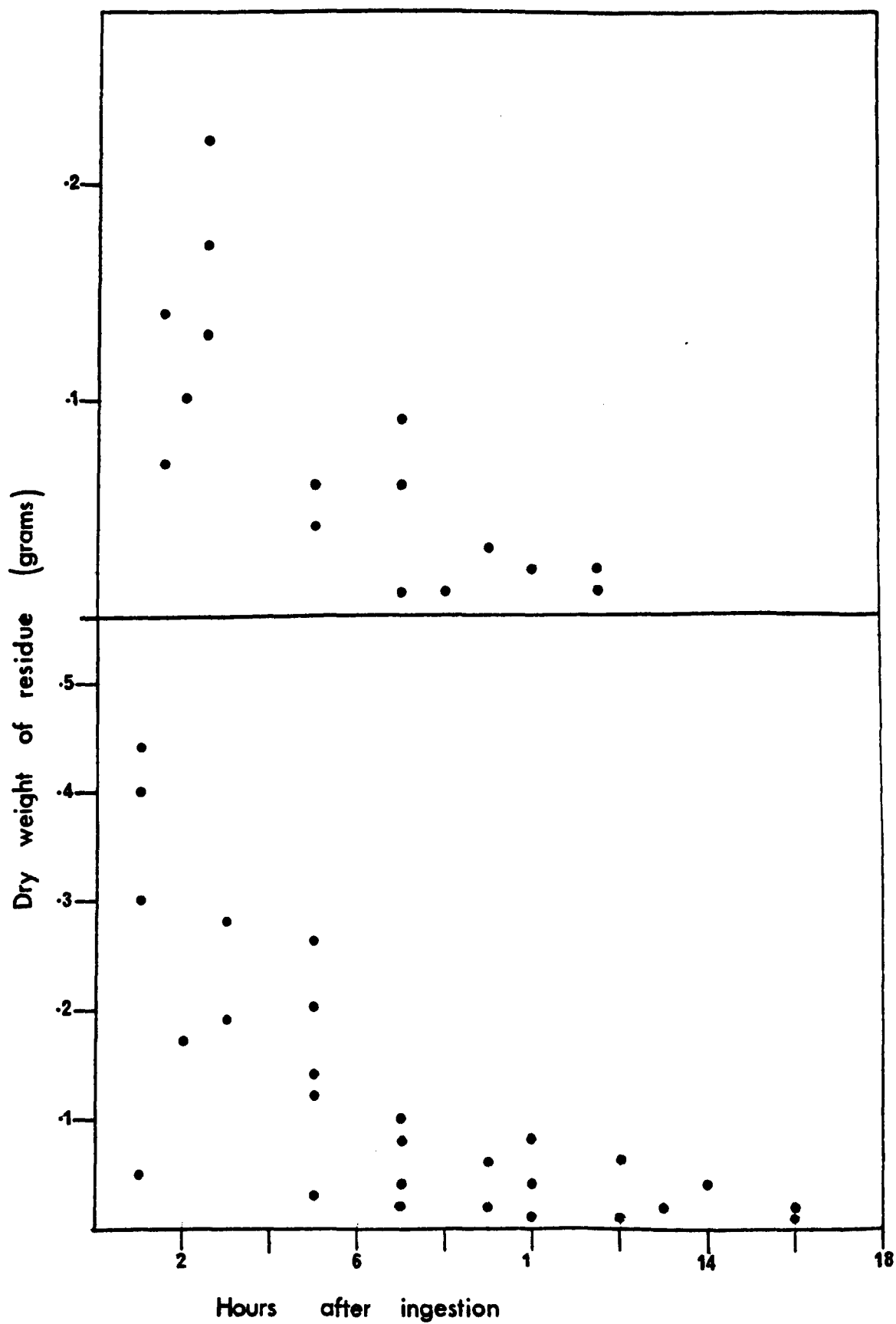
have a physiological basis.

The applicability of the square root relationship having been verified above, attempts were made to estimate the rate of evacuation (g/hr) from the GET data. At each of the three temperatures the equations describing $\log_{10}$ GET vs $\log_{10}$ fish size (Table 3.b) were used to calculate the time required to clear the stomach of meals of specified size in fish of 400, 200 and 100 gms. These meal sizes, expressed in the original equations as % body weight, were transformed into $\sqrt{gms}$ and the rate of evacuation averaged over the first two hours after ingestion. Fig. 3.4 and legends give a worked-out example of this procedure. It will be noticed that the evacuation lines for the three meals are parallel. This was so in every other case tested and indicates that once the line describing evacuation of the largest meal the stomach can hold has been established, the depletion curve of any other meal can be constructed by starting at the appropriate point on the Y-axis and drawing a line parallel to that of the maximum meal. In other words, the depletion curves of meals of various sizes would be statistically indistinguishable. Similar trends have been observed by Tyler (1970) for young Gadus and Beamish (1972) for Micropterus.

The procedure outlined in Fig. 3.4 makes it possible to investigate the effect of meal size on the rate of evacuation. This is done by plotting the $\log_{10}$ rate of evacuation (gm/hr) against $\log_{10}$ meal size (gm) and is illustrated in Fig. 3.5 for fish of 50, 100, 200 and 400 gms at 9.5, 12.5 and 15.5°C. It is obvious from this plot that the specified temperature does not affect the exponent describing the change in evacuation rate with change in meal size though the elevation of

Fig. 3.4.   Estimating the rate of evacuation

from G.E.T. data.   The diagonal lines

connect the square root of meal size

to GET.   Evacuation rate was

averaged over the first two hours.

Fish Size	**200 gm**					**100gm**				**50 gm**			

Meal Size (MS) gms	$\sqrt{MS}$	Residue after 2 hrs $\sqrt{R}$	Rate g/hr
1.0	1.0	0.76	0.21
2.0	1.4	1.17	0.32
4.0	2.0	1.77	0.44

MS	$\sqrt{MS}$	$\sqrt{R}$	g/hr
0.5	0.71	0.48	0.14
1.0	1.0	0.78	0.20
2.0	1.41	1.19	0.29

MS	$\sqrt{MS}$	$\sqrt{R}$	g/hr
0.25	0.50	0.29	0.09
0.50	0.71	0.51	0.13
1.00	1.00	0.82	0.17

$\sqrt{\text{Meal Size}}$ (gm)

Gastric   Evacuation   Time   (hours)
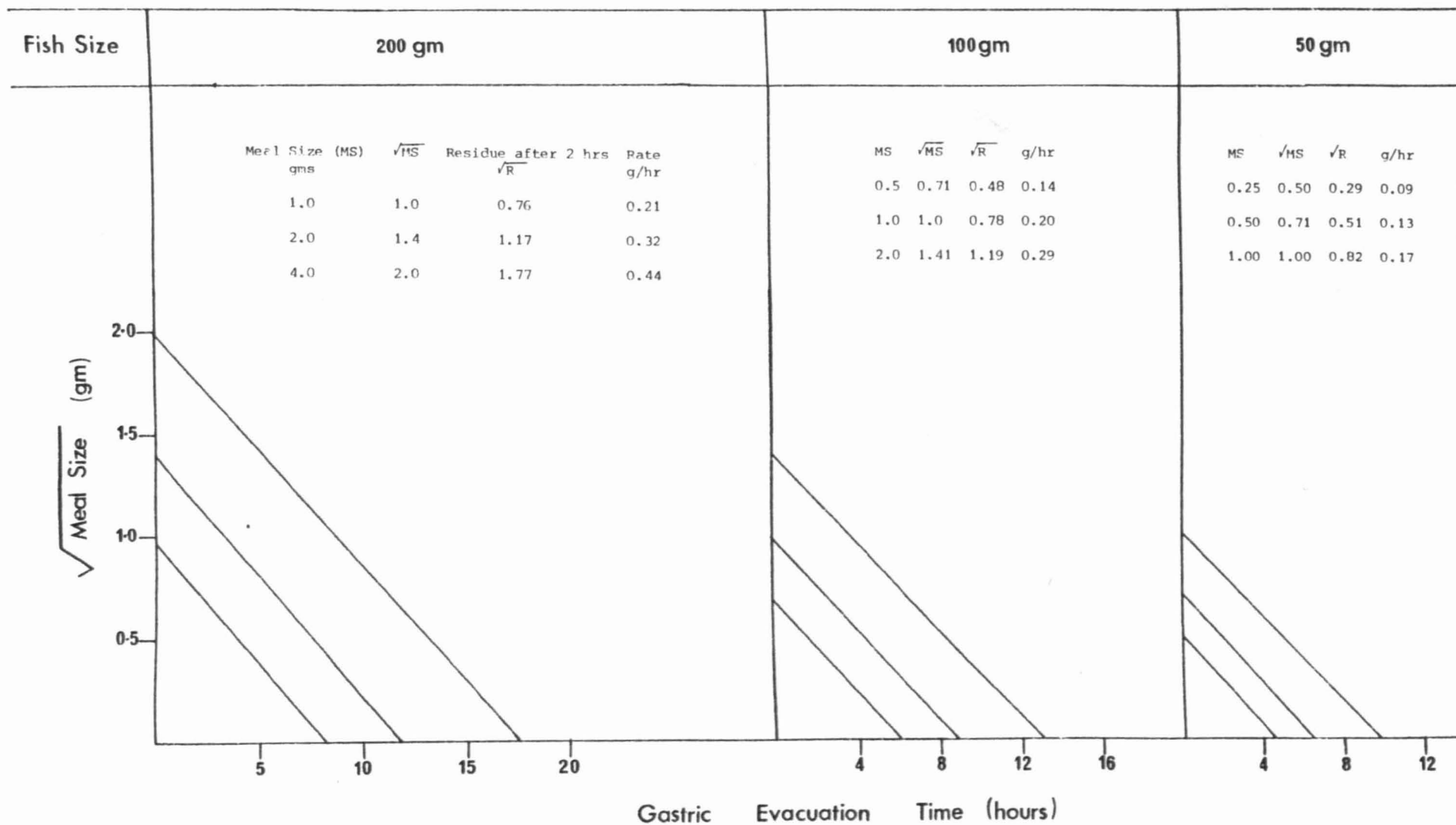
Fig. 3.3. The relationship between evacuation
rate and meal size.

Circles   60-100 gm fish

Squares   120-160 gm fish

Triangles 200-260 gm fish

Stars   300-360 gm fish

Open symbols $9.5^{\circ}C$

Solid symbols $15.5^{\circ}C$

The points for the $12.5^{\circ}C$ (dashed)

line have been omitted for visual

clarity.
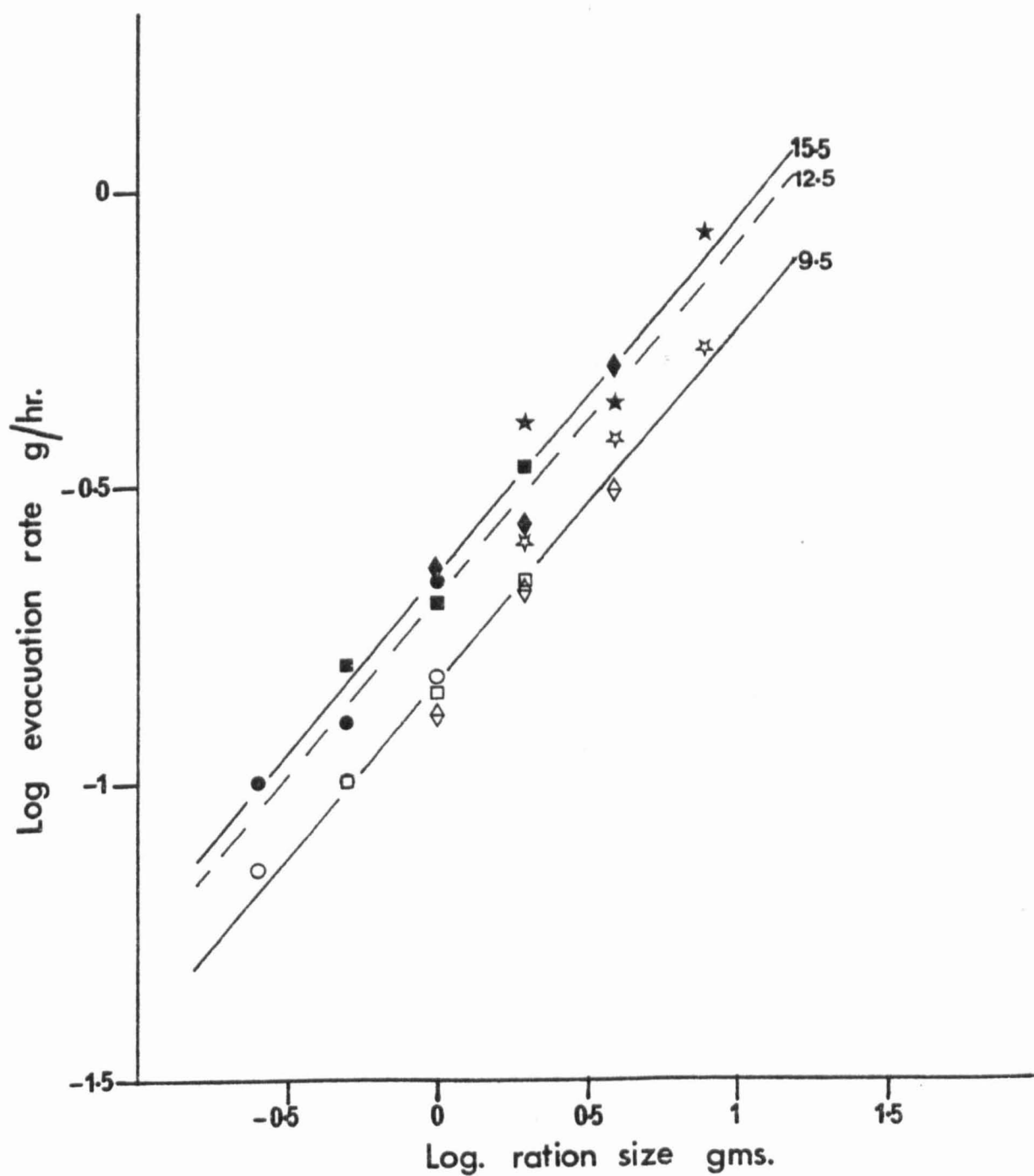
Worksheet 3.3e.   Testing for differences in the slope of the simple linear regressions of $\log_{10}$ ration (Y) on $\log_{10}$ meal size (X) obtained for fish of 50, 100, 200 and 400 gms of 3 temperatures

Regression	x^2	xy	y^2	SS	DF
9.5°C	2.084	1.2136	0.7182	0.0115	10
12.5°C	2.084	1.2462	0.7558	0.0106	10
15.5°C	2.084	1.2627	0.7849	0.0198	10
Pooled				0.0419	30
Common	6.252	3.7225	2.2589	0.0425	

To test H_O: $B_1 = B_2 = B_3$ H_A: All 3 B's are not equal.

F = 0.215   Since $F_{0.05}(1)$ 2,30 = 19.5   Reject H_A.

<u>Common slope = 0.595</u>

the lines alter with temperature. All the points were therefore pooled
and a total regression slope of 0.60 was obtained (Worksheet 3.3e).

DISCUSSION

The findings of the present study on the effects of temperature, fish size and meal size on gastric evacuation times agree with what a review of the literature would predict, viz:

i)   A rise in temperature will shorten the GET for a meal of given size. GET was found to vary with temperature raised to the power -1.03 (Fig. 3.2; Table 3b; Worksheet 3.3b, p. 54-57).

ii)   When fed weight-specific meals (i.e. % body weight units) of equal size, small fish will complete gastric evacuation earlier than larger fish at the same temperature. GET varied with fish size raised to the power 0.42 (Fig. 3.2; Table 3b; Worksheet 3.1, p. 54-57).

iii)   When fed meals of equal absolute size (gms) small fish require a longer time to complete gastric evacuation than larger fish. GET varied as fish size raised to the power -0.068 (Worksheet 3.3c).

iv)   For a fish of given size at a specified temperature, the larger the meal (% body weight or gms), the longer the time to complete gastric evacuation. For meals expressed as % body weight GET altered as meal size raised to the power 0.211 (Worksheet 3.3a, p. 54-57). For meals expressed as gms the exponent was ca. 0.50 (Fig. 3.3; Worksheets 3.3c and d, p. 54-57).

v)   The rate of evacuation as gms/hr is faster the larger the meal (gms). Gastric evacuation rate was found to vary as meal size raised to the power 0.60 (Fig. 3.5; Worksheet 3.3e, p. 59-61).

In the preface to this chapter it was made obvious that the literature is replete with gastric evacuation data. Unfortunately very few attempts have been made to construct models that would describe these data and predict the performance of fish under various conditions. To date only one model, that of Fänge and Grove (1978) has been formulated for this purpose. This is the surface-area model which predicts that:

i)   GET will change according to meal size raised to the power 0.33.

ii) If fish are given weight specific meals, GET for a given meal size should vary as fish size to the power 0.33.

iii) The rate of gastric evacuation (g/hr) should vary as meal size to the power 0.67.

The beginnings of another model also exist in the statement by Hunt and Knox (1968) that the stomach may function as a constant frequency pump whose stroke volume is regulated by radial distension. Since most fish stomachs tend to approximate to a cylindrical shape, the radius will vary according to the square root of the volume. If volume is determined by the amount of stomach contents then the radius at any time is proportional to the square root of the volume or (if the same food type is used and density is therefore constant) to the square root of the weight of the food. Since radius is also proportional to circumferential tension, the strength of stimulus received by receptors in the stomach wall and therefore perhaps the muscular response, will be proportional to the (meal size)$^{\frac{1}{2}}$. Rate of emptying will therefore vary as meal size to the power 0.5, i.e.

$$\frac{dW}{dt} = -f(M)^{0.5}$$

The time taken to clear the stomach (GET, t_λ) will also vary in the

same way, i.e.

$$GET \propto (Meal\ size)^{0.5}$$

This relationship will hold whether meal sizes are expressed in gms or
% body weight.

