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FECUNDITY AND THE ENERGETICS OF REPRODUCTION AND GROWTH OF NORTH SEA PLAICE (PLEURONECTES PLATESSA L.).

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A.D. Rijnsdorp, F. van Lent
and K. Groeneveld
Netherlands Institute for Fishery Investigations
P.O. Box 68, 1970 AB IJmuiden
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Abstract.

The fecundity and the growth of female plaice were studied in combination with the calorific content of the ripe eggs and of the total body during the spawning period. With these data an energy budget of mature females was calculated. A comparison of the fecundity, growth and maturity is made between the present and two historic periods: around 1900 and 1947-1949.

The fecundity in 1983 was with approximately 6 %, significant lower than in 1982. Condition factor in 1982 and 1983, and age in 1983 had a significant positive influence on the fecundity. In both years no significant difference could be shown between the fecundity in the Southern Bight, German Bight and Flamborough area. Present fecundity is substantial higher than in both historic periods.

The length at which 50 % of the females became mature was 30.8 cm in 1979-1980 and increased to 33.8 cm in 1982. The corresponding age was estimated at 4 years. In the period around 1900 this age was estimated at 5 years.

Growth was shown to be isometric. The condition factor peaks in October-November. A drastic decline occurs in the spawning period when the females shed their eggs. A corresponding decline was observed in the energy contents of the female body.

The present growth rate is higher than in 1947-1949. The growth rate around 1900 was lower for the younger age groups and higher for the older ones.

In the energy budget the following features are calculated:
1. the net energy production during the summer feeding period between March and December,
2. the energy expenditure in somatic growth, egg production and metabolic losses during the spawning period.

Summer production appears to be almost linearly related with the weight of the fish. The proportion of the summer production, which is spent in egg production increases with the weight of the fish. Winter metabolism was found to be related to the weight to the power of 0.74. The ratio of the energy expenditure in egg production and somatic growth increases with the age and the weight of the fish. Summer production and ratio of energy expenditure are proposed as the important parameters to use in a comparison of energy budgets. This is explored in a comparison of the energy budgets of the two historic periods.

Introduction.

For several marine fish species preyed upon by commercial fishermen, changes in the basic biological parameters as growth, fecundity and age of first maturity have been described (e.g. DE VEEN, 1976; OOSTHUIZEN & DAAN, 1974; BURD, 1962). The observed changes are not yet fully understood. Their importance in our understanding of the productivity of a fish stock, however, can not be underestimated.

For North Sea plaice the fecundity has been studied by REIBISCH (1899), FRANZ (1909 a+b), SIMPSON (1951) and recently by HORWOOD & BANNISTER (in preparation). Maturity data are given by e.g. WALLACE (1914). Growth data are published among others by WALLACE (1907), OSEA & DE VEEN (1972) and BANNISTER (1978).

In these studies on plaice, as on many other marine species, the basic biological parameters are studied in isolation. Possible interactions can therefore not be evaluated. Interactions between the basic biological parameters are likely to occur, because they are influenced by the total energy consumption and by the partitioning of energy between somatic growth and reproduction. A detailed description of the energy budget will serve as a conceptual framework from which questions about the causation of changes in biological parameters can be stated more explicitly. With this in mind we have embarked on a study of the energy budget of North Sea Plaice.

North Sea plaice seems a good candidate to study changes in these basic biological parameters into more detail. The stock has attracted the interest of both fishermen and fishery biologists for several generations. A summary of the changes in the stock in relation to the fishery is given by BANNISTER (1978). The annual yield increased from 50.000 tonnes before the second world war to a record of 154.000 tonnes in 1982 (ANONYMUS, 1983). Possible factors involved in this change are given by DE VEEN (1972), who described a change in the growth rate of plaice in the southern North Sea and the German Bight, and by BANNISTER (1978), who concluded that the average recruitment in the period 1922-1938 of 281 million was significantly lower than in the period 1945-1971 (377 million).

Plaice shows a seasonal pattern of feeding in summer and spawning in winter. From December till March, the time of spawning, it does not feed. (TODD, 1911). In this period it is dependent on the energy reserves build up during the summer feeding period for winter metabolism and growth of the gonads as shown by DAWSON & GRIMM (1980) for Irish Sea plaice.

This paper presents a preliminary analysis of the energy budget of female North Sea plaice, connecting growth and fecundity. The energy budget calculated for the present situation will be compared with the energy budget of two historic periods for which growth and fecundity data were available: the period around 1900 and the period 1947-1949. Changes in the growth rate and the fecundity between these periods will be discussed in the context of the changes in the energy budget.