In the present work GET varied as meal size to the power ca. 0.5
(Worksheets 3.3c and d). This value is much closer to the square root
model than it is to the surface-area model of Fänge and Grove. The
exponent for the rate of evacuation was 0.6 and was not significantly
different from the 0.67 predicted by the surface-area model ($t_{0.05}$ 34,
- 2.03; calculated t = -16.75). When tested with the square root
prediction of 0.5, there was a significant difference (t = 2.5).
It is more than likely that neither model can adequately describe all
gastric evacuation data on its own, mainly because in the view of .
this writer, each gives insular consideration to one of a pair of
factors that may frequently work in concert. Descriptively it would be
difficult to discuss the transfer of food from stomach to intestines
without mentioning either enzymes and the surface-area nature of their
release and activity, or the churning action resulting from gastric
motility. It may be unrealistic to free mathematical models from these
constraints and the solution may lie in a successful combination of
these two models.

Swenson and Smith (1973) worked with the walleye Stizostedion
vitreum vitreum and concluded that the evacuation rates obtained by
force-feeding single meals were too retarded to be of much use in field
determinations of daily ration. This view is confirmed in the present
study. In November, gastric evacuation was completed in 6 hours between
16.30 and 22.30 hours by all 3 size-groups (Figs. 2.2d, 2.2iv). If

the median length of each size-group is taken as its average length
(i.e. 17.5, 22.5 and 32.5 cm respectively) and a length-weight relation-
ship of 0.01 L^3 adopted (see Chapter 4, p. 74) this means that meals
of 0.6% body weight (smalls) and 1.5% body weight (large) took only
6 hours to evacuate in the wild. Laboratory values at that temperature
(ca. 10°C) would be 14.3 hours (x 2.3) and 22.79 hours (x 3.8)
respectively. This is not to say that laboratory data are valueless.
It is possible that the direction (though not the amount) of the changes
in GET caused by such factors as meal size and temperature indicate
the trends in field situations.

The results obtained here may then be taken as support for the
postulations in Chapter 2 that larger meal sizes and higher temperatures
will mean greater evacuation rates in summer. Large fish have been
shown to have a faster evacuation rate (gm/hr) than small fish.
However the time required to evacuate a weight-specific meal of equal
size (% body weight) is longer for larger fish. It follows from this
that unless they are more efficient at foraging, the daily ration of
large fish (% body weight) will be less than that achieved by smaller
individuals. These expected differences in ration size between
seasons for fish of a given size and between different sized fish
during a given season should be reflected in seasonal changes in
condition and in seasonal patterns of growth. This possibility will be
investigated in the next chapter.

GET was significantly altered only when the inorganic content of
the diet exceeded 50% (Worksheet 3.2, p. 53). This may mean the
existence of a calorie threshold below which gastric evacuation rate
may be increased to raise total food intake in compensation for the drop

in nutritive value. This phenomenon, referred to in the literature as "calorie counting", has been reported for the goldfish <u>Carassius</u> (Rozin and Meyer, 1961, 1964), <u>Salmo</u> <u>gairdneri</u> (Lee and Putnam, 1973; Grove et al., 1978). In each case an increase in the daily ration followed dilution of the diet and Grove <u>et al.</u> were able to show for <u>S. gairdneri</u> that this was due to increased evacuation rates. The mechanisms responsible for this are as yet unknown but may either depend on decreased production of enterogastrone from the intestines or a change in activity of extrinsic nerves supplying the stomach (Fänge and Grove, 1978).

Chapter 4

Studies on seasonal trends in growth and condition.

Preface

Seasonal variations in temperature and prey density provide an a priori reason for expecting the growth and condition of fish populations to follow a seasonal schedule. The literature on condition is a chronology of successive attempts to obtain a mathematical description of general applicability. Condition is a measure of fatness and can therefore be an index to the suitability of the environment for the growth of fish. To be of any use, a mathematical description of condition should make possible the measurement of temporal changes in this feature within a population, as well as allow comparisons between monospecific populations inhabiting different localities. Fatness has logically been thought of as the amount of mass associated with a unit length of fish and measurements of condition are based on length-weight relationships. For most species of fish, the relationship between length (L), and weight (W) is adequately described by the equation:

$$W \approx aL^n \qquad \dots\dots\dots\dots\dots\dots\dots\dots\dots \text{(i)}$$

where a is a constant and n is an exponent usually lying between 2.5 and 4.0 (Le Cren, 1951). Ideally growth would be isometric so that $n = 3$ and this has been reported for Salmo trutta by Allen (1938).

In the majority of cases, condition has been measured as a condition factor obtained by dividing the weight observed at length (L) by the cube of the length (L^3). Fulton (1911) used the expression:

$$\text{Condition factor (C)} = \frac{W}{L^3} \qquad \dots\dots\dots\dots\dots\dots\dots\dots \text{(ii)}$$

Menzies (1920) obtained an average value of C for Salmo gairdneri and used it to calculate a new condition factor K, where

$$K = \frac{W}{C(= 0.000427)L^3} \qquad \dots\dots\dots\dots\dots\dots\dots\dots \text{(iii)}$$

Hile (1936) working with ciscoes <u>Leucichthys</u> <u>artedi</u> multiplied the right hand side of (ii) by 100 to obtain the expression

$$K = \frac{100W}{L^3} \quad \dots\dots\dots\dots\dots\dots\dots\dots \text{(iv)}$$

The reason for this appears to be that C obtained from (ii) is usually an awkward decimal number similar to that obtained by Menzies (op. cit.) for the denominator of equation (iii). Equation (iv) is the most widely used expression in studies on condition. (e.g. Todd, 1915 on <u>P. platessa</u>; Johnstone, 1924, and Stanek, 1964 on <u>Gadus</u> <u>morhua</u>). By dividing the observed weight at length by the cube of the length, equations (ii) - (iv) measure condition as the extent to which the observed weight deviates from that predicted by isometric growth. In practice, most fish species grow allometrically (Le Cren, 1951; Weatherly, 1972) and $n \neq 3$. In such cases the condition factor (K or C), will vary with the length of the fish in the manner

$$C \text{ (or K)} \propto L^{n-3}$$

For this reason equations (ii) - (iv) are inapplicable when $n \neq 3$ and they can only then be used to compare fish of the same length (Ricker, 1975).

The negative condition factor, K_n, (Le Cren, 1951), compares the observed weight with that predicted by an empirical length-weight relationship:

$$W = a L^n$$

in which the exponent n is derived from observed data. For each length the observed weight (W) can be compared with that predicted by the empirical relationship $(\hat{W})$ thus:

$$K_n = \frac{W}{\hat{W}} \quad \text{(Le Cren, 1951)} \quad \dots\dots\dots\dots\dots \text{(v)}$$

As with K in equation (iv), K_n is usually an awkward decimal number and it is customary to multiply the right hand side of (v) by 100 (see e.g.

Tyler and Dunn, 1976). Equation (v) can only be used to compare groups

of fish that are homogenous with respect to n. Homogeneity can be

tested for by an analysis of covariance and, when no significant

differences exist, a common exponent can be established. This exponent

can then be substituted into equation (v) and adjusted 'a' values obtained

for each group of fish being tested; these 'a' values will be reliable

measure of the condition of each group (Le Cren, 1951).

The length of the growing season and the shape of the growth curve

have been established for several freshwater species e.g. the cisco

Leucichthys artedi (Hile, 1936), the black crappie Pomoxis nigromaculatus

(Deason and Hile, 1947), O-group sockeye salmon Onchorhynchus nerka

(Ricker and Foerster, 1948), brook trout Salvelinus fontinalis (Cooper,

1953) and lake trout Salvelinus namaycush (Fry, 1953; Lawrie, 1962).

Relatively few marine fish have been investigated in this way, and they

include the Atlantic herring, Clupea harengus (Hodgson, 1925), O-group

winter flounder, Pseudopleuronectes americanus (Pearcy, 1962), and O-group

plaice Pleuronectes platessa (Lockwood, 1972). From the above and other

reports in the literature, growth in northern temperate waters starts

in March and is virtually over by the end of September. In some cases

(e.g. Lawrie, 1962; Lockwood, op. cit.) seasonal growth curves have been

interpreted as sigmoid: growth rate was slow at the start of the growing

season, increased to a maximum after a few weeks, and later tapered off

at the approach of winter. Other reports (e.g. Cooper, op. cit.; Macer,

1967) contain growth curves which rise abruptly with no sign of an initial

period of slow growth. According to Gerking (1966) such curves are the

result of inadequate sampling and measurement during the earliest parts

of the growing season.

Mathematical descriptions of seasonal growth of fish are scarce.

Ricker and Foerster(op. cit.) fitted their seasonal growth curve by
inspection. Semi-monthly instantaneous growth rates were obtained by
reading logarithms of weights from the curve, calculating the differences
between successive values and dividing by 0.4343. The annual instanta-
neous growth rate was taken as the sum of the semi-monthly rates. Allen
(1951) obtained instantaneous annual growth rates for S. fontinalis by
the expression

$$\frac{\log_e W_2 - \log_e W_1}{365}$$

where W_1 and W_2 refer respectively to the average weight per individual
at the start and end of the year. Lockwood (1972) fitted his seasonal
data on the growth of O-group plaice to the Von Bertalanffy equation.
Instantaneous growth rate (K) was calculated as the slope of the plot
of increase in average length per unit time $(\Delta \bar{l}/\Delta t)$ against median length
for time interval Δt $((\bar{l}_1 + \bar{l}_2)/2)$. The asymptotic length was taken as
the intercept value of this regression on the X-axis.

Materials and Methods

The fish used in these investigations were collected by otter trawl from the study area as they were needed. For studies on condition factor, the aim was a sample size of at least 30 fish of each sex with as wide a size range as possible. Each fish was sexed, its total length recorded to the nearest centimetre and its ungutted weight in grams to two places of decimal . In January and March mature and immature fish of each sex were treated separately.

Growth data were based on otoliths extracted from stratified sub-samples and read in the manner described in Chapter 1 (p. 11). Whenever possible, 10 fish of each sex were sampled at each centimetre length within the size range 14 cm and over. It was not always possible to achieve the required sample size with larger fish (> 30 cm) and generally the sample size decreased with the age of the fish. A mathematical description of seasonal growth requires that dates of sample collection be known with some accuracy. As it was not possible to catch the required numbers of fish in a single day's fishing, samples were collected over a period of not more than two weeks. In each case the midpoint of each collection period was taken as the date of collection. A study of seasonal growth also requires that a 'birthday' be assigned to the fish to mark the start of the growing season. In plaice, the opaque bands on the otolith are laid down in the season of heaviest feeding and growth (Blacker, 1974). As a first approximation therefore, the start of the growing season in spring was assumed to correspond to the appearance of a dark band on the edge of the otolith, outside the hyaline band characteristic of winter. To determine when this occurred, otoliths collected in different months were classified into 4 categories on the basis of the condition of their edges, viz.:

Those with a dark band typical of summer ('+').

Those with the hyaline band typical of winter ('++').

Those with an incipient and discontinuous dark band on the edge of the existing hyaline band ('+++'). (This condition was also found to be restricted to late autumn and winter).

Those with a very thin but mostly continuous dark band outside an existing hyaline band ('spots'). Fish with otoliths in this condition were assumed to be at the start of the new growing season.

The various otolith conditions described above are illustrated in Plate 3 .

Plate 3.   The 4 otolith conditions used in determining
          the length of the growing season.
          Magnification x 10.

SPOT

Note the incomplete but distinct opaque band at the edge.
This condition was most frequent in April but also occurred in February. In April this fish would be taken as 5 spot. For reasons explained in the text, it would be retained as a 4 year old in February.

+

Extensive opaque band around the edge. Typical of summer, May - August.

⧺

The edge is a hyaline band. Typical of autumn/winter i.e. September - February.

⧻

The very faint beginnings of a dark band can be seen at 12 o'clock, within the hyaline zone occupying the edge.

Table 4a. The length-weight relationship of male and female plaice in different months.

$Y = \log_{10}$ weight (gms). $X = \log_{10}$ length (cm). N = sample size. r = correlation coefficient. Equations and predictive regressions.

Month	Group	Males Equation	N	r	Females Equation	N	r
May	Mature and immature	Y = 0.023 + 2.76X	30	0.9364*	Y = 0.017 + 2.88X	30	0.9729*
June	"	Y = 0.059 + 2.51X	30	0.9524*	Y = 0.020 + 2.83X	30	0.9883*
July	"	Y = 0.086 + 2.40X	30	0.8605*	Y = 0.035 + 2.67X	30	0.9587*
September	"	Y = 0.009 + 3.09X	22	0.9833*	Y = 0.013 + 2.97X	30	0.9476*
November	"	Y = 0.024 + 2.74X	32	0.9808*	Y = 0.009 + 3.04X	35	0.9828*
January	Immature	Y = 0.030 + 2.68X	44	0.9725*	Y = 0.014 + 2.92X	27	0.9689*
	Mature	Y = 0.037 + 2.62X	35	0.9145*	Y = 0.010 + 3.01X	49	0.9559*
	Spent	–			Y = 0.022 + 2.75X	42	0.9580*
March	Immature	(Y = 0.012 + 2.93X	18	0.9842*)	Y = 0.007 + 3.10X	16	0.9539*
	Mature				Y = 0.007 + 3.08X	25	0.9472*
	Spent				Y = 0.038 + 2.60X	16	0.9766*

*Significant at $\rho < 0.001$.

(   ) mature and immature combined, and may include some spent males.

Results

(a) <u>Condition</u>: The results obtained are presented as length-weight

relationships in Table 4a. An analysis of covariance in the manner of

worksheet 3.1 (p. 53) showed that the slopes of all groups were homogenous

($F_{0.05}$ (1) 17,562 = 1.62, calculated F = 1.53). The value of the common

exponent was 2.83, with a correlation coefficient of 0.9606 (significant

at $\rho < 0.001$). The common slope was then divided by the correlation

coefficient to give a geometric mean slope of 2.946 (Ricker, 1973). Next

it was necessary to determine whether the 'a' values of males and

females were significantly different within each month. The test employed

was the modified Newman-Keuls test described earlier on p. 54 . The

results of these tests are contained in Table 4b and show no significant

differences in 'a' between males and females within the months of May, June,

July, September and November. In January and March when spawning is

imminent, data were collected for immature and mature fish of each sex

separately. With the exception of spent female plaice, there was no

detectable difference in the 'a' values of immature and mature fish of

either sex in a given month. The number of spent males caught were too

few to allow a similar comparison. On the basis of these findings, male

and female fish have been combined in Table 4c which gives for each month,

the condition factor of the plaice in the study area. These factors

were obtained as adjusted 'a' values with the common (GM) slope as

outlined earlier (p. 69). This table also gives the calculated weight of

a 30 cm fish as an illustration of the changes in condition with time of

year. Statistical comparisons of the condition factors in Table 4c

revealed the following: The fish were fattest in June and July. In each

of the intervals July to September, September to November and November to

January, there was a significant loss of condition. Spent females were

significantly leaner than other fish in January and in March. The

steepest decrease in condition occurred between January and March. This

Table 4b. Testing for significant differences between the unadjusted 'a' values of the predictive linear regressions (Log_{10} fish weight vs. Log_{10} fish length; Table 4a) obtained for several groups of plaice in different months

Month	Between Groups	Critical q at $\alpha = 0.05$	Calculated q
May	♀ vs ♂	2.829	0.631
June	"	2.829	1.042
July	"	2.829	0.944
September	"	2.858	0.422
November	"	2.829	2.57
January	♂ (mature vs immature)	2.829	0.624
	♀ (mature vs immature)	2.829	0.212
	♀ (spent vs others)	2.829	5.590*
March	♀ (mature vs others)	2.858	0.721
	♀ (spent vs others)	2.858	7.03*

* significant at $\alpha = 0.05$

Table 4c. Variation of the condition factor with time of year

Month	Condition factor x 100	Calculated wt. of a 30 cm fish	
May	1.30	292.11 gms	*Power is*
June	1.43	321.32 "	*2.946*
July	1.41	316.82 "	
September	1.35	303.34 "	
November	1.30	292.11 "	
January	1.26	283.12 "	
	1.12*	251.66 "	
March	1.16	260.65 "	
	1.09*	244.92 "	

*spent females.

Table 4d (i) % Occurrence of the four otolith conditions in female plaice in different months

Date	Age-group	+	++	+++	spot	sample size
			% Occurrence of Otolith Conditions			
31.10.76	II	11.0	42.9	31.9	14.3	91
"	III	4.9	54.1	37.7	3.3	61
"	IV	0	82.5	17.5	0	40
"	V	0	84.6	15.4	0	26
14.2.77	II	20.8	51.4	22.9	5.7	35
"	III	29.4	29.4	29.4	11.8	17
"	IV	0	57.9	31.6	10.5	19
"	V	0	75.0	25.0	0	8
18.4.77	II	9.1	6.1	6.1	78.8	33
"	III	14.1	3.1	10.9	71.9	64
"	IV	5.3	26.3	15.8	52.6	19
"	V	0	50.0	0	50.0	8
6.6.77	II	87.6	2.4	0	0	41
"	III	100	0	0	0	69
"	IV	100	0	0	0	49
"	V	56.3	3.1	6.3	34.4	32
15.9.77	II	25.4	74.6	0	0	63
"	III	4.4	95.6	0	0	45
"	IV	0	100	0	0	15
"	V	0	100	0	0	4
2.11.77	II	21.1	68.4	8.8	1.8	57
"	III	14.0	73.7	12.3	0	57
"	IV	6.4	93.6	0	0	47
"	V	17.5	82.5	0	0	40

Table 4d (ii) % Occurrence of the four otolith conditions in male plaice in different months

Date	Age-group	+	++	+++	spot	sample size
				% Occurrence of Otolith Conditions		
31.10.76	II	12.9	49.4	27.1	10.6	85
"	III	0	82.2	13.3	4.4	45
"	IV	0	83.3	16.7	0	12
"	V					
14.2.77	II	12.1	39.4	33.3	15.2	33
"	III	5.3	52.6	42.1	0	19
"	IV	0	63.6	36.4	0	11
"	V					
18.4.77	II	15.1	26.4	5.7	54.7	54
"	III	15.8	13.2	5.3	65.8	38
"	IV	16.7	50.0	0	35.3	12
"	V					
6.6.77	II	75.5	15.3	0	8.2	49
"	III	37.7	23.3	9.8	29.5	61
"	IV	25.0	25.0	25.0	25.0	24
"	V					
15.9.77	II	12.8	87.2	0	0	39
"	III	4.0	96.0	0	0	24
"	IV	9.1	90.9	0	0	11
"	V					
2.11.77	II	7.5	88.1	1.5	3.0	67
"	III	15.8	71.9	12.3	0	57
"	IV	14.3	81.0	4.8	0	21
"	V					

period coincides with the spawning period, but it is interesting that the dramatic loss of condition also affected fish that were not spent. Condition improved between March and May and between May and June. In summary, there appeared to be 3 parts to the calendar year: Peak condition in June, July and perhaps part of August; intermediate condition in spring (improving) and autumn (deteriorating), and poor condition in winter.

(b) Growth: The percentage occurrence of the 4 otolith conditions showed that the highest incidence of the spot condition was in April (Fig. 4.0). The start of the growing season was therefore set tentatively as the first day of April. Fig. 4.1 is based on data pooled from all ages and both sexes. Examined in more detail (Table 4d) the data for April suggests that for both sexes, the younger fish were more synchronised in the start of their growing season. On the same basis female fish showed better synchrony than male fish. As April shows the highest incidence of the 'spot' condition in each age group, these differences could be taken as evidence that female fish may start their growing season earlier than males, within each sex, younger individuals may begin seasonal growth earlier than older ones. This view is strengthened by the data for June (Table 4d) which shows age groups II, III and IV well into their summer growth (i.e. '+' condition). In contrast only age group II amongst the males are well into their summer growth at this time. 16.3% age III and 25% age IV were still in the hyaline winter ('++') condition. In September there was a return to the winter otolith condition by all age groups of both sexes. It is interesting to note that this time the situation was reversed: For each sex the better synchrony was amongst the older fish (Table 4d). If the 'spot' and hyaline ('++') conditions respectively mark the start and end of the growing season, these observations may mean that female fish have a longer growing season than males. In addition younger

Fig 4a

Percentage occurrence of the 4 otolith conditions in different months.
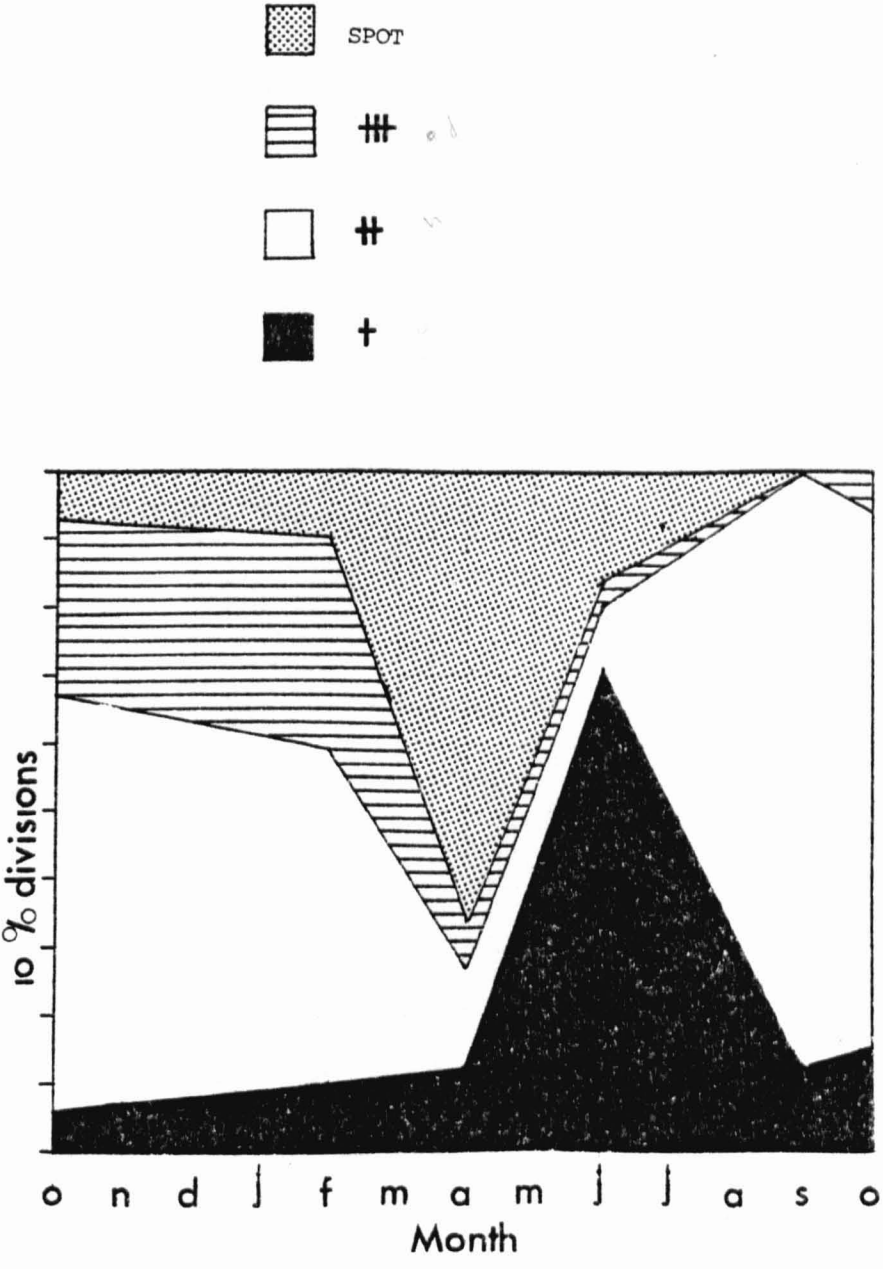
Table 4e. <u>The average length of age II fish of various otolith</u>

<u>conditions in (i) November and (ii) February.</u>

<u>Top: females, Bottom: males.</u>

	Numbers	Average length (cm)	$\pm$	
spot	13	22.46	2.99	
+	10	21.20	4.92	
++	39	25.36*	5.39	(i)
+++	29	28.48*	4.30	
spot	2	17.50	0.71	
+	7	21.0*	3.16	
++	18	22.33*	3.50	(ii)
+++	8	27.25*	3.62	
spot	9	23.89	1.27	
+	11	22.64	3.23	
++	42	24.69	3.94	(i)
+++	23	26.39*	3.29	
spot	5	20.40	3.21	
+	4	20.75	0.50	
++	13	21.77	3.63	(ii)
+++	11	25.82*	3.31	

* significantly different from the appropriate spot condition

at $t_{0.05(2)}$ $(\nu_1 + \nu_2)$.

age groups may have a longer growing season than older fish.

The data in Table 4d show that the onset of seasonal growth is not perfectly synchronous amongst members of each age group. At any one time, each year class may exhibit several otolith conditions though one usually predominates. In February a small proportion of each age group (n) were found to have initiated the formation of a thin opaque zone outside the hyaline band characteristic of winter, i.e. they had become 'spots' a month earlier than the bulk of the population. Theoretically these fish then belonged to the age group above (i.e. n + 1) the majority of whom were still in their winter condition prior to becoming n + 2 fish in April. It was reasoned that including these precocious growers in age group n + 1 would have the effect of artificially reducing the average length of that age group (see Table 4e for the size relationships of fish in different otolith conditions). As a result all new members of each age group in February (i.e. spots) were retained in the age group below when it came to assigning length-at-age values. Incidentally it will also be noticed from Table 4e that ('++') fish (i.e. winter condition) tended to be larger than those still in the summer otolith condition ('+'). This may mean that the smaller members of an age group have a longer growing season than the larger ones.

Figs. 4.2M and F show the changes in the average length of each age group with time of year. In each case the minimum length for each age group occurs in April, after which average length increases asymptotically with time. These trends justify the initial choice of April 1 as the probable 'birthday' of plaice in the study area. Despite the precautions outlined above, all age groups independent of sex were smaller in February than they were in the preceding October. The fish cannot possibly have shrunk between October and February and this effect must have originated either from changes in the population being sampled, or a

bias in the sampling method. Of these two possibilities the first is the more likely, as the same area was fished by the same crew using the same gear throughout the study. Whatever its origins this bias also affected the April samples and fish of age n + 1 were smaller in April than they were as members of the n age group in October.

Because of the discrepancies outlined above two separate curves have been fitted to each set of data. Each curve was fitted by use of the equation:

$$\ell_t = \ell_n - \Delta\ell\,(e^{-Kt})$$

where for each age group

ℓ_t = length on any day after April 1.

ℓ_n = the asymptotic length.

K = the instantaneous seasonal growth rate.

$\Delta\ell$ = the distance between the Y-axis intercept of the curve (i.e.

$\quad\ell_o$, length on April 1) and the asymptotic length ℓ_n.

Thus $\Delta\ell = \ell_n - \ell_o$, and is the seasonal growth increment. It will be recognised that this relationship is the function

$$Y = A - B\,(e^{-Kt})$$

of which the von Bertalanffy equation

$$Y = A\,(1 - e^{-K(t-t_o)})$$

is a modification allowing A to be equated to B with the factor t_o included to account for the fact that in practice, the growth curves of fish do not go through the origin of the abscissa and $A \neq B$. In fitting the dashed curves shown in Fig. 4.2, the length on April 1 was taken as the asymptotic length achieved during the previous year's growth. The data for April and February were omitted from these calculations. The solid curves were fitted using all the observed data except those for February; the assumed length on April 1 was excluded in these calculations. The

Fig. 4.2.   Seasonal growth of plaice in the study area.   The stars on the y-axis at the start

of the growing season are, in each case, the asymptotic length of the age-group

below.   These lengths were assumed to be the length-at-age on April 1 when fitting the

dashed curves.   The standard deviation about all points ranged between 2.76 and 5.21 cm.

There was no obvious relationship between standard deviation and either age or sample size.

Top: Fig. 4.2 M Seasonal growth of male plaice of ages II - IV in the study area.

Bottom: Fig. 4.2 F   Seasonal growth of female plaice of ages II - V in the study area.

Days Since 1st April Of Year Of Metamorphosis
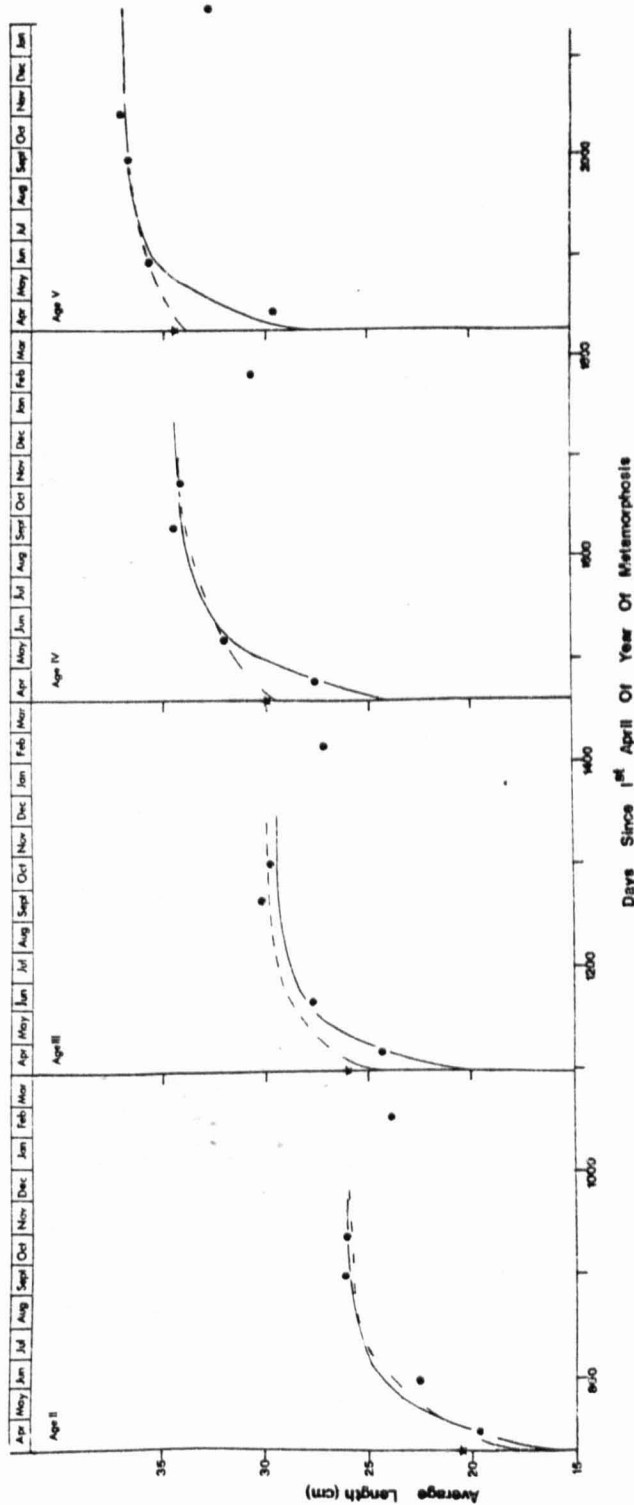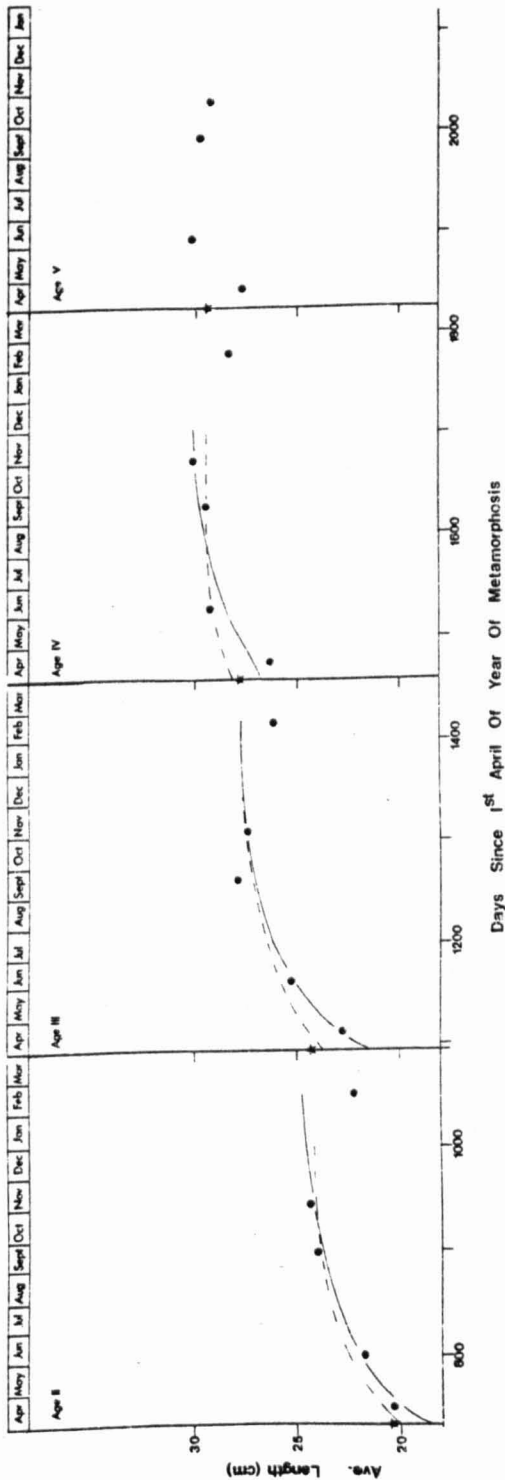
Table 4f. Seasonal growth parameters for male and female plaice of ages II - V for the equation $\ell_t = \ell_n - \Delta\ell(e^{-Kt})$. Top: Dashed curves Fig. 4.2. Bottom: Continuous curves Fig. 4.2. ℓ_t = length in cm on any day after April 1. ℓ_n = asymptotic length at age. $\Delta\ell$ = seasonal growth increment. K = instantaneous seasonal growth rate.

	Growth Parameters							
	Females				Males			
Age-group	ℓ_o (cm)	ℓ_n (cm)	$\Delta\ell$ (cm)	K	ℓ_o (cm)	ℓ_n (cm)	$\Delta\ell$ (cm)	K
II	16.7	26.0	9.3	0.0231	20.0	24.42	4.4	0.0124
III	24.3	30.0	5.7	0.0235	23.8	27.8	4.0	0.0106
IV	29.6	34.5	4.9	0.0119	28.2	29.5	1.3	0.0213
V	33.9	37.0	3.1	0.0134				
II	15.72	26.0	10.28	0.02606	18.51	25.0	6.49	0.01103
III	20.16	29.5	9.34	0.02652	21.46	27.8	6.43	0.01314
IV	24.01	32.4	10.19	0.02311	26.67	39.04	3.74	0.01033
V	27.93	36.8	8.87	0.02583				

parameters for these curves are given in Table 4f.