Material and methods.

Fecundity estimates:

Ovary samples were obtained from the landings of commercial beam trawlers in the fish market. Fish as well as vessels were sampled at random within weight strata and area strata respectively. Sampling positions are shown in figure 1 and are summarized in table I. On board of commercial vessels the fish is stored on ice for not more than 1 week. For each fish the length, weight, age, sex and maturity stage were recorded. The usual technique of separating the oocytes from the connective tissue by using Gilson fluid was abandoned because of environmental reasons. In the present study the ovaries were stored in alcohol (50 - 70 %). The oocytes were separated from the connective tissue by washing them above a small meshed sieve under a gentle flow of water. This method was developed by P. VAN LEEUWEN of our laboratory and is a further development of the method described in VAN LEEUWEN (1971). Only ovaries of ripening females (maturity stage 2) were used. After taking the weight of the ovary a subsample of 1.50 to 3.00 gram was taken by cutting a section out of the middle region of the ovary. Oocytes were counted with a wet counting device. The difference between the actual number of oocytes and the estimated number was less than 1 %. Nine samples of 300 - 1200 oocytes counted by hand gave a mean difference of 0.36 % and a range of -1.8 % to + 4.1 % with the wet counting device.

In 1982 two subsamples of the same ovary (left or right) were taken. From a pilot test it appeared that the number of oocytes per unit ovary weight did not differ for the different positions within the ovary (Table II). The deviation from the estimated number of eggs had a geometric mean of 2.0 % and ranged from 0.08 % to 11.5 %. In 1983 the two subsamples were taken from the left and the right ovary separately. The deviation from the estimated number of eggs had a geometric mean of 1.9 % and ranged from 0.08 % - 21.3 %. Differences in the number of oocytes per unit weight between both ovaries were not correlated with the differences between the weights of both ovaries (linear regression: r = .013, n = 151).

Growth and maturity data.

The growth and maturity of female plaice was analysed using 1st quarter data from the market sampling programme. Mean length for the youngest age groups were obtained from the "Tridens" survey of demersal young fish along the continental nursery area from the Dutch coast to the Skagerrak in 1982 (Annales Biologiques, in press).

Condition factors were obtained from the market sampling data of gutted fish. Maturity staging is explained in table III. Maturity ogives were calculated using GM regression of logit transformed percentages mature females (P): logit P = 0.5 ln (P/1-P). The length at which 50 % of the females become mature was estimated from the regression.

Maesurements of energy contents.

In other studies the energy contents of the body have been estimated with bomb calorimetry of different parts of the body (e.g. McKINNON, 1972) or with chemical analysis (e.g. DAWSON & GRIMM, 1980). The approach adopted in this study is to measure the energy contents of the total body of individual fishes by bomb calorimetry.

Unsorted fish samples were obtained from commercial beam trawlers (table I). The samples have been stored on ice for not more than 1 week. At the laboratory, females of the maturity stages 1, 2 and 7 (juveniles, ripening and spent) and males of the stages 1, 3 and 6 (juveniles, prespawning and postspawning) were sorted. Length, total fresh weight and age were recorded and the fish were frozen individually at -20 °C. Only the results of the mature females will be presented in this paper.

After homogenising the individual fish, a subsample of 30 gram was oven dried at 70 °C to constant weight. The oven dry material again was grounded in a coffee grinder. A pellet of 0.15 - 0.20 gram was combusted in a PARR microbomb calorimeter. The calorific measurements of the same sample were all within 1 % of the mean, so only one measurement per fish was taken. In order to test the homogeneity of the minced fish 36 samples were oven dried and combusted separately. The mean difference was 2.06 % with a range of 0.0 - 4.6 %. All energy values are uncorrected for the endothermic combustion of bony material.

Energy values of ripe eggs.

The energy content per egg was calculated from the dry weight per egg and the energy value per unit dry weight. Eggs of ripe running females were obtained from market samples. The dry weight per egg was obtained from samples stored in 4 % formaldehyde in seawater. The eggs were washed and a sample of 500 eggs was counted by hand and oven dried at 70 °C to constant weight. From these eggs no proper pellet could be made for combustion. The energy value was therefore estimated from ripe eggs frozen at - 20 °C and subsequently freeze dried and combusted.

Results.