Discussion

(a) Condition: Todd (1915) obtained condition factors for North Sea plaice
that ranged from 0.88 to 1.15 during the year. It is doubtful if these
values can be validly compared with those of the present work. Todd
used the popular equation (iv) (p. 68) to compare his fish with an ideal
isometrically-growing fish and his range of factors must have depended
in part on the fish length used in the calculations. The North Sea plaice
showed an improvement in condition from the end of spawning in March, and
attained peak condition in November. Their condition therefore continued
improving for over two months after the plaice of the present study had
commenced a decline. Though feeding continued till November in both
studies, this discrepancy may mean that, by the end of August, food
was already becoming a limiting factor to growth and condition to plaice
in this study area. This is consonant with the interpretation placed
on the feeding chronology data in Chapter 2. A similar discrepancy
exists between Bagenal (1957) and MacKinnon (1972) on the timing of peak
condition in the related species , Hippoglossoides platessoides. Bagenal
obtained maximum condition between November and December, and minimum
values in April. In MacKinnon's study, minimum values were also recorded
in April but peak condition occurred two months earlier in September.
Tyler and Dunn (1976) have shown for another flatfish species,
Pseudopleuronectes americanus, that condition is largely dependent on
ration. It is thus possible that differences between localities in the
timing, duration and intensity of benthic productivity may be depicted
by parallel differences in the condition factors of their respective fish
populations. These discrepancies may ultimately be manifested as
differences in total fish production. With regard to the differences
between Todd's results and the present work, it may be mentioned that after
reviewing the Irish Sea fisheries, Brander (1977) concluded that the
Irish Sea and Bristol Channel are much less productive of fish than the

Table 4g.   Simple linear regression equations relating gonad weight to fish length in mature female plaice

caught in the study area at different times of the year.   G = gonad weight (gm).   L = fish

length (cm).

Month	Sample size	Equation	Correlation coefficient r	Calculated Ovary weight of a 30 cm fish (gm)	(% body weight)	Water content of ovary % wet weight
July	20	$G = 1.6 \times 10^{-7} L^{4.79}$	0.849*	1.95	0.62	85.37
October	20	$G = 0.00001 L^{3.94}$	0.6864*	6.94	2.30	70.17
November	36	$G = 3.39 L^{0.65}$	0.9908*	30.93	10.59	67.54
March	28	$G = 0.046 L^{2.11}$	0.7390*	60.18	23.18	69.06

* significant at $p < 0.001$.

Ripe and running females were not included in these samples.

6 ripe and running females caught in the study in February 1977

ranged from 33-38 cm, their ovaries averaged 34.2% body weight

and contained 87.8% water.

North Sea.

From the interpretations placed on the feeding chronology data in Chapter 2, feeding conditions were already deteriorating in the study area by the end of November. However the enlargement of gonads in preparation for spawning also commenced at this time. Table 4g is a list of equations relating ovary weight to fish length during the period July to March. By March, the ovaries of a 30 cm female weighed about 60 gms on average; testes weight for a male fish of similar size was 4.85 gms. Yet at this time there were no significant differences in weight at length (i.e. condition) between mature and immature fish of each sex. Indeed the development of the gonads was accompanied by a loss of condition. It is tempting to infer from these observations that the elaboration of gonad tissue is achieved at the expense of somatic tissue without a net change in the overall weight of the fish. This would explain why significant differences between mature and immature fish were only detectable when the former were spent. Unfortunately comparison between immature and spent males was not possible as so few of the latter were caught. Given the relatively small size of the testes, however, it is doubtful whether any significant difference would have been detected.

There exists an extensive body of literature purporting to link gonad maturation in fish with somatic tissue depletion. Such depletion is usually characterised by a mobilisation of amino acids as well as alterations in the levels of sex hormones and other substances in the blood. In an extensive and thorough review of the literature, Love (1970) commented, "..... some depletion seems to be the invariable accompaniment of maturation in fish .....". Because most of the relevant reports deal with fish species that go through a fasting period prior to and during spawning (e.g. Salmo salar, Cowey et al., 1962), it is difficult to discern the extent to which these biochemical events are a direct response

to the onset of maturation. Indeed, Love concedes that "..... many of the phenomena described are not the direct result of maturation at all, but can be duplicated by straightforward depletion .....". Where the interest is trophic ecology (as it is in the present case) the problem could be solved with much less difficulty by energy budget studies. In one such study, MacKinnon (1972) was able to estimate how much of the depletion occurring during the fasting-spawning-overwintering period of H. platessoides is attributable to gonad elaboration. This amounted to 20 Kcals out of a total of 92 Kcals stored in the liver and other somatic tissues during the summer feeding period. In the chapter that follows a similar exercise will be undertaken as a conclusion to the present study.

(b) <u>Seasonal Growth</u>: Proximate limits for the start and end of the growing season of plaice are mentioned incidentally in several reports. Dawes (1930, 1931) observed that 2-year old plaice contained in floating boxes at Plymouth Sound started growth in April and stopped in October and November. Blegvad (1934) monitored the growth of North Sea plaice transplanted to the Baltic and noted that growth occurred mainly between May and September. In the north-east Irish Sea Hill (1971) took April 1 as the birthday of plaice because it corresponded to the middle of the spawning season as defined by Simpson (1959). For O-group plaice in a bay on the east coast of England, Lockwood (1972) took May 1 as the 'birthday', based on the earliest date of larval settlement. The birthday for the present work, taken as April 1, falls well within the range established by these studies. It must be pointed out, however, that the population was not perfectly synchronised. Some individuals started growth as early as February and the date April 1 was chosen only because it apparently marked the 'average' start of seasonal growth.

There was a noticeable difference in the degree of synchrony with which individuals of the different age-groups began their growing

season. The general tendency was for younger fish to be better synchronised
than those belonging to older age groups; this trend was reversed when it
came to ending the growth season. There were also differences between the
sexes: At each age female fish appeared to commence growth earlier than
males. It has already been pointed out that these differences may allow
some groups of fish to have a longer growing season than others. In
this way, female fish could attain a greater size at age than males;
younger fish may grow more during a growing season than older individuals.
Gerking (1966) observed similar differences in the growth rates of
bluegill (Lepomis macrochirus) populations inhabiting different lakes, and
was able to show that a fast growth rate was characterised by a longer
growing season. Two features were found to characterise longer growing
seasons, viz.: An earlier time of annulus formation in the scales, and
"..... a considerably longer period of growth in the late summer and
autumn".

The very pronounced reductions in average length-at-age observed in
February and April deserve some comment if not a cogent explanation.
Since this phenomenon occurred during the spawning season it is likely to
be connected with this activity. The onset of maturity in plaice is
determined by both size and age (Simpson, 1959; present work). Two
statements follow logically from this:

1) During the spawning season it is the larger members of each age group
   that will undertake spawning migrations.

2) The structure of inshore plaice populations will undergo alterations
   during the spawning season and show a higher proportion of smaller fish.

To test (2) above, the length-frequency of catches obtained in the study
area in March (1975 and 1977) by postgraduate Marine Biology classes were
compared by inspection with the November catches presented in Fig. 1.2
(p. 6). No obvious differences were apparent and the modal length still

occurred between 19 and 22 cm. The length at which 50% of males and females are mature in the study area is between 25-26 cm. The length-frequency plots of Fig. 1.2 show that fish greater than 26 cm usually have a frequency of less than 4%. Because of their relatively low frequency, it is possible that the departure of numbers of these fish will fail to markedly alter the gross population structure. However, when the population is stratified into age-groups the effects of such selective migration will become progressively more marked in older age-groups. This stems from the fact that the frequency of larger fish is much higher in older year classes than in the population as a whole. It is therefore not surprising to find that in Figs. 4.2M and F, the discrepancy between the average length-at-age in October and that obtained for February increases steadily with the age of the fish, e.g. for female fish the reduction in average length was ca. 2 cm for age II, 3 cm for age III and over 4 cm for age V. These differences are not as severe for male fish, possibly because they have a shorter length-at-age. In a recent survey of the north-east Irish Sea, Brander and Wallace (1976) treated their catch data statistically. Their main conclusions were that 'large female plaice were very scarce in March and numbers also dropped off at greater depths outside 6 miles in June'. None of these factors, i.e. depth up to 10 fm, distance from coast, or month (June, October, March) affected the distribution of large/ male plaice significantly.

Because it was not possible to ascertain what proportion, if any, of the migrant fish returned at the end of the spawning season, two separate curves have been fitted to each set of data. The dashed curve takes ℓ_o for each age group as the asymptotic length of the age group below, thereby assuming that all the migrant fish eventually return. The solid curves on the other hand assume that none of the migrants return and regard the April lengths as the true size-at-age of a year class at the start of the growing season.

Lockwood (1972) is responsible for the only mathematical description
of seasonal growth of fish that exists in the literature. He obtained the
Bertalanffy parameters K and L_∞ for O- and I-group plaice by regressing
the increase in average length per time interval on the median length for
interval. This regression gave two lines, one with a positive, and the
other with a negative slope. The former was taken to represent the
sigmoid portion of the growth curve during which growth rate was
increasing. The instantaneous seasonal growth rate K, was taken as the
slope of the second line. Attempts to treat the data obtained here in
similar fashion gave wildly improbable results with age II females
attaining a larger asymptotic length than age IV fish. The reason for
this could well have been the paucity of points available for the regression
to obtain K. Lockwood used 7 points in his plot and there was considerable
scatter about the least squares line. Indeed, analysis of his raw data
shows that the correlation for his regression was 0.4429, a value
insignificant at p= 0.10.

The function used in the present study to describe seasonal growth
bears little resemblance to the Bertalanffy equation except to the extent
that they both assume growth to be exponential. The various parameters
cannot be imbued with any physiological significance and serve only as
convenient mathematical tools for describing the observed data.
Nevertheless the equations contained in Table 4f will give length-at-age
estimates for any interval after April 1. As each equation is a
description of the available data these estimates will be only as
reliable as the original data.

Chapter 5

Estimates of annual food consumption and annual production.

Preface

In this chapter, the results obtained on feeding chronology, diet, condition and growth will be used to estimate the total annual food intake and annual production of the plaice population. It is realised that these estimates will be very proximate because of the quality of the available data. In particular it is conceded that little was known about the efficiency of the trawl used in the estimation of stock size. Nevertheless the computations that follow should indicate the possible extent to which production in the fishable population is influenced by such factors as its age structure, the timing and duration of benthic production, and the metabolic consequences of reproduction and winter fasting.

Table 5a. <u>Establishing the true sex ratio of the total stock</u>

Fish Length	r_c	r_s	Total numbers	Total Females at length	Total males at length
14	0.5	0.4	670	479	191
15	1.5	1.2	2680	1218	1218
16	1.84	1.47	7897	3197	4700
17	1.0	0.8	14072	7818	6254
18	1.43	1.14	34701	16215	18486
19	1.58	1.26	47145	20861	26284
20	1.16	0.93	57531	29809	27722
21	1.22	0.98	48198	24342	23856
22	2.42	1.94	43603	14831	28772
23	2.02	1.62	40779	15565	25215
24	2.27	1.82	32260	11440	20820
25	2.12	1.70	27138	10051	17087
26	2.03	1.62	23452	8951	14501
27	1.86	1.49	19959	8016	11943
28	1.03	0.82	17135	9415	7720
29	0.51	0.41	10913	7740	3173
30	0.41	0.33	9956	7486	2470
31	0.37	0.30	8472	6517	1955
32	0.22	0.18	6747	5718	1029
33	0.15	0.12	6318	5641	677
34	0.07	0.06	4451	4199	252
35	0.13	0.10	2968	2698	270
36	0.06	0.05	3111	2963	148
37	0.03	0.02	1723	1689	34
38	0.07	0.06	1532	1445	87
39	0.03	0.02	1005	985	20
40				1292	
41				574	
42				814	
43				574	
44				335	
45				144	
46				239	
47				192	
48				192	
49				48	
50				48	

r_c = sex ratio of catch

= No. of males ÷ No. of females

r_s = sex ratio of stock and is related to r_c by

r_s = r_c ÷ r_q (Beverton, 1964)

where r_q is the relative catchability of males to females and is given by

r_q = F_m ÷ F_f

F_m = fish mortality of males

F_f = fish mortality of females

The maximum values for these factors in the Irish Sea for 1976 were

F_m = 0.6 F_f = 0.48 (ICES Irish Sea Working Group, unpublished data)

∴ r_s = $0.8r_c$

N.B. The Nos. in column 4 were estimated by proportion from the length frequency of catches (1974-1977) and the total stock size.

Production: Production, as defined by Ivlev (1945) and Clarke (1946), is

the total quantity of biomass elaborated during a stated period of time,

regardless of whether or not all of it survives to the end of that time.

In this study production has been calculated as the product of average

population biomass during a time interval Δt, and average individual

growth increment during the same period (after Ricker, 1946; Ricker and

Foerster, 1948; Pearcy, 1962). Because growth rates were seen to vary

seasonally (Chapter 4), and also because the intensity of feeding showed

a similar pattern, production estimates have been carried out for sub-

sections of the year which will, in what follows, be called growth periods.

The trends in growth, feeding intensity and condition were used as a basis

for the limits of these growth periods. In keeping with the simplistic

assumption made in Chapter 1 (p. 6), i.e. that the stock size in the

study area remains relatively stable from year to year, the total stock

at the start of the growing season in April was assumed to be 478,630

individuals. The length/frequency data for the catches of 1974-1977 (Appendix

1.1 p. 136 - 139) have been used to assign a length frequency

structure to this stock (Table 5a). Using methods outlined by Beverton

(1964) the sex ratio of these catches (given in Table 1c, p. 10) have been

used to segregate the total population into male and female segments

(Table 5a). The age structure of each sex population was then obtained

by proportionately distributing the numbers at each length on the basis of

the length/age matrices obtained from the stratified samples described in

Chapter 1 and contained in Appendices 1.4M and 1.4F (p. 142-143). The results

of these computations are contained in Table 5b as total numbers at age for

each sex. This data was used in conjunction with the mortality coefficients

in Figs. 1.6M and 1.6F to estimate numbers at age for each sex at the

start and end of each growth period.

In Worksheets 5aM and 5aF, production has been computed for each age

group during 4 growth periods. For each period two separate estimates

Table 5b F.   Length/Age Matrix of Total Female Population

	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
14	120	359														
15	244	974														
16	337	1683	1178													
17		6254	1564													
18		12161	3040	1013												
19		15478	3365	2019												
20		18879	9936	994												
21		11802	9589	2951												
22		6921	6427	1483												
23		3632	7783	2594	1038	519										
24		1476	5536	3690	369	369										
25		2010	6031	1005	335	670										
26		1399	4476	1678	1119	280	280									
27		776	3103	3103	776	259										
28		607	4859	2733	1215											
29			3049	3049	469	469	704									
30			3630	2495	907	227		227								
31			1892	3364	631	421	210									
32			1112	2065	1747	318	477									
33			564	2115	1974	705	141	141								
34			215	1184	1400	969	215	215								
35			159	476	635	1190			280							
36				382	956	956	382	287								
37				225	676	394	56	225	113							
38				248	206	206	330	83	165	165	41					
39					170	272	204	136	68	102	34					
40					76	138	554	231	138	46	92		46			
41					44	155	199	22	44	66	22	22				
42					98	195	65	130	98	65	65	33	65			
43					36	144	144	36	72	72		36		36		
44						19	37	37	37	37	74	56		19	19	
45						18	18	36	27	9	18			18		
46					40		80	40	40	40						
47									38	38	19		58		19	19
48					32	32		32	64				32			
49									10	19	10	10				
50													16	16	16	
Total Nos. at Age	701	84406	77508	38846	14919	8925	4096	1878	1194	659	375	157	185	121	54	19

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Table 5b   M.   Length/Age Matrix of Total Male Population

	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
14		191										
15	183	1196	133									
16	336	3525	839									
17	195	4300	195	195								
18		13119	5370									
19		17249	8214		821							
20		17326	6064	2599	866	866						
21		14165	7455	2237								
22		7193	14386	6474	719							
23		4880	12201	7321	814							
24		4759	8923	5949	595		595					
25		5126	7689	2563	1282		427					
26		372	6693	5206	1487		744					
27			7025	2810	1405	703						
28			2989	3238	747	498	249					
29			1169	919	418	334	167	84	84			
30			659	741	329	412		82	82	165		
31			196	977	326	261	130	65				
32			94	234	234	281	94	47				47
33			118	265	118	88	29	29		29		
34				46	69	23	92	23				
35				68	68	34		34			68	
36				49				25	49	25		
37					17				17			
38							87					
39							20					
Total Nos. at Age	664	93401	90412	41891	10315	3500	2634	389	232	219	68	47

were made using data from the two sets of growth curves in Figs. 4.2M and F. Average length at age obtained from these curves was converted to weight using appropriate condition factors reported earlier in Table 4c (p. 75). These factors indicate that there was some production in March resulting in improved condition without a change in length at age. For this reason the start of the first growing season has been taken as March 1 though growth in length is calculated from April 1. This time-lag between improvement in condition and growth in length is again evident towards the end of the year: while columns V and IX show some slight increase in length between July and September in all cases, production for this period (Columns VIII and XII) is sometimes negative (ages IV males; II, III, IV and V females). Production is negative for all age groups between December and the end of February reflecting the sharp loss of condition reported earlier for this period. It will be recalled that in fitting the dashed curves in Figs. 4M and F, it was assumed that all migrant fish returned to the study area in April; the opposite assumption was made for the continuous curve i.e. that all migrant fish stayed away permanently. As a result size at age values at the start of the growing season were higher for the dashed curves. This is reflected as a discrepancy between production values derived from the two curves in Columns VIII and XII in Worksheets 5M and F with the dashed curves giving constantly lower production estimates. To some extent, therefore, columns VIII and XII give minimum and maximum estimates of production in the study area. It is more than likely that some of the migrants do return, so that the true value probably lies somewhere between these two estimates. Since there is no growth and virtually no feeding between mid December and the end of February the negative production obtained for this period is in effect an index of the metabolic requirements of the population during winter.

The relationship between the age-groups appears to be the same for

Worksheet 5a   F   Computation of Production by Female Plaice of Age II-V in the study area

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
				Data from continuous curve Fig. 4F				Data from dashed curve Fig. 4F			
Growth Period	Year class	N	N̄	ℓ̄ (m)	W̄ (gm)	ΔW̄ (gm)	N̄ΔW̄ (kilos)	ℓ̄ (cm)	W̄ (gm)	ΔW̄ (gm)	N̄ΔW̄ (kilos)
End Feb - End April		77508		15.72	38.83			16.7	46.41		
			75491			35.01	2642.940			66.83	5045.064
End April - End July		73473		18.81	73.84			21.35	107.24		
			67907			131.50	8921.771			90.45	6142.188
End July - End Sept		62341		25.77	205.34			25.44	197.69		
	2		59125			-8.37	-494.876			-1.83	-108.199
End Sept - Mid Dec		55909		25.91	196.97			25.86	191.19		
			52348			-5.34	-279.538			-4.67	-244.886
Mid Dec - End Feb		48787		25.91	191.63			25.98	185.31		
			45735			-5.90	-269.837			-5.88	-268.922
			42683		25.91	186.73			25.98			

Annual Production Σ_{2}^{3} = 10520.460kg   Annual Production Σ_{2}^{3} = 10565.245 kg

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
End March - End April		38846		20.16	80.81			24.3	140.11		
			37835			95.60	3617.060			78.28	2961.724
End April - End July		36824		25.28	176.41			27.18	218.39		
	3		34034			118.22	4023.499			92.32	3142.019
End July - End Sept		31244		29.13	294.63			29.66	310.71		
			29633			-7.95	-235.82			-9.74	-288.625
End Sept - Mid Dec		28021		29.43	286.68			29.92	300.97		
		26236				-8.68	-227.729			-9.15	-240.059
Mid Dec - End Feb		24451		29.5	278.0			29.99	291.82		
		22922				-8.56	-196.212			-9.18	-210.424
		21392		29.5	269.44				29.99	282.84		

Annual Production Σ_{3}^{4} 6980.748   Annual Production Σ_{3}^{4} 5364.635

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
End March - End April		14919		24.01	135.24	·		29.6	250.54		
			14531			132.07	1919.109			73.34	1065.704
End April - End July		14142		29.11	267.31			31.07	323.88		
	4		13071			180.97	2365.459			115.03	1503.557
End July - End Sept		12000		33.59	448.28			33.35	438.91		
			11381			-7.78	-88.544			-2.58	-29.363
End Sept - Mid Dec		10762		34.05	440.50			33.94	436.33		
			10077			-11.89	-119.816			-3.37	-33.960
Mid Dec - End Feb		9391		34.17	428.61			34.28	432.96		
			8804			-13.19	-116.125			-13.59	-119.646
			8216		34.17	415.42			34.28	419.37		

Annual Production Σ_{4}^{5} 3960.083 kg   Annual Production Σ_{4}^{5} 2386.292 kg

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
End March - End April		8925		27.93	211.15			33.9	373.62		
			8693			125.14	1087.842			83.69	727.517
End April - End July		8460		32.71	336.29			34.93	457.31		
	5		7820			232.62	1819.088			110.68	865.518
End July - End Sept		7179		36.42	568.91			36.4	567.99		
			6809			-18.69	-127.260			-17.33	-118.000
End Sept - Mid Dec		6438		36.72	550.22			36.73	550.66		
			6028			-16.97	-102.295			-13.13	-79.148
Mid Dec - End Feb		5618		36.8	533.25			36.9	537.53		
			5267			-16.41	-86.432			-16.54	-87.116
			4915		36.8	516.84			36.9	520.99		

Annual Production Σ_{5}^{6} 2590.943 kg   Annual Production Σ_{5}^{6} 1308.771 kg

Total Annual Production Σ_{2}^{5} = 24052.234 kilos   Total Annual Production Σ_{2}^{6} = 19624.943 kilos

Mean = 21838.588 $\pm$ 3130.568 (14.34%)

Worksheet 5a   M   Computation of Production for Male Plaice of Ages II - IV in the study area

I Growth Period	II Year class	III N	IV N̄	V ℓ̄ (cm)	VI w̄ (gm)	VII Δw̄ (gm)	VIII N̄Δw̄ (kilos)	IX ℓ̄ (cm)	X w̄ (gm)	XI Δw̄ (gm)	XII N̄Δw̄ (kilos)
				Data from continuous curve Fig. 4M				Data from dashed curve Fig. 4M			
End Feb - End April	2	90412		18.51	62.84			20.00	78.94		
			86919			30.13	2618.869			28.89	2511.089
End April - End July		83425		20.34	92.97			21.39	107.83		
			74291			59.82	4444.088			47.69	3542.928
End July - End Sept		65156		23.31	152.80			23.45	155.52		
			60234			7.11	428.264			1.67	100.591
End Sept - Mid Dec		55312		24.14	159.91			24.0	157.19		
			50187			2.88	144.539			-1.31	- 65.745
Mid Dec - End Feb		45061		24.60	162.79			24.24	155.88		
			40957			-4.99	-204.375			-1.48	-196.590
			36853		24.6	157.78			24.24	151.08		

Annual Production $\sum_2^3$ 7431.385 kg   Annual Production $\sum_2^3$ 5892.273 kg

I Growth Period	II Year class	III N	IV N̄	V ℓ̄ (cm)	VI w̄ (gm)	VII Δw̄ (gm)	VIII N̄Δw̄ (kilos)	IX ℓ̄ (cm)	X w̄ (gm)	XI Δw̄ (gm)	XII N̄Δw̄ (kilos)
End Feb - End April	3	41891		21.46	97.15			24.89	131.78		
			40273			45.48	1831.316			36.73	1479.227
End April - End July		36854		23.52	142.63			26.70	168.51		
			34422			80.57	2773.381			59.44	2046.044
End July - End Sept		30189		26.51	223.20			27.23	227.95		
			27909			4.58	127.823			0.08	2.233
End Sept - Mid Dec		25628		27.22	227.78			27.54	228.03		
			23253			0.46	10.696			-1.00	- 23.253
Mid Dec - End Feb		20878		27.59	228.24			27.54	227.03		
			18977			-7.02	-133.219			-6.99	-132.649
			17075		27.59	221.22			27.54	220.04		

Annual Production $\sum_3^4$ 4609.997 kg   Annual Production $\sum_3^4$ 3371.602 kg

I Growth Period	II Year class	III N	IV N̄	V ℓ̄ (cm)	VI w̄ (gm)	VII Δw̄ (gm)	VIII N̄Δw̄ (kilos)	IX ℓ̄ (cm)	X w̄ (gm)	XI Δw̄ (gm)	XII N̄Δw̄ (kilos)
End Feb - End April	4	10315		26.67	184.30			28.81	217.22		
			9917			45.41	450.331			42.05	446.761
End April - End July		9518		27.65	229.71			29.4	259.27		
			8476			71.23	603.746			43.48	368.537
End July - End Sept		7434		29.34	300.94			29.47	302.75		
			6893			-2.34	-16.083			-14.93	-102.614
End Sept - Mid Dec		6311		29.84	298.60			29.50	287.82		
			5726			-2.46	-14.086			- 9.82	- 56.229
Mid Dec - End Feb		5141		30.14	296.14			29.50	278.00		
			4673			-9.11	-42.571			- 8.50	- 39.721
			4205		30.14	287.03			29.50	269.44		

Annual Production $\sum_4^5$ 981.337 kg   Annual Production $\sum_4^5$ 616.734 kg

Total Annual Production $\sum_2^5$ 13022.719 kg   Total Annual Production $\sum_2^5$ 9880.609 kg

Mean 11451.664 ± 2221.807 (19.4%) kilos

Note: The values for N for the start and end of each growth period were calculated using the Z values of Fig. 1.6. For simplicity average values (N̄) for each period were taken as arithmetic means and not as average integrals.

both sexes: i.e. that production decreases with age. No doubt this is due to the larger numbers of young fish and their larger growth increments.

Use of appropriate condition factors in converting length to weight has made it possible to estimate how much of the production achieved in the spring/summer months is retained into the next age-group. Though slight increases in length may occur beyond September, columns VIII and XII in the worksheet show that the fish were already using up reserves at this point. By the end of February mean values from the two curves show that between 7.3 and 13.4% of the summer production has been dissipated. Because the condition factor employed for the winter calculations was not that obtained for spent fish, the loss does not include the reproductive products.

Assuming that recruitment in the population is complete by age II, the age-groups in Worksheet 5a M and F represent 94% of the fishable population in the study area. The fishable population thus produces ca. 33,300 kg annually. When the reductions due to loss of condition in winter are ignored this value becomes 35,900 kg.

This gives a value of ca. 0.14 gms/m^2. Based on commercial landings, Clarke (1946) calculated that the total demersal production of the George's Bank of the North Sea approaches 3.68g/m^2/yr (= 33lb/acre). Harvey (1950) estimated in very proximate fashion, that

daily demersal production in the English Channel is 0.001 gm dry wt/m²

which, assuming 75% water content, gives ca. 1.46 g/m²/yr. Pearcy (1962)

working with estuarine O- and I-group winter flounder Pseudopleuronectes

americanus, obtained yearly production estimates of 3.68 gm/m². Lockwood

(1972) obtained half-yearly production estimates (May-October) of between

2.49 and 5.19 gm/m² for O-group plaice. Considering that the present

study excludes O- and I-group fish which must be the most numerous and

fastest growers in the population, the present study does not compare too

badly with these earlier reports. In terms of P/B ratios, the fishable

population more than replaces itself annually, producing 1.26 of the biomass

available at the start of the year. Pearcy's winter flounders on the

other hand produced about twice the average biomass and the same is true

of Lockwood's O-group plaice.

Daily food Intake

The estimation of the daily food intake (d.f.i.) of fish populations

in the wild has proved to be difficult. It is not feasible to observe

the feeding activities of fish directly in the field and information is

therefore derived from the stomach contents of freshly caught specimens.

However, the amount of such contents will on any occasion be the outcome

of two concurrent processes, viz. ingestion and gastric evacuation. In

fish populations where the feeding is not synchronised amongst individuals,

consecutive samples of stomach contents will tend to oscillate about a

mean. When the ingestion rate exceeds the rate of gastric evacuation,

consecutive samples of fish from a population which is synchronised will

show a rise in stomach contents. This trend will be reversed when the

rate of gastric evacuation exceeds that of ingestion. These considerations

mean that the average stomach contents obtained from a single sample of

fish are a static picture from what is essentially a dynamic flow.

Originally these factors were not quite appreciated and in 1935 A.J.

Bajkov suggested catching large numbers of fish and killing some immediately to establish the average stomach contents in the wild. Serial slaughter of the remaining individuals could then be used to estimate total gastric evacuation time from which daily food intake (D.f.i.) could be estimated by use of the expression

$$D = \frac{A24}{N}$$

where D = D.f.i., A = original stomach contents, N. = number of hours required to empty the stomach of A.

Since the mid-sixties the literature has seen a spate of feeding chronology and gastric evacuation studies which now make it possible to fault the rationale of Bajkov's equation in some respects. The equation assumes in effect that feeding is not synchronised amongst the members of a fish population and that consecutive samples throughout a 24-hour period will give average stomach contents that oscillate about A. In other words the population as a whole (not the separate individuals) feeds at an unchanging intensity. This is probably true of the cod, Gadus morhua (see Daan, 1973). However, when feeding is synchronised and the population behaves essentially like a single 'corporate' individual, alterations in the relationships between evacuation rate and ingestion rate will result in a fairly smooth rise and fall of stomach contents. It follows then that estimates of daily food intake must be preceded and guided by investigations of the feeding chronology.

The weight of stomach contents of fish at any given time of day depends on, amongst other factors, the digestibility of the various items and the time since they were ingested. Failure to take this into account is another shortcoming of Bajkov's equation and one which several subsequent expressions have sought to rectify. For example, Swenson and Smith (1972) estimated the daily food intake of Stizostedion vitreum vitreum from the expression

$$C = \Sigma_t \, \Sigma_s \, \frac{(\Sigma f.sc)}{F}$$

where C = daily food intake in gms for the average fish; sc = undigested weights of stomach contents for foods of a given size not more than 90% digested and consumed during a given period; Σf = summation of corrected weights of stomach contents for all fish in the sample having consumed food of a given size during a time period; F - number of fish in the sample which could have contained food of a given size during a time period in a state of digestion not exceeding 90%; Σ_s = summation of food sizes; Σ_t = summation of time. This is one of the most carefully constructed equations of its kind in the literature. It makes provision for loss of weight of food items due to digestion and also recognised that the extent of such digestion will vary with the digestibility and size of each food item. Daan (1973) working with the more macrophagous cod, assumed that the average stomach contents from a sample of freshly killed specimen would be half the original weight and used a much simpler expression for estimating food consumption viz.:

$$\phi_L = \frac{2.W_L}{D_L}$$

where ϕ_L = daily ration of fish of length L; weight of the stomach contents at length L; D_L = digestion time in days at length L.

Perhaps more relevant to the present study, is the method devised by Lockwood (1972) to estimate the daily ration of 0-group plaice in a bay on the east coast of England. Trawls were carried out at 3 hourly intervals over a 24-hour period. Each catch was divided into two groups designated A and B. Sample A were killed immediately and their stomach contents preserved. Sample B were kept alive on deck. After 3 hours, when the next catch was taken, sample B were killed. This process, repeated over the 24-hour sampling period, gave 8 pairs of samples: 'A' samples preserved at the time of capture and 'B' samples preserved after holding alive on

deck for 3 hours. The following assumptions were then made:

1) During each 3 hour period all fish free in the sea were feeding/ digesting/behaving normally.

2) The mean stomach contents of sample A_t (where t is the time of death) is representative of the population at the time of capture.

3) Sample B_t have digested as much food during the 3 hours spent in the tanks on deck as sample A_z ingested while still free.

On the basis of these assumptions, the difference between A_t and B_t was the amount eaten in 3 hours (and the difference between $A_t - 3$ and B_t was the amount digested).

$\therefore$ food intake per 3 hours = $A_t - B_t$ and daily food intake D.f.i. = $\Sigma(A_t - B_t)$.

Lockwood realised that assumption (3) was likely to be unjustified because of the stress occasioned by trawling/handling which was bound to depress the evacuation rate of sample B_t. As the fish feed on a tidal cycle he reasoned that cessation of feeding should theoretically be the same in tanks (B_t) as in the sea (A_t) and $A_t = B_t$. On the basis of this he assumed that the mean value of the difference when $A_t < B_t$ was an estimate of the food not digested, C, due to stress that would have been digested in unstressed, i.e. free fish.

$\therefore$ when $A_t < B_t$, $B_t - A_t = C$

As fish were stressed by an equal amount throughout the 24 hour period the mean value of C, $\bar{C}$ was added to each estimate of food intake

f.i. = $(A_t - B_t) + \bar{C}$

D.f.i. = $\Sigma(A_t - B_t) + \bar{C}$

Lockwood's method was considered unsuitable for the present study for several reasons. Some of these were practical: e.g. there would not have

been enough room on deck on the R.V. 'Prince Madog' to hold sufficiently large samples of each of the three size-groups under reasonable conditions. There were also theoretical considerations most of which centred around assumption (3) and the stress effects of trawling and handling. Evidence for this is extensive (see e.g. Windell, 1966) and it is not surprising that the correction factor $\bar{C}$ usually accounted for ca. 50% of the estimated D.f.i. in each case. As there were only a few short periods in the study when stomach contents fell steadily, it was thought that estimates of C would be unreliable. The problem therefore was to obtain reliable estimates of the gastric evacuation rate in the wild and this was done as follows. The series of Figs. (2.2 i-v and 2.2 a-e) was examined in detail. It was considered that a period of no feeding and gastric evacuation would be characterised by the following:

a) A consistent fall in both feeding and total averages of stomach contents.

b) A fall in S.I. and an increase in I.O and perhaps E.

Figs. 2.2ii and 2.2b have been modified in Fig. 5a to illustrate the process. It was found that conditions (a) and (b) above were not necessarily met simultaneously, e.g. in Fig. 5a the period marked (i) for small fish shows a drop in average stomach contents but also a rise in S.I. This means that the fish were still feeding and the decline in stomach contents during this period is an underestimate of the gastric evacuation rate. For those periods which met both conditions simultaneously, gastric evacuation was calculated as the slope of the regression of the square root of total average against time. Where more than one period was available an average slope was calculated (after Thorpe, 1977; see Notes on Fig. 5a). The gastric evacuation rate obtained for each size group was used to predict the amount of food evacuated between hauls by use of the following equation

$$C_2 = (\sqrt{C_1} - R\Delta t)^2$$

where C_2 is the predicted stomach content for haul $n + 1$; C_1 = observed

Fig. 5a. Estimating average gastric evacuation rates for

each size-group population from the variation

in average stomach contents with time of day.

Gastric evacuation for each period (i.e.

(i), (ii), (iii)), was calculated by regressing

the square root of total averages against

time. An average was obtained for each size-

group as the arithmetic mean of the individual

rates obtained for each period. Where a

decline in stomach contents was <u>not</u>

accompanied by a fall in S.O the period in

question was excluded from the calculations

e.g. period (ii) smalls.