Growth:

The distribution of plaice is size dependent. The smaller fish dominate the coastal waters and move into deeper water as they grow. A growth curve based on market sampling data therefore seriously overestimates the mean length of the younger age groups. This is illustrated in figure 2 in which the mean length of female plaice in the market sampling data is compared with those of the "Tridens" survey of the continental nursery areas in 1982. Up to age group 4 the market sampling does not give a reliable estimate of the mean length of female plaice.

A BERTALANFFY growth curve is calculated for the combined data using the least square method of TOMLINSON & ABRAMSON (1961). The results are shown in table IV.

Historical growth data:

Because in a major part of the old literature the age of plaice was based on the presence of the start of a new growth zone in the otolith only the data of WALLACE (1907) could be used. The birth date of 1 April used by WALLACE has been converted to 1 January to be consistent with the convention presently in use.

Growth data of female North Sea plaice for the period 1947-1949 have not been published. However, from the basic data of the fecundity study of SIMPSON (1951) the mean length at age in the 1st quarter can be calculated.

Table IV gives the present and the historical mean length at age data. Compared with data given by WALLACE (1907) for the beginning of this century the younger age groups at the moment grow faster. At present the growth in length of age group 6 and 7 tend to level off, whereas in 1900 these age groups still continued their growth. Growth in the period 1947-1949 was slower than at present. The mean length of the youngest age groups in SIMPSON's data are strongly biased, because he selected only the mature females, which have a faster growth Therefore.

they should be compared with the market sampling data and not with the "Tridens" data.

Age of first maturity:

Maturity - length relations were studied in a part of the available material from the Dutch market sampling programme. Figure 3 summarises the results of the preliminary analysis of the data collected between 1979 and 1980 in the Southern Bight and in 1982 in the total North Sea. Maturity ogives were calculated using a geometric mean regression of the logit transformed data. Results of the calculations are given in table V.

In 1979 - 1980 50 % of the female plaice in the Southern Bight became mature at a length of 30.8 cm. In 1982 this length has shifted to 33.8 cm. In the total North Sea half of the females reached maturity in 1982 at a length of 34.1 cm, which does not differ from the 50 % maturity length in the Southern Bight in that year.

The maturity - age relationship for 1982 shows that more than 60 % of the 4 year old females are already mature (figure 4). From the comparison of the mean length per age group in the market sampling data and the "Tridens" survey, we have seen that up to age 4 the recruitment to the fishery is size dependent. This implicates that the maturity - age relation will also be biased and that less than 60 % of the 4 year old females will be mature. From the mean length at age (table IV) it can be deduced that the 50 % maturity age will approximately be 4 year.

Historical maturity data:

The criterium of distinction between juvenile and mature plaice presently in use is similar to the criterium used in the study of WALLACE (1914). Figure 3 compares the maturity-length relation between both periods. When we take into account the change in the relation between 1979 - 1980 and 1982, no major change can be observed between 1900 and present. The maturity - age relation, however, differs because of the difference in growth rate. The maturity - age relation presented by WALLACE (1914) shows that nearly 50 % of the 5 year old females had become mature (figure 4). However, the method of ageing used in this study differed from the method presently in use and used by WALLACE (1907) in an earlier paper. This means that the age of the females could be partly underestimated. However, from the mean length at age (table IV) and the length - maturity relation (figure 3) the age of 50 % maturity can be estimated at 5 year. At present 50 % mature at age 4.

Fecundity:

The fecundity - size relationship was determined for four models (table VII). A linear relationship between fecundity and weight gives the best correlation. Geometric mean regression (RICKER, 1974) was used to describe the functional relation between the fecundity and the weight. Figure 7 shows the GM regression and the data points for 1982 and 1983. In both years the intercept of the regression line with the x axis differs from the origin. For the highest weights there is no indication that the fecundity is underestimated by the linear GM regression. So the curve - linear relationship as suggested by the log F - log W regression (table VII) is probably caused by the positive intercept of the x axis.

A comparison of both years shows that the fecundity in 1983 was significantly lower than in 1982 (table VIII). A F-test of the slopes yields a F = 7.563 with d.f. = 1.253 ($P < 0.01$). Also the elevations differ significantly (F = 5.941, d.f. = 1;254, $P < 0.05$).