Time of Day (hours)

10 Percent Divisions
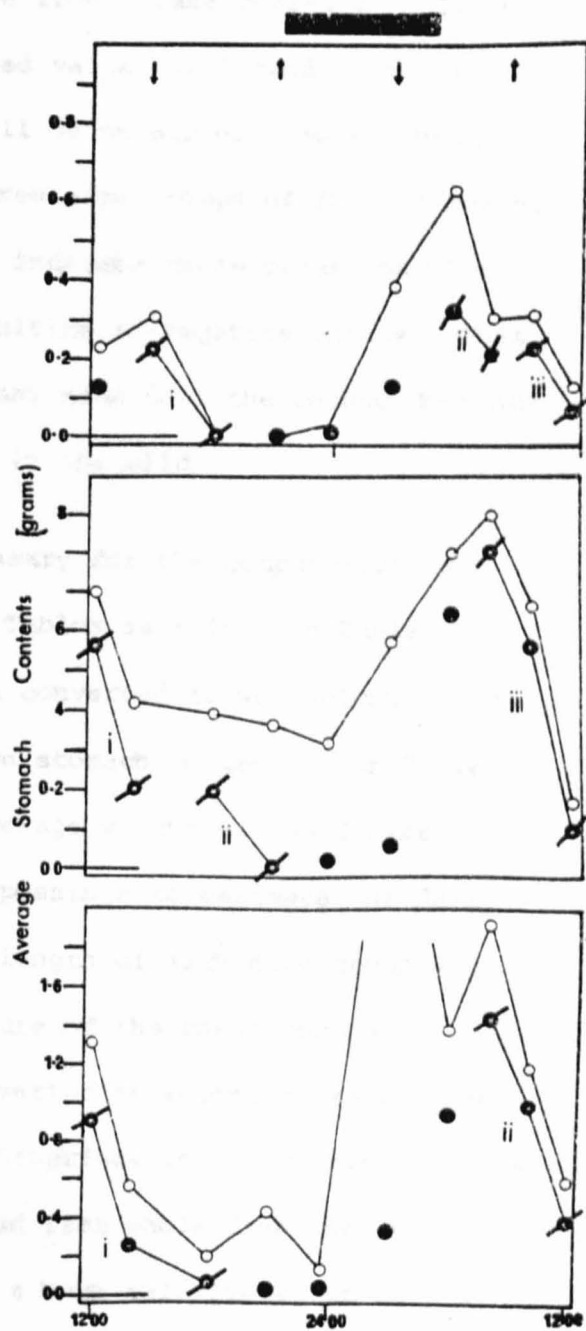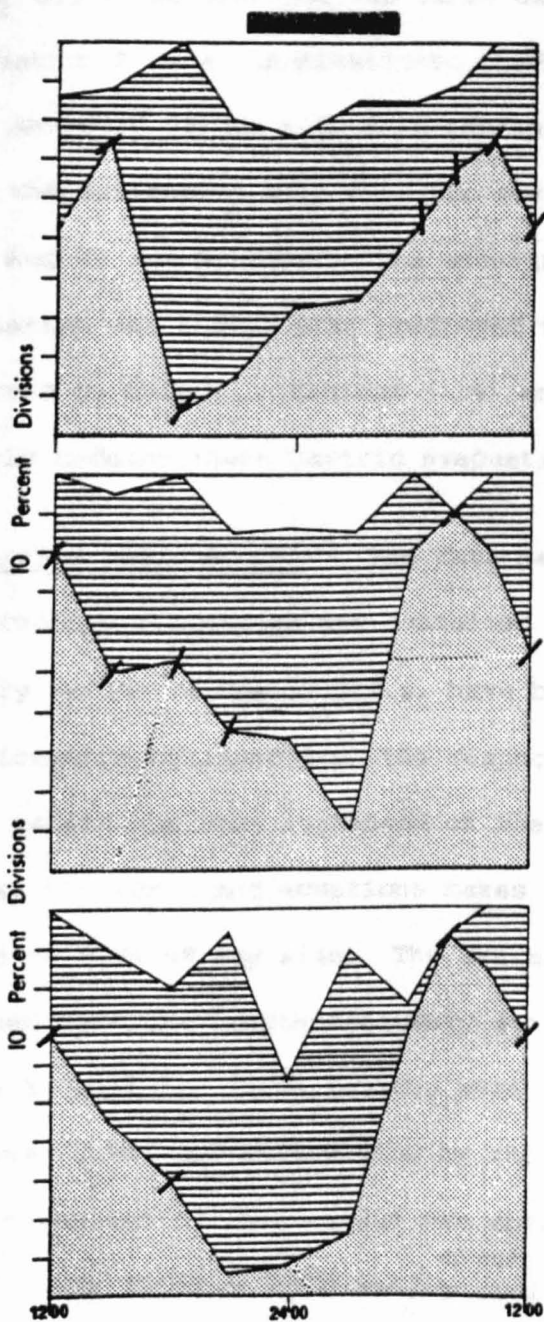
Average Stomach Contents (grams)

stomach content for haul n; R = gastric evacuation rate; Δt = time
interval between hauls C_1 and C_2. The difference between predicted values
of C_2 and those observed was taken as the food intake during Δt. If the
evacuation R is an underestimate, predicted values will tend to be higher
than observed values i.e. food intake will be negative. Tables 5b-5f
show the estimation of D.f.i. for the three size-groups of fish in March,
May, August and November. The asterisks indicate those occasions when
evacuation was faster than predicted resulting in negative intake. This
occurred on only 10 occasions (12%) and may mean that the method does not
greatly underestimate gastric evacuation in the wild.

Conversion Efficiencies: The data necessary for the computation of
conversion efficiencies are contained in Tables 5a - 5n. In Table 5g
the dry weight values of D.f.i. have been converted to wet weight using
relationships obtained from the respective stomach contents. In Table 5h
daily ration has been regressed on the average weight of the 3 size-
groups; the resultant equations makes it possible to estimate the daily
ration of fish of any size. The average length of each size group was
obtained from the length-frequency structure of the total population
(Table 5a p. 91). These lengths were converted to weight by raising to
the power 2.946 and multiplying by the appropriate condition factor. The
caloric content of fish tissue was obtained from whole fish that were
minced, oven dried at 60°C and/ignited *aliquots* in a bomb calorimeter at 20 atm. O_2.
Table 5k shows that caloric content of plaice tissue can be considered
constant throughout the year. The proportion of each food type in the
mean of each size group is based on the frequency of occurrence by weight
shown in Fig. 2.1a-c (p. 28). All molluscs have been grouped together
because of the similarity of their caloric contents; Pectinaria is
separate from other polychaetes because of its comparatively low caloric
value (Table 5n). Common values are similarly given for small (19.4 -
20.4 cm) and medium (20.5 - 25.4 cm) fish in Table 5n because of the

Table 5b   Estimation of D.f.i. in March

Hauls o'clock	SMALLS				MEDIUMS				LARGE			
	Initial gm	Final gm	Expected gm	Intake gm	Initial gm	Final gm	Expected gm	Intake gm	Initial gm	Final gm	Expected gm	Intake gm
1234→1434	0.026	0.012	0.00	0.012	0.065	0.032	0.00	0.032	0.165	0.00	0.00	0.00
1434→1640	0.329	0.329	0.00	0.329	0.032	0.603	0.00	0.603	0.00	1.053	0.00	1.053
1640→1900	0.329	0.216	0.1088	0.1072	0.603	0.346	0.1197	0.2263	1.053	0.140	0.2033	0.00
1900→2100	0.216	0.018	0.0653	0.0*	0.346	0.00	0.0674	0.00*	0.140	0.00	0.00	0.00
2100→2400	0.018	0.001	0.000	0.001	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2400→0300	0.001	0.024	0.000	0.024	0.00	0.451	0.00	0.451	0.00	0.688	0.00	0.688
0300→0600	0.024	0.133	0.000	0.133	0.451	0.266	0.0137	0.2523	0.688	0.452	0.0078	0.442
0600→0800	0.133	0.047	0.0242	0.023	0.265	0.239	0.0211	0.2179				
0800→1000	0.047	0.103	0.001	0.102	0.239	0.040	0.0142	0.0258	0.452	0.220	0.00	0.220
1000→1200	0.103	0.052	0.0125	0.0395	0.040	0.055	0.00	0.055	0.220	0.00	0.00	0.00

D.f.i. = 0.7714 gms dry   D.f.i. = 1.8633 gms dry   D.f.i. = 2.4052 gm dry

Table 5c   Estimation of D.f.i. in May

Hauls o'clock	SMALLS				MEDIUMS				LARGE			
	Initial gm	Final gm	Expected gm	Intake gm	Initial gm	Final gm	Expected gm	Intake gm	Initial gm	Final gm	Expected gm	Intake gm
1145→1445	0.1213	0.223	0.00	0.233	0.564	0.208	0.1538	0.0542	0.886	0.255	0.2491	0.0059
1445→1745	0.233	0.00	0.0086	0.0*	0.208	0.204	0.0095	0.1945	0.255	0.060	0.0037	0.0563
1745→2045	0.00	0.00	0.00	0.0	0.204	0.013	0.0086	0.0044	0.060	0.027	0.00	0.027
2045→2345	0.00	0.011	0.00	0.011	0.013	0.017	0	0.017	0.027	0.510	0.00	0.510
2345→0245	0.011	0.131	0.00	0.131	0.017	0.057	0.0	0.057	0.510	0.330	0.0740	0.256
0245→0545	0.131	0.329	0.00	0.329	0.057	0.657	0.0	0.657	0.330	0.941	0.0175	0.9235
0545→0800	0.329	0.209	0.0618	0.1472	0.657	0.809	0.2932	0.5158	0.941	1.802	0.4101	1.3919
0800→1000	0.209	0.233	0.0389	0.1931	0.809	0.562	0.4359	0.1261	1.802	1.000	1.0974	0.0*
1000→1200	0.233	0.069	0.0491	0.0199	0.562	0.095	0.2606	0.0	1.000	0.393	0.4973	0.0*

D.f.i. = 1.0642 gms dry   D.f.i. = 1.626 gms dry   D.f.i. = 3.1706 gm dry

Table 5d   Estimation of D.f.i. in August

Haul	SMALLS				MEDIUMS				LARGE			
	Initial	Final	Expected	Intake	Initial	Final	Expected	Intake	Initial	Final	Expected	Intake
1200→1500	0.023	0.175	0.00	0.175	0.085	0.021	0.00	0.021	0.358	0.207	0.0294	0.1776
1500→1800	0.175	0.137	0.0190	0.118	0.021	0.536	0.00	0.536	0.207	0.911	0.0008	0.9102
1800→2100	0.137	0.273	0.008	0.265	0.536	0.548	0.1632	0.3848	0.911	0.283	0.2783	0.0047
2100→2400	0.273	0.081	0.0586	0.234	0.548	0.299	0.1698	0.1292	0.283	0.186	0.011	0.175
2400→0300	0.081	0.068	0.0041	0.064	0.299	0.007	0.0478	0.000*	0.186	0.00	0.00	0.00
0300→0600	0.068	0.143	0.00	0.143	0.007	0.434	0.00	0.434	0.00	0.00	0.00	0.00
0600→0900	0.143	0.229	0.0095	0.2195	0.484	0.472	0.1093	0.3627	0.00	0.181	0.00	0.181
0900→1130	0.229	0.122	0.0599	0.0521	0.472	0.340	0.1710	0.1690	0.181	0.595	0.0049	0.5901

D.f.i. = 1.2606 gms dry   D.f.i. = 2.0367 gms dry   D.f.i. = 2.0386 gms dry

Table 5e   Estimation of D.f.i. in November

Haul	SMALLS				MEDIUMS				LARGE			
	Initial	Final	Expected	Intake	Initial	Final	Expected	Intake	Initial	Final	Expected	Intake
1030→1330	0.117	0.00	0.0026	0.0*	0.06	0.094	0.00	0.094	0.342	0.645	0.00	0.645
1330→1630	0.00	0.09	0.00	0.09	0.094	0.493	0.0001	0.4849	0.645	1.813	0.0409	1.7721
1630→1930	0.09	0.115	0.0001	0.1499	0.493	0.078	0.1629	0.00	1.813	0.166	0.5559	0.00*
1930→2230	0.15	0.00	0.0093	0.00*	0.078	0.011	0.00	0.011	0.166	0.021	0.00	0.021
2230→0110	0.00	0.004	0.00	0.004	0.011	0.01	0.00	0.01	0.021	0.060	0.00	0.060
0110→0430	0.004	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.060	0.060	0.00	0.060
0430→0730	0.00	0.128	0.00	0.128	0.00	0.210	0.00	0.210	0.060	0.137	0.00	0.137
0730→1000	0.128	0.075	0.0133	0.0617	0.210	0.052	0.0439	0.0081	0.137	0.258	0.00	0.258

D.f.i. = 1.527 gms dry   D.f.i. = 0.818 gms dry   D.f.i. = 2.953 gms dry

Table 5g   <u>Converting the dry weights of D.f.i. to wet weight</u>

Y = wet weight (gms)   X = dry weight (gms)

Month	SMALLS 15 - 19.4 cm				MEDIUMS 19.4 - 25.4 cm				LARGE 30 - 35 cm			
	D.f.i. gms dry	Wet wt. (Y) vs Dry wt (X)	D.f.i. gms wet	D.f.i. % body wt	D.f.i. gms dry	Wet wt (Y) vs Dry wt (X)	D.f.i. gms wet	D.f.i. % body wt	D.f.i. gms dry	Wet wt (Y) vs Dry wt (X)	D.f.i. gms wet	D.f.i. % body wt
March	0.7714	$Y = 3.4335X + 0.1856$	2.8342	5.32	1.2283	$Y = 3.2120X + 0.4351$	4.3804	3.90	3.3182	$Y = 2.6289X + 0.6726$	10.3958	3.15
May	1.0642	$Y = 3.5009X + 1.207$	4.9327	8.26	1.626	$Y = 3.8574X + 3.3278$	9.60	7.67	3.1706	$Y = 3.9646X + 0.9398$	13.1349	3.55
August	1.2606	$Y = 3.1473X - 0.0320$	3.9355	5.32	2.0367	$Y = 2.8134X + 0.3805$	6.1109	4.26	2.0396	$Y = 2.7991X + 1.1726$	10.4811	2.81
November	0.4336	$Y = 3.5930X - 0.0309$	1.527	2.56	0.818	$Y = 3.3923X + 0.6466$	3.4215	2.70	2.953	$Y = 3.6422X + 3.0561$	11.1521	3.02
February	0.2085	$Y = 5.075X + 0.0084$	1.0665	1.65	0.473	$Y = 4.5259 + 0.2384$	2.3792	2.13	0.163	$Y = 3.7125X + 0.0496$	0.6547	0.20

Table 5h   The relationship between daily food intake (D.f.i. gms) and fish size (W gms)

Month	Equation	Correlation (r)	Level of signficance
March	$D.f.i. = 0.102W^{0.804}$	1.00	$\rho \leq 0.005$
May	$D.f.i. = 0.524W^{0.562}$	0.9247	$\rho = 0.50$
August	$D.f.i. = 0.328W^{0.591}$	0.9919	$\rho = 0.01$
November	$D.f.i. = 0.01\ W^{1.211}$	0.9970	$\rho = 0.05$

Table 5k   The caloric content of plaice tissue in different moths

Month	% Water	KCals/gm wet	KCales/gm dry
March	72.4	1.40	5.07
May	71.8	1.45	5.13
June	71.0	1.51	5.19
August	72.1	1.51	5.42
September	72.2	1.45	5.21
Means:	71.9 ± 0.55	1.46 ± 0.05	5.204 ± 0.13

Table 5m   The caloric content of prey items

Item	% Water	KCals/gm wet	KCals/gm dry
Molluscs	67.76	1.37	4.25
Pectinaria	71.48	0.813	2.85
Other Polychaetes	80.12	0.950	4.78

Table 5n   The composition by weight of Plaice diet in the study area in different months   ( ) = large fish > 30 cm

| Month | Fraction of diet due to each item | | |
	Molluscs	Pectinaria	Other polychaetes
Feb/March	0.21	0.63	0.20
	(0.38)	(0.12)	(0.50)
May	0.90	0.03	0.03
	(0.62)	(0.27)	(0.04)
August	0.70	0.20	0.04
	(0.51)	(0.20)	(0.04)
November	0.2	0.70	0.1
	(0.2)	(0.50)	(0.3)

Large fish ( ) = > 30 cm   i.e. Age III[+] females.

similarity of their diet compositions as outlined earlier in Chapter 2.