In order to test whether geographical differences occur in fecundity within the North Sea as concluded by BAGENAL (1966), three areas were compared. Table VIII shows the relationship between the fecundity and the weight for the different areas for two years. In both years no significant difference between the areas could be shown for the slopes (1982: F = 2.96, d.f. = 2;96; 1983: F = 0.079, d.f. = 2;149) as well as for the elevations (1982: F = 1.68, d.f. = 2;98; 1983: F = 0.245, d.f. = 2;151).

Individual variation in fecundity is large (figure 7). The influence of age and condition of the individual fish on the fecundity was analysed with a stepwise multiple regression analysis. Because plaice grows isometrically the cube of the length was chosen as index of size. Table 9 gives the results of the analysis. It is shown that in 1982 only size (L^3.) and condition contribute significantly to the variance in the fecundity. In 1983 also the age of the fish explains a significant, although small part of the variation in the fecundity.

Historical fecundity data:

Fecundity studies of North Sea plaice have been published by REIBISCH (1899) and FRANZ (1909a & b) for the beginning of this century and by SIMPSON (1951) for the period 1947-1949. The basic data presented by these authors have been reanalysed. The results are presented in figure 8 and table X. The relation between the fecundity and the cube of the length has been used to compare the three periods because no weight data were published by FRANZ (1909 a& b). A comparison of the relation between fecundity and size shows that the fecundity at present is at the highest level. In the period 1947-1949 fecundity was at its lowest level. Both GM regression lines have a similar intercept. In comparison the 1900 regression line intersects the x-axis at a higher length. The slope is not significantly different from that of the present 1982-1983 line.

Seasonal change in the weight - length relationship:

Weight - length relationships are usually expressed in the condition factor: $CF = W/L^3$ assuming isometric growth. To check this assumption the log weight - log length relation is calculated for three maturity stages in the market sampling data of the 1st quarter of 1982.

The slopes of the GM regression for all three maturity stages do not differ significantly from 3 (table VI). It can therefore be concluded that the condition factor is a proper measure of the weight - length relationship. With a F-test no significant difference between the slopes of the regression for ripening females and the spent females could be found (F = 0.686, d.f. = 1;536, SNEDECOR, 1947). The elevations of the regression lines, however, differed significantly (F = 727.59, d.f. = 1;537) and show that the condition of the fish strongly decreases during spawning.

A more detailed picture of this seasonal change in the weight - length relationship is shown in figure 5 for ripening and spent female plaice in the Southern Bight in 1982. The condition factor is at its lowest level in March and April after spawning (spent females). From April onwards the condition factor increases steadily towards a maximum in October and November. During winter the conditon factor slightly decreases from 1080×10^{-5} in October and November to 1017×10^{-5} in February.

During summer reproductive tissue is produced at a low rate. Not earlier then in October the gonad starts to increase significantly in weight from 4 % of the body weight in October to 13 % in December. The peak gonad weight is recorded in January and February with 16 % of the body weight.

In figure 6 the mean condition factor for ripening and spent females is shown for different ages. It appears that up to an age of about 10 - 12 the condition does not change. For females older than 10 - 12 years a slight decrease in the condition factor seems to occur. The number of these older females sampled is very limited so no firm conclusion can be drawn. For the moment we accept that the age of the female does not influence its condition up to an age of 12 years.

Energy budget:

The measurement of the calorific contents of female plaice are summarised in table 11 and are plotted in figure 9. The energy measurements of ripe eggs are given in table XII. The line drawn in figure 9 connects the average energy values for each month. After spawning both the condition factor and the energy contents per unit body weight are at the lowest level. During spawning energy reserves are depleted while the water content as percentage of the body weight increases. This decline in energy reserves during the spawning season can also be observed for the ripening females, for which the condition factor as well as the energy value per unit of fresh body weight decreases (figure 5 and 9).

The energy loss during the spawning season can be calculated by subtracting from the total energy contents at the beginning of the spawning season in December, the energy contents at the end of the spawning season in March. The condition factor (gutted weight) of ripening females in December is estimated at 1075×10^{-5} (figure 5) and decreases to 865×10^{-5} in March (spent females). Energy values per unit fresh weight decreases from 5.81 kjoules in December to 4.10 kjoules in March (table XI).

Consequently a 5 year old female plaice with a length of 34.9 cm and a weight of 487 gram, will have an energy contents of $487 \times 5.81 = 2832$ kjoules. In March after the spawning season her weight has fallen to 391 gram and her energy contents to 1602 kjoules, a 43 % decrease.

In the above calculation only constants were used. The percentual decrease in energy contents over the spawning season therefore will also be a constant. In table XIII the energy loss during the spawning season is partitioned in the energy loss for egg production and the energy loss for winter metabolism for ages 4 to 12. The total net production laid down in the summer feeding season is estimated from the difference between the total energy contents after spawning in March and at the start of the fasting period in December. The energy allocated to somatic growth is calculated from the difference between the total energy contents in March between two successive years. The energy invested in egg production was estimated from the number of eggs produced ($F = -35.6 + 0.2815\ W$, table VIII) and the energy value of ripe eggs (6.136 kjoules per 1000 eggs, table XII). In the fecundity estimation the average 1st quarter weight has been used, because most of the fecundity samples were taken in the first quarter.

The total loss of energy during spawning can only be partly explained by the energy loss due to egg production. The difference between the two is an estimate of the energy needed for metabolism during the spawning season.

Figure 10 summarises the energy partitioning for the different age groups. The age range has been restricted to 4 - 12 years because the assumption of a constant condition factor might not hold outside this range as shown in figure 6. From figure 10 it can be seen that the proportion of the egg production of the total energy loss during spawning is not constant but increases as the fish gets older and becomes bigger. The energy for egg production and that for winter metabolism are complementary. Consequently the proportion of winter metabolism changes in relation with weight and age. Metabolic rates (MR) are known to be a function of body weight (W): $MR = a.W^b$ in which the exponent $b = 0.70 - 0.80$ (e.g. WINBERG, 1956; JONES, 1976). Calculation of the regression of the log-log transformed winter metabolism against body weight in December shows a similar relation to the weight: log winter metabolism = 0.503 + 0.74 log weight.

Discussion.

The energy value per unit dry weight found in this study were for both the ripening and the spent females about 9 % lower than those found for Irish Sea plaice by chemical analysis (DAWSON & GRIMM, 1980). Calorific values obtained by bomb calorimetry are usually slightly lower than those obtained by chemical analysis (BRADFIELD & LLEWELYN, 1982). BEUKEMA & DE BRUIN, 1979, estimated the difference between both methods at 6 % for Macoma flesh.

The seasonal pattern in energy reserves as observed for North Sea plaice is similar, to the pattern of Irish Sea plaice (DAWSON & GRIMM, 1980). These authors calculated the energy budget for a 7 year old female (35.8 cm and 527 gram). The gross energy content decreased from 3506 kjoules in December to 1862 kjoules in March, a decrease of 53 %. The proportion of this decrease allocated in egg production was 60 %. For North Sea plaice we have found that the female body looses 43 % of its energy from December till March (table XIII), of which between 37 and 56 % is allocated in egg production. A female of the same weight as the Irish Sea example (527 gram) will loose approximately 46 % in the production of eggs. The estimated total energy losses during the spawning season are rather similar taking into account the different methods and the rather crude assumption made.

In an attempt to make a quantitative comparison of the changes in growth rate and fecundity, we have calculated the energy budget for both historic periods to compare with the energy budget of the present period.

Two types of hypotheses have been formulated to explain changes in the basic biological parameters: 1. Increase in the ~~l~~availability of food, due to a reduced competition for food when the stock size is reduced by fishing, or to an increased level of nutrients. 2. Selection of faster growing genotypes due to the relatively increased fishing mortality of the slower growing individuals.

Therefore, two aspects are of particular importance if we compare the energy budgets: 1. the level of summer production, and 2. the partitioning of energy over somatic growth and reproduction.

The energy budgets for both periods are given in table XIV and can be compared with the energy budget of the present period in table XIII. Only those age groups are included for which at least 50 % had become mature. The length at age data were estimated from the least square fitted BERTALANFFY growth curve (TOMLINSON & ABRAMSON, 1961) for the observed mean length at age data of WALLACE (1907) and SIMPSON (1951) presented in table IV. The fecundity data used are given in table X. The total summer production is plotted in figure 11 against the weight of the female at the start of the feeding season in March. Summer production seems linearly related with fish weight. The relation for 1982-1983 appears to be slightly curvi-linear with a decreasing slope for increasing weights. The functional relation between summer production and weight will have an intercept with the y-axis of approximately the energy contents of a female plaice at the end of her first growing season. This appears not to be the case. Assuming a winter length of 10 cm, a condition factor of 1100 $.10^{-5}$ and an energy value of 5 kjoules per gram fresh weight (unpublished data RIVO) the total energy contents at the end of the first growing period is estimated at 54 kjoules. The intercept with the y-axis, as observed in figure 11, is approximately 335 kjoules in the period 1947-1949 and 1050 kjoules in 1982-1983. This implicates that the summer production relative to the weight of the fish decreases as the fish grows. The lines of 1982-1983 and 1947-1949 run almost parallel but differ in level. The slope for 1900 seems to be somewhat higher than for 1947-1949 and 1982-1983.