Worksheets 5b M and F give the steps involved in the computation of conversion efficiencies. Each initial and final weight is an average calculated from values obtained from each growth curve as Columns VI and X of Worksheet 5a. Daily food intake for each growth period was calculated by substituting the average weight per individual ((initial + final)/2) in the appropriate equation contained in Table 5h. The D.f.i. for March was used for period 1; the D.f.i. for May was used for period 2 and that for August for period 3. Conversion efficiencies have been calculated only up to the point when 90% of the annual increment has been achieved; this is usually up to the 3rd growth period for male fish and only up to the second growth period for female fish. Gross conversion efficiencies have been calculated as

$$K_1 = \frac{\Delta W}{R \Delta t} \times 100$$

where K_1 - gross efficiency, ΔW = growth increment during growth period; Δt = length of growth period in days; R = daily ration. Net conversion efficiency K_2 was calculated as

$$K_2 = \frac{\Delta W}{\rho R \Delta t}$$

where ΔW and Δt remain as in the K_1 equation and ρR is the assimilated fraction of R. ρR was taken as $0.8R$ after Winberg (1956). Growth efficiency of the third order K_3 was calculated as

$$K_3 = \frac{\Delta W}{\rho R \Delta t - T_R}$$

where T_R is the amount of ρ that meets metabolic needs. According to Edwards, Finlayson and Steele (1968), oxygen consumption in resting plaice obeys the formula:

$$QO_2 = 0.214 W^{0.721} \text{ at } 10^\circ C$$

where QO_2 = oxygen consumption as ml/hr, and W = fish weight. The resting metabolic rate for each age group was obtained using this formula and then

Computation of the Conversion Efficiencies of Male Plaice of ages II-IV in the study area

Age	Growth Period	Length of Growth Period	Initial weight	Final weight	Growth Increment	D.f.i.	Total Intake	Routine Metabolism	CONVERSION EFFICIENCIES Gross (K_1)	Net K_2	3rd Order K_3
		days	gm (Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	Kcal	g(Kcal)	g(Kcal)	g(Kcal)
II	End February - End April	61	70.84 (103.43)	100.4 (146.58)	29.56 (43.16)	3.66 (3.62)	223.26 (221.03)	66.51 (65.84)	13.24 (19.53)	16.55 (24.41)	26.37 (38.89)
	End April - End July	92	100.40 (103.43)	154.16 (225.07)	53.76 (78.49)	7.99 (10.27)	735.08 (944.58)	78.08 (100.33)	7.31 (8.31)	9.14 (10.39)	10.54 (11.98)
	End July - End September	61	154.16 (225.07)	158.55 (231.48)	4.39 (6.41)	6.42 (7.41)	391.74 (452.07)	188.18 (217.16)	1.12 (1.42)	1.40 (1.77)	3.51 (4.44)
III	End February - End April	61	114.47 (167.13)	155.57 (227.13)	41.10 (60.01)	5.28 (5.23)	322.08 (318.86)	92.36 (91.44)	12.76 (18.82)	16.07 (23.52)	24.86 (36.67)
	End April - End July	92	155.57 (227.13)	225.58 (329.35)	70.01 (102.22)	10.02 (12.88)	921.84 (1184.56)	228.60 (293.75)	7.60 (8.63)	9.49 (10.79)	13.75 (15.63)
	End July End September	61	225.58 (329.35)	227.91 (332.75)	2.33 (3.40)	8.00 (9.23)	488.00 (563.15)	245.99 (283.87)	0.48 (0.60)	0.60 (0.76)	1.61 (2.04)
IV	End February - End April	61	200.76 (293.11)	244.49 (356.96)	43.73 (63.85)	7.90 (7.82)	481.90 (477.08)	132.46 (131.13)	9.08 (13.38)	11.34 (16.73)	17.28 (25.48)
	End April - End July	92	244.49 (356)	301.85 (440.70)	57.36 (83.75)	12.27 (15.77)	1128.84 (1450.56)	296.35 (380.79)	5.08 (7.28)	6.35 (7.22)	9.45 (10.74)

Computation of Conversion Efficiencies in Female Plaice

Age	Growth Period	Length of Growth Period	Initial weight	Final weight	Growth Increment	D.f.i.	Total Intake	Metabolic Requirements	CONVERSION EFFICIENCIES Gross K_1	Net K_2	3rd Order K_3
		days	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)	g(Kcal)
II	End February – End April	61	42.62 (62.23)	90.54 (132.19)	47.92 (69.96)	2.98 (2.95)	181.78 (179.96)	55.47 (54.92)	26.36 (38.88)	32.95 (48.59)	53.27 (78.56)
	End April – End July	92	90.54 (132.19)	201.52 (294.22)	110.98 (162.03)	8.63 (11.09)	793.96 (1020.24)	188.68 (242.45)	13.98 (15.88)	17.47 (19.85)	24.86 (28.24)
III	End February – End April	61	110.46 (161.27)	197.40 (288.20)	86.94 (126.93)	5.86 (5.80)	356.85 (353.28)	101.52 (100.51)	24.36 (35.93)	30.45 (44.91)	47.26 (69.70)
	End April – End July	92	197.40 (288.20)	302.67 (441.90)	105.27 (153.69)	11.67 (15.00)	1073.64 (1379.63)	278.05 (357.29)	9.81 (11.14)	12.26 (13.92)	18.12 (20.59)
IV	End February – End April	61	192.89 (281.62)	295.60 (431.58)	102.71 (149.96)	8.48 (9.27)	517.28 (565.49)	128.24 (140.19)	19.86 (26.52)	24.82 (33.15)	35.96 (48.03)
	End April – End July	92	295.60 (431.58)	443.60 (647.66)	148.0 (216.08)	14.53 (16.09)	1336.76 (1479.79)	427.81 (473.58)	11.07 (14.60)	13.89 (18.25)	23.07 (30.42)
V	End February – End April	61	292.39 (426.89)	396.80 (579.33)	104.41 (152.44)	11.18 (12.22)	681.98 (754.95)	164.36 (179.68)	15.31 (20.19)	19.14 (25.24)	27.39 (35.93)
	End April – End July	92	396.80 (579.33)	568.45 (829.94)	171.65 (250.61)	16.89 (18.70)	1553.88 (1720.15)	518.56 (574.04)	11.05 (14.57)	13.81 (18.21)	23.69 (31.09)

corrected to ambient temperature using the expression

$$Log\ Q_{10} = \frac{10(\log R_1 - \log R_2)}{10 - T_2} \qquad \text{(Hoar, 1966)}$$

where Q_{10} was taken as 2.63 (after Backiel, 1971), R_1 as the oxygen consumption at $10^\circ C$ and R_2 as the oxygen consumption at ambient temperature T_2. Metabolic rates obtained in this way were corrected for activity by multiplying by 2 (Winberg, 1956) and then converted to calories using the factor

$$1\ ml\ O_2 = 4.77\ cals$$

Worksheets 5b M and F show 4 clear trends:

1) In all cases conversion efficiencies measured in grams are lower than values expressed in energy units.

2) Female fish display consistently superior efficiencies when compared with males of similar age.

3) In both males and females the efficiency of conversion declines with age.

4) Conversion efficiency also declines as the growth season progresses in all age groups of both sexes.

The greater efficiencies obtained with energy units are a simple consequence of the fact that 1 gm of plaice tissue has a higher caloric content than 1 gm plaice diet as obtained in this study. Commonly quoted values for the energy content of plaice usually give 1.1 Kcals per gram wet weight (Hatanaka et al., 1956a,b) which is 0.36 Kcals/gm lower than in the present study. The inferior performance of males as compared with females is explained partly by their slower growth rates. Preliminary checks made during the 24 hour trips reported in Chapter 2 showed no obvious differences in either diet or average stomach contents between male and female fish of the same size. Unless they assimilate less efficiently than females (there appears to be no evidence for or against this) it is

likely that these differences may have a sex-linked genetic basis. The decline in conversion efficiency with age shown by both sexes has been observed in this and other species, e.g. P. platessa (Dawes, 1930a,b), Limanda yokohamae, Hatanaka et al., 1956a), Megalops cyprinoides, Ophiocephalus striatus (Pandian, 1967), Stizostedion vitreum vitreum (Kelso, 1972). Kelso maintains that this is due not to a decreased ability to grow per se, but to the increase in metabolic requirement that accompanies growth in size. This explanation may be too simplistic for the present case, because not only does efficiency decrease with age, it also declines as the growing season progresses. Temperature and ration also vary throughout the season but not in a unidirectional manner: both rise to a maximum in May/July and then drop off as autumn approaches. Besides, the literature is far from dogmatic on the effects these two variables can exert on efficiencies of conversion. Paloheimo and Dickie (1966a, b) reviewed various earlier works (including that of Dawes 1930-31a on 2 year old plaice) and concluded that gross efficiency K_1 decreases with ration size. Though LeBrasseur (1969) was able to confirm this for Onchorhynchus keta Brett et al. (1969) were unable to do the same with another species of the same genus O. nerka. These workers found that K_1 increased to an optimum as ration increased. On the other hand Kelso (1972) found no relationship between K_1, K_2 or K_3 and ration when 2 year old walleye S. vitreum vitreum were fed young crustaceans.

If temperature affects conversion efficiencies at all it must be via its effects on metabolism, though the data of Kohler (1964) who fed Atlantic cod (G. morhua) at 2.3 and 13.6°C show no correlation between temperature and net efficiency (quoted in Jones, 1976). Whatever effects of temperature may exist, the use of K_3 which eliminates T, the metabolic requirement, should remove them to some extent. The K_3 values in Worksheets 5bM and F, however, show similar trends to those of gross and

net efficiencies and the suspicion arises that in the wild, the interactions between simultaneous change in temperature, food density, fish size and day length (via its effects on blood levels of growth and other hormones), provide field situations more complex than the laboratory regimes under which empirical relationships are established.

Published values on the conversion efficiencies of plaice and related species range between 4.6% for Limanda yokohamae (Hatanaka et al., 1956a) and 45% for O-group plaice (Lockwood, 1972). Beverton and Holt (1957) suggested a net efficiency of 20% for plaice in the North Sea and this fits well with the range of values obtained in the present study.

Energy Budget Calculations. Table 5m gives the annual energy intake of the population and the manner in which it is ultimately utilised. Because the fish fast during late autumn and winter, gonad maturation as well as the metabolic requirements for this period must be at the expense of somatic tissue. Estimates for these two processes have therefore been subtracted from the total growth production in each case to give the final yield that is retained into the next year of life. Gonad weight for female fish was obtained from the relationship between fish length and ovary weight given in Table 4g (p. 84) for the month of March. There was no correlation between male fish length and testes size and an average testes weight of 5.0 gms wet, has been adopted. Wet weights of gonads were converted to energy as 1 gm wet ovary = 1.86 Kcals,

$$1 \text{ gm wet testes} = 0.5 \text{ Kcals.}$$

The proportion of each male and female age-group involved in gonad elaboration was obtained from Table 1.g M which contains the results of the probit analysis of maturity data.

The differences in conversion efficiencies between males and females recorded earlier are reflected in the greater proportion of the annual intake used for growth by the female fish. For both sexes metabolic requirements approach a third of the annual intake. Though a

Table 5m   Annual Energy Budget of the Plaice Population. Values are million Kcals.(   ) = adjacent value expressed as % annual intake.

	Age	Annual Intake	Routine Metabolism		Growth Production		Autumn/Winter loss of condition	Reproduction		Production retained into next yr	
FEMALES	2	135.72	42.66	(31.43)	16.61	(12.23)	1.22	1.44	(1.06)	13.95	(10.78)
	3	97.78	30.85	(31.55)	10.03	(10.26)	0.95	1.71	(1.75)	7.37	(7.54)
	4	41.49	17.01	(40.99)	5.00	(12.05)	0.37	1.17	(2.82)	3.46	(8.34)
	5	30.40	11.46	(37.70)	3.29	(10.82)	0.44	0.89	(2.92)	1.96	(6.45)
MALES	2	133.04	37.64	(28.29)	10.06	(7.56)	0.34	0.042	(0.032)	9.68	(7.28)
	3	81.10	28.64	(35.31)	6.04	(7.48)	0.21	0.029	(0.036)	5.80	(7.15)
	4	25.0	7.80	(31.10)	1.37	(5.48)	0.20	0.009	(0.036)	1.16	(4.64)
All Groups		544.53	176.06	(32.33)	52.4	(9.62)	3.73	5.29	(0.97)	43.38	(7.97)

Winter losses =   (i)   2.12% of annual metabolic requirements

(ii)   7.11% of total growth production

large proportion of older female fish are mature, the younger fish expend a comparable amount on reproduction. Expressed as a fraction of the annual calorie intake however, the older fish are seen to expend proportionally more on reproduction. The fraction of the total growth production lost later as reproductive products is 8.7% for age II, 17% for age III, 23.4% for age IV and 25% for age V (Mean = 18.52%). These values are much lower for male fish, being 0.42% age II, 0.48% age III and 0.66% for age IV (Mean = 0.52%).

With regard to its impact on the local benthic community, the population crops 491.15 tonnes annually (2.08 g/m²). Nicholaidou (1977) has shown that in Beaumaris Bay, production of P. koreni alone approaches 138.82 g/m² and it is therefore likely that the requirements of the fish population are met. From personal observations, only one other species in the study area (Limanda limanda) takes P. koreni and A. alba to any extent. However, the aspects of duration and timing of production by the benthic community should not be ignored. Nicholaidou's data show that 93% of the annual production of P. koreni occurs between the first week in June and the first week in October; production was negative in December and January and minimal in February and March. This is unfortunate from the point of view of fish production: instead of sustained production that can meet the needs of the fish population, there is a glut of production in a few short months probably in excess of the maximal rate at which the fish can exploit it.

Summary

(1)   The area occupied by the population was estimated as 23672.5

hectares (= 236.73 Km^2). Population size was 478,630 fish. Biomass

was 26.36 tonnes (= 0.11 gm/m^2). Assuming that recruitment was complete

by age II, 94% (by numbers) of this population were in the fishable

phase.

(2)   Data on diet and feeding chronology was obtained from fish collected

by trawling at known intervals (usually 3 hours) during a 24-hour

period. Such trawls were carried out in March, May, August, November

and February.

(3)   The diet of 'small' (15.5 - 19.4 cm) and 'medium' (19.5 - 20.4 cm)

fish was found to be similar in each of the months for which data was

collected. The two chief items were the polychaetes Pectinaria koreni

and the lamellibranch Abra alba. The diet was dominated by P. koreni

in February and by A. alba in May. In each case the dominant item

formed over 80% of the diet by weight and by numbers. In August A. alba

was still dominant but not to the extent observed in May. In November

there was a return to the February situation and the diet was dominated

by P. koreni. The large fish (30 - 35 cm) had a more catholic diet and

no single species ever accounted for more than 65% either by numbers

or by weight. In addition to P. koreni and A. alba, Nereis spp. and the

bivalve Tellina fabula were also prominent in the menu of these fish.

(4)   Variation in the average stomach contents with time of day indicated

that

a) Generally the amount of food in the stomach at any time of day was

related to the size of the fish; the largest having the most and the

smallest the least.

b) Feeding did not appear to be entrained to the state of the tide.

c) Feeding was usually restricted to daylight hours.

d) There was a winter fast from about the second week in December whilst February probably marked the earliest resumption of feeding.

(5)   When average stomach contents were considered in conjunction with the occurrence of food in specific regions of the alimentary canal, the feeding chronology appeared to vary between seasons for each size-group. In the cooler months - February, March and November - the following phases were recognisable

   a)   Feeding Peak

   b)   Gastric Evacuation

   c)   Feeding Pause

   d)   Resumption of Feeding.

In the warmer months of May and August, these phases were not recognisable. It was concluded that feeding pauses occurred in the cooler months not because a certain hunger threshold was required to stimulate resumption of feeding, but as a result of lowered swimming speeds, and an impoverished benthos. It appeared that in the cooler months ingested food is retained in the stomach for some degree of physical and chemical breakdown before evacuation into the intestines. In late spring and summer increased feeding frequency, larger meals and higher temperatures may stimulate the gastro-intestinal tract to such an extent that this retention period is drastically reduced and food is transferred into the anterior regions of the intestines almost immediately after ingestion. The effect of this would be to eliminate the feeding phases shown by each population in the cooler months.

(6)   The interpretations placed on the feeding chronology data were supported by data from laboratory studies on gastric evacuation time (GET) which showed that

a) A rise in temperature will shorten the GET for a meal of given size. GET was found to vary with temperature raised to the power

-1.03 (Fig. 3.2; Table 3b; Worksheet 3.3b, p. 54-57).

b) When fed weight-specific meals (i.e. % body weight units) of equal size, small fish will complete gastric evacuation earlier than larger fish at the same temperature. GET varied with fish size raised to the power 0.42 (Fig. 3.1; Table 3b; Worksheet 3.1, p. 54-57).

c) When fed meals of equal absolute size (gms) small fish require a longer time to complete gastric evacution than larger fish. GET varied as fish size raised to the power -0.068 (Worksheet 3.3c).

d) For a fish of given size at a specified temperature, the larger the meal (% body weight or gms), the longer the time to complete gastric evacuation. For meals expressed as % body weight GET altered as meal size raised to the power 0.211 (Worksheet 3.3a, p.54-57). For meals expressed as gms the exponent was ca. 0.50 (Fig. 3.3; Worksheets 3.3c and d, p.54-57).

e) The rate of evacuation as gms/hr is faster the larger the meal (gms). Gastric evacuation rate was found to vary as meal size raised to the power 0.60 (Fig. 3.5; Worksheet 3.3e, p. 59-61).

(7)   The factors shown to affect the rate of gastric evacuation in the laboratory also vary seasonally in the field. Not surprisingly the condition and growth of the population were found to vary in the same way. Regarding condition, there appeared to be 3 parts to the calendar year: Peak condition in June, July and perhaps part of August; intermediate condition in spring (improving) and autumn (deteriorating), and poor condition in winter. There was no difference in condition between immature and mature fish during the spawning season but spent fish were significantly leaner than other fish.

(8)   Seasonal growth started in April and was virtually over by the end of September. As a result of differences in the timing of the start and

end of their growing seasons, younger fish of each age-group may have
a longer growing season than older fish; younger fish of each sex may
have a longer growing season than older individuals, and female members
of a year-class may have a longer growing season than their male
counterparts. These observations may account for differences between
these groups in their seasonal growth increments. Average lengths-at-
age showed a drop between October and February. This was attributed
to a size-linked spawning migration undertaken during this period.
The function

$$Y = A - B (e^{-kt)}$$

was used to describe seasonal growth data.

(9)   The variations in average stomach contents with time of day were
used to establish gastric evacuation rates in the wild. These rates
were then used for estimates of daily ration for each size group at
different times of year. When these estimates were utilised in con-
junction with growth data it became possible to make estimates of the
total annual production of the plaice population in the study area.
Net production was 22.85 tonnes for females and 11.68 tonnes for females.
Total annual production for the whole population excluding winter losses was
35.9 tonnes (0.15 g/m²). Assuming that gonad maturation occurred at
the expense of somatic tissue ca. 15% of female production and 0.47%
of male production was later lost as reproductive products.

(10)   Total food intake by the population was 491.15 tonnes annually (=
544.5million Kcals). Further energy budget calculations indicated
that in energy units this was eventually distributed as follows:

Growth   9.62%

Routine metabolism   32.33%

Reproduction   0.97%

Losses (due to egestion,   58.4%

   conversion etc.)

(11) Because spawning and winter metabolism were at the expense of

      somatic tissue only 82.7% of total growth production was retained

      into the next growing season.

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Appendix

Appendix 1.1

Details of catch data 1974 - 1977.

1974

Fish Length (cm)	13 October (i)	13 October (ii)	1 November Only	Only	16 Nov. Only	Total at each Length	% Catch at each Length
Distance Trawled (metres)	5562	7417	6488	3707	7417	at each	at each
Area Trawled (hectares)	17.18	22.91	20.04	11.45	22.91	Length	Length
14	3	1			1	5	0.23
15	18	1	4		6	29	1.32
16	20	2	15	7	15	59	2.69
17	27	14	18	13	19	101	4.61
18	69	5	29	21	29	153	6.98
19	83	9	24	36	43	195	8.89
20	96	16	36	38	37	223	10.17
21	111	21	33	33	25	223	10.17
22	104	14	27	40	33	218	9.84
23	90	17	26	26	36	195	8.89
24	78	13	18	35	18	162	7.39
25	89	9	18	25	21	122	5.56
26	56	1	8	15	10	90	4.10
27	36	5	11	20	13	85	3.88
28	18	7	19	13	14	71	3.24
29	14	1	12	5	10	42	1.92
30	14	2	10	7	8	41	1.87
31	7	3	10	2	14	36	1.64
32	3	3	13	4	18	41	1.87
33	1		4	1	26	32	1.46
34	5	1	2	1	14	23	1.05
35			1		8	9	0.41
36	1		2		11	14	0.64
37	1				8	9	0.41
38			1		4	5	0.23
39			1			1	0.05
40					2	2	0.09
41			1		1	2	0.09
42					3	3	0.14
43							
44							
45							
46					1	1	0.05
47					1	1	0.05
48							
49							
50							
Total Catch	914	145	343	342	449	?-	
Catch/Hectare	53.20	6.33	17.12	29.86	19.60		

1975

Date	21 October		22 October		28 October		Total at each Length	% Catch at each Length
Haul	(i)	(ii)	(i)	(ii)	(i)	(ii)		
Distance Trawled (metres)	5189	4264	7802	7802	4079	2233		
Fish Length (cm) / Area Trawled (hectares)	16.03	13.17	24.1	24.1	12.60	6.9		
14								
15					2		2	0.19
16				1			1	0.10
17			2	1	1		4	0.39
18			4	8	29		41	3.98
19			1	19	39		59	5.72
20			2	22	77		101	9.80
21			5	14	51		70	6.79
22			2	9	50		61	5.92
23	3		4	10	62		79	7.66
24	5		1	11	68		85	8.24
25	1		3	10	59		73	7.08
26	3		3	8	71		85	8.24
27	3		3	9	53		68	6.60
28	1		6	12	32		51	4.95
29	2			5	24		31	3.01
30	3	1	1	6	19		30	2.91
31		2	4	4	16		26	2.52
32	1	3	5	1	7	1	18	1.75
33	1	6	3	4	8		22	2.13
34	1	1	2	3	6	3	16	1.55
35	1		4	4	8	2	19	1.84
36		4	6	3	5	1	19	1.84
37	1		2		10	1	14	1.36
38	2	1	4	3	1		11	1.07
39	1	1	3	3	4	2	14	1.36
40			3	2	1	3	9	0.87
41			1		3		4	0.39
42	1	2	1	1		1	6	0.58
43			1	2	1		4	0.39
44					1	1	2	0.19
45		1			1		2	0.19
46		1			1		2	0.19
47								
48				2			2	0.19
49								
50								
Total Catch	30	23	76	177	710	15		
Nos per hectare	1.88	1.75	3.15	7.34	56.35	2.17		

1976

Date	27 October			2 November		3 November		Total at each Length	% Catch at each Length
Haul	(i)	(ii)	(iii)	(i)	(ii)	(i)	(ii)		
Distance Covered (metres)	5099	3616	4357	6303	5193	4820	5377		
Area Trawled (hectares)	15.75	11.17	13.46	19.47	16.04	14.89	16.61		
Fish Length (cm)									
14	1							1	0.04
15	1	1	5	1				8	0.33
16	7	3	20	2	5	2		39	1.58
17	11	6	23	3	11	2	9	65	2.64
18	25	9	88	21	21	6	18	198	8.03
19	24	19	94	27	49	14	27	254	10.31
20	19	12	94	32	65	14	30	266	10.80
21	23	13	54	35	77	6	33	241	9.78
22	21	11	54	35	80	7	31	239	9.70
23	10	7	34	35	82	6	24	198	8.04
24	18	6	31	26	67	8	24	180	7.31
25	10	5	31	19	68	2	15	150	6.09
26	20	3	28	11	44	4	17	127	5.16
27	15	3	17	11	39	4	14	103	4.18
28	16	5	21	9	36	4	6	87	3.53
29	6	4	16	7	22	3	5	63	2.56
30	3	6	9	6	19	5	13	61	2.48
31	5	5	8	4	13	4	10	49	1.99
32	1	11	8	1	5	1	4	31	1.26
33	1	7	4	3	8	1	4	28	1.14
34	3	2	2	3	3	4	1	18	0.73
35		1	2	1	4	1	2	11	0.45
36		1	2	1	3	1	1	9	0.37
37		1	1				2	4	0.16
38		2				1	2	5	0.20
39							1	1	0.04
40	1	4			1	2		8	0.33
41		1				1		2	0.08
42	2	1					1	4	0.16
43					1	2	1	4	0.16
44			1				1	2	0.08
45									
46	1							1	0.04
47	1					1		2	0.08
48						1		1	0.04
49		1						1	0.04
50				1				1	0.04
Total Catch	245	150	647	294	723	107	296	2462	
Nos/hectare	15.50	13.34	48.10	15.10	15.10	7.20	17.82		

45.07

1977

Date	19 October		25 October		26 October		1 Nov	Total	%
Haul	(i)	(ii)	(i)	(ii)	(i)	(ii)	ONLY	at each	Catch
Distance Trawled (metres)	3801	2965	6209	4756	6397	4756	3153	Length	at eac Length
Fish \ Area Trawled (hectares)	11.74	9.16	19.18	14.69	19.76	14.69	9.74		
Length (cm)									
14	1		1		2	1		5	0.24
15	2		2		1			4	0.19
16	9	10	8	1		1		29	1.41
17	23	10	11	5	3	4	2	58	2.81
18	43	64	21	11	11	17	3	170	8.24
19	74	101	27	17	10	16	10	255	12.36
20	104	132	28	32	11	23	11	341	16.53
21	67	91	22	21	6	27	12	246	11.92
22	53	80	7	8	12	16	12	188	9.11
23	38	48	31	35	7	19	10	188	9.11
24	22	31	12	9	6	9	6	95	4.61
25	28	12	10	8	11	23	2	94	4.56
26	19	14	11	13	8	10	3	78	3.78
27	11	15	7	13	5	10	6	67	3.25
28	12	12	14	9	8	10	3	68	3.30
29	10	9	5	2	5	5	5	41	1.99
30	6	8	3	2	6	4		29	1.41
31	11	1	2	1	2	5	4	26	1.26
32	5	2	2	1	1	5	3	19	0.92
33	4	3	1		3	4	5	20	0.97
34	2		2	2	1	6	2	15	0.73
35		2			1	1	5	9	0.44
36	1		1	1	1	2	2	8	0.39
37						1		1	0.05
38					2	2		4	0.19
39									
40						1	1	2	0.1
41							1	1	0.05
42									
43					1			1	0.05
44						1		1	0.05
45									
46									
47									
48									
49									
50									
Total Catch	545	645	228	191	123	223	108		
Nos/hectare	46.5	70.4	11.9	13.1	6.2	15.3	11.1		

Appendix 1.2 Single factor analysis of variance of catch data

Data are in $\log_e$ units

YEARS			
1974	1975	1976	1977
6.81	3.40	5.50	6.30
4.98	3.14	5.01	6.47
5.84	4.33	6.47	5.43
5.84	5.18	5.68	5.25
6.11	6.57	6.58	4.81
	2.71	4.67	5.41
		5.69	4.68
Group sums: 29.58	25.33	39.60	38.35

$\underset{i \ j}{\Sigma \ \Sigma} \ X_{ij} \ = \ 132.86$

$\Sigma \ \Sigma \ X^2{}_{ij} \ = \ 734.09$

$N \ = \ 25$

$C \ = \ \dfrac{(132.86)^2}{25} \ = \ 706.07$

Total SS = $734.09 - 706.07 \ = \ 28.02$

Groups (i.e. years) SS = $\dfrac{(29.58)^2}{5} \ + \ \dfrac{(25.33)^2}{6} \ + \ \dfrac{(39.60)^2}{7} \ + \ \dfrac{(38.35)^2}{7} \ -$

$706.07 \ = \ 12.18$

Error SS = $28.02 - 12.18 \ = \ 15.84$

Source of Variation	SS	DF	MS
Total	28.02	N-1 = 24	
Groups	12.18	K-1 = 3	4.06
Error	15.84	N-K = 21	0.75

$F \ = \ \dfrac{4.06}{0.75} \ = \ 5.41$

$F_{0.05(1)}{}^{3,21} \ = \ 3.07$ 　　　　　 Reject H_o

Appendix 1.2 <u>Single factor analysis of variance of catch data</u>

| | YEARS | | | |
	1974	1975	1976	1977
	314	30	245	545
	145	23	150	645
	343	76	647	228
	342	177	294	191
	449	710	723	123
		15	107	223
			296	108
Group Sums:	2193	1031	2462	2063

$$\sum_i \sum_j X_{ij} = 7749$$

$$\sum_i \sum_j X^2_{ij} = 3922895$$

$$N = 25$$

$$C = \frac{(7749)^2}{25} = 2401880.$$

Total SS = 3922895 - 2401880 = 1521015.

Groups (i.e. years) SS = $\frac{(2193)^2}{5} + \frac{(1031)^2}{6} \quad \frac{(2462)^2}{7} + \frac{(2063)^2}{7} - 2401880 = 211046$

Error SS = 1521015 - 24046 = 1309969.

Source of Variation	SS	DF	MS
Total	1521015	N-1 = 24	
Groups	211046	K-1 = 3	70349
Error	1309969	N-K = 21	62380

$$F = \frac{70349}{62380} = 1.13$$

$F_{0.05(1)}$ 3,21 = 3.07   Do not reject H_O.

Appendix 1.3

Calculation of the Distance between Trawl Doors during Fishing

Data

(i)   DD' is the distance between the doors.

(ii)   AB and A'B' are the sides of the ship.

(iii)   S and S' are the shackles from which the warps leave the ship during fishing.

(iv)   Each warp subtends an angle of 10° with the side of the ship so that

$$DSB = D'S'B' = 10^{\circ}$$

(v)   As the shackles S and S' are directly opposite each other, the line joining them must be perpendicular to the sides of the ship and its long axis.

Thus $BSM = B'S'M = 90^{\circ}$

(vi)   The line PMX represents the axis of the ship and assuming that the net was towed directly behind the ship, PMX bisects SS' as well as DD'. It is also parallel to AB and A'B'.

(vii)   The distance between the shackles S and S' is 18 ft, so

$$SM = MS' = 9 \text{ ft}$$

Procedure: Construct a line each from S and S' to meet PMX at a point Z.

Deductions: $DSB = ASZ = 10^{\circ}$

(Vertically Opposite Angles)

$SZM = ASZ = 10^{\circ}$

(Alternate angles on parallel lines)

In triangle SZM Sine 10° = $\text{sm}/_{ZS}$

        ZS = 51.829 ft

In triangle ZDP Sine 10° = $\text{DP}/_{ZD}$

        But ZD = ZS + SD = 51.829 + 240

        DP = 50.676 ft

        DP = ½DD'

    ∴ <u>DD' = 101.35 ft</u> (= 30.89 metres)

Length/Age Matrix for Stratified Female Samples

Length \ Age	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV
14	1	3														
15	1	4														
16	2	10	7													
17		24	6													
18		24	6	2												
19		23	5	3												
20		19	10	1												
21		16	13	4												
22		14	13	3												
23		7	15	5	2	1										
24		4	15	10	1	1										
25		6	18	3	1	2										
26		5	16	6	4	1	1									
27		3	12	12	3	1										
28		2	16	9	4											
29			13	13	2	2	3									
30			16	11	4	1		1								
31			9	16	3	2	1									
32			7	13	11	2	3									
33			4	15	14	5	1	1								
34			2	11	13	9	2	2								
35			2	6	8	15			3							
36				4	10	10	4	3								
37				4	12	7	1	4	2							
38				6	5	5	8	2	4	4	1					
39					5	8	6	4	2	3	1					
40					1	3	12	5	3	1	2		1			
41					2	7	9	1	2	3	1	1				
42					3	6	2	4	3	2	2	1	2			
43					1	4	4	1	2	2		1		1		
44						1	2	2	2	2	4	3		1	1	
45						2	2	4	3	1	2			2		
46					1		2	1	1	1						
47									2	2	1		3		1	1
48					1	1		1	2					1		
49									1	2	1	1				
50													1	1	1	
Nos. at Age	4	164	205	155	111	96	63	37	37	32	23	7	7	6	3	1
Av. Length	15.25	19.74	25.12	29.57	33.99	36.40	38.65	40.14	40.14	41.59	42.00	43.86	45.00	45.67	46.67	47.00
S.D.	0.96	3.03	4.52	4.69	4.55	4.74	4.32	4.33	4.33	4.06	3.32	2.55	3.65	2.34	3.87	0

S.D. = Standard Deviation

Appendix 1.4 M   Length/Age Matrix of Stratified Male Samples

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Length \ Age	0	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
14		1											
15	1	9	1										
16	2	21	5										
17	1	22	8	1									
18		22	9										
19		21	10		1								
20		20	7	3	1	1							
21		19	10	3									
22		10	20	9	1								
23		6	15	9	1								
24		8	15	10	1		1						
25		12	18	6	3		1						
26		1	18	14	4		2						
27			20	8	4	2							
28			12	13	3	2	1						
29			14	11	5	4	2	1	1				
30			8	9	4	5		1	1	2			
31			3	15	5	4	2	1					
32			2	5	5	6	2	1				1	
33			4	9	4	3	1	1		1			
34				2	3	1	4	1					
35				2	2	1		1			2		
36				2				1	2	1			
37					1				1				
38							1						
39							1						
40													
	4	172	200	131	48	29	16	8	5	4	2	1	Numbers of Age
	16	19.35	24.16	27.48	29.17	30.34	31.05	32.5	33.6	32.3	35.0	32.0	Av. Length at Age
	0.82	2.87	4.11	3.96	3.96	2.82	3.98	2.45	3.80	2.87	0	-	Standard Deviation

Appendix 1.5.   Testing for significant differences between male and

female plaice in the slope of the simple linear regression

$\log_e N_t$ (Y) vs t (X)

$H_0 : \beta_{0\female} = \beta_0$

	Females	Males
Σx^2	82.5	42
Σxy	-53.77	-41.26
Σy^2	35.18	41.17
n	10	8
b	- 0.652	- 0.982
Residual SS		
$(\Sigma y^2 - \frac{(\Sigma xy)^2}{\Sigma x^2})$	0.135	0.637
Residual DF (n - z)	8	6

$(S^2_{y.x})_p$ $\dfrac{0.135 + 0.637}{8 + 6}$ =   0.005

$S_{0\female} - 0 = \sqrt{\dfrac{0.005}{82.5} + \dfrac{0.005}{42}}$ =   0.045

$t = \dfrac{-0.652 + 0.982}{0.045}$ = $\underline{7.33}$

$\nu = 8 + 6 = 14$

$t_{\alpha (2) 14} = 2.145$ Therefore reject H_0.

Appendix 2.1   The Percentage Occurrence by numbers and by weight ( ) of the principal prey items in the diet of three size-groups of plaice in the study area

	FEBRUARY			MAY			AUGUST			NOVEMBER		
	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
POLYCHAETES												
Pectinaria koreni	56.25 (57.1)	73.6 (67.28)	11.54 (12.21)	3.32 (3.7)	6.84 (5.2)	24.76 (15.68)	28.32 (23.20)	18.21 (16.25)	19.23 (20.0)	42.2 (75)	53.2 (72.4)	37.2 (48.2)
Nephthys sp.	...	0.56 (0.53)	3.85 (4.98)	2.77 (3.5)	5.25 (4.6)	4.38 (3.4)	1.50 (0.97)	1.43 (1.20)	2.44 (0.87)	0.8 (1.6)	1.2 (1.5)	1.4 (2.11)
Others	28.57 (26.23)	8.99 (7.25)	42.31 (45.2)	1.70 (2.8)	2.56 (0.53)	1.99 (1.12)	10.77 (4.26)	5.74 (2.01)	3.83 (7.63)	3.8 (2.0)	25.4 (9.38)	38.7 (28.29)
BIVALVES												
Abra alba	4.46 (4.2)	5.62 (7.2)	19.23 (20.46)	88.9 (84.3)	81.78 (88.63)	62.28 (59.07)	45.61 (61.58)	64.21 (75.11)	48.25 (57.12)	47.7 (18.19)	12.9 (6.2)	6.6 (1.52)
Cultellus pellucidus	2.68 (3.01)	3.37 (3.43)	1.99 (2.23)	1.47 (1.91)	1.22 (0.73)	0.76 (0.63)	6.26 (4.90)	3.51 (3.17)	... ...	3.4 (2.01)	3.4 (4.33)	12.5 (15.54)
Ensis ensis	4.46 (5.57)	5.06 (5.32)	7.69 (9.71)	0.18 (0.24)	0.12 (0.1)	1.71 (1.25)	2.25 (2.73)	1.27 (1.20)	14.68 (13.06)	0.8 (0.3)	2.4 (3.21)	2.7 (3.42)
Other bivalves	3.57 (3.99)	12.81 (8.99)	13.39 (5.21)	1.28 (2.68)	1.81 (0.53)	2.65 (10.28)	2.4 (0.8)	2.5 (0.87)	2.41 (1.0)	...	0.6 (0.8)	0.5 (0.06)
Miscellaneous	...	...	...	0.18 (0.87)	0.36 (0.21)	1.47 (8.62)	3.25 (1.56)	3.13 (0.19)	9.26 (0.32)	1.3 (0.9)	0.9 (2.18)	0.5 (0.86)

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