It is expected that the summer production will be a function of - among others - the availability of food and the temperature. No important difference could be observed in the sea temperatures near Den Helder (VAN DEN HOEVEN, unpublished). Temperatures in 1982-1983 and in 1947-1949 being slightly above average, those around 1900 slightly below average. We therefore tentatively conclude that food availability might be one of the major factors involved in the change in the level of summer production. However, the increase in the summer production is not correlated with the change in stock biomass. BANNISTER (1978) estimated the total stock biomass in the period 1947-1949 at 350 thousand tonnes. For 1982 the total stock biomass was estimated at 650 thousand tonnes (ANONYMUS, 1983).

The way in which an increase in summer production affects the growth and the fecundity, depends on the partitioning of the available energy over both parameters. The second aspect of our comparison concerns this partitioning. It is generally accepted that life history patterns have become adapted to the particular environmental conditions of a species. So the trade-off between the energy expenditure in reproduction and in somatic growth will be adapted to maximise the life time reproductive success of the individual plaice (e.g. MANN & MILLS, 1979). This could imply that the ratio of the energy input in reproduction and somatic growth will have a fixed value for each age. In figure 12 this ratio is plotted against age. The ratio ~~increases~~ increase geometrically with age. Comparing the periods, we see that the ratio increased for each age group going from 1900 to 1947-1949 and to 1982-1983. So, plaice has invested an increasing proportion of the available energy in reproduction at a progressively younger age.

If age determines the energy partitioning, the positive influence of age on fecundity as shown in 1983 (table IX) and reported frequently for other fish species (WOOTTON, 1979), can be explained. Summer production is weight dependent (figure 11) and is partitioned in reproduction and growth as determined by age. Because this ratio increases with the age of the fish, the fecundity of a fish of an older age will be higher than that of a younger fish of the same weight. This younger fish, however, will show a higher somatic growth.

One may wonder whether the energy partitioning of between egg production and somatic growth is causally affected by age. In figure 12 the energy ratio is plotted against the weight of the fish at the start of the spawning season. It appears that there is hardly any difference in the ratio for fish of a similar weight. The question which we are left with is: if weight or age determines the partitioning?

The description of the energy budget can of course not give an answer to the above mentioned question. Nevertheless it has pinpointed down a significant question to be tackled in future research. In this context a description of the energy budget on a monthly base is also important. A preliminary analysis of the seasonal growth pattern (DE CLERCK, 1982; unpublished RIVO data) suggests that the energy for somatic growth and reproduction are not stored at the same time. Somatic growth mainly takes place in summer, whereas the energy reserves for egg production are mainly build up in autumn. The number of eggs to be shed in the next spawning period is already present early in the season (BARR, 1963; YAMAMOTO, 1956). During the summer and autumn a low percentage of oocystes which are in a stage of atresia (resorption) can be observed (BARR, 1963; DUNN & TYLER, 1969), suggesting that the fish could have a mechanism to tune the number of developing oocystes to the actual feeding conditions. In a tank experiment low food availability inhibited the vitellogenesis in American plaice (TYLER & DUNN, 1976), and thus the energy expenditure in reproduction. So good feeding conditions in autumn might lead to a high condition factor and a low level of atresia and thus to a high fecundity. This could explain the influence of the condition factor on the fecundity as observed in 1982 and in 1983 (table IX).

The comparison of the energy budgets of the two historic periods leans heavily on the assumptions made about the constancy of condition factors and energy values, on the accuracy of the growth and fecundity data and on the feature whether plaice feeds or not in the spawning season. Energy values of biological materials are rather constant. The proportion of fat being the main variable.

The similarity of the condition factor could be tested for the females sampled for the fecundity study by SIMPSON (1951) and REIBISCH (1899). The average condition factor and its standard deviation were not significantly different between the historic periods and the present value (1048x 10^{-5}). SIMPSON 1947-1949; ripening females: 1032 ± 106 (x 10^{-5}) n = 197. REIBISCH (1899): ripening females 1083 ± 134x 10^{-5} ; n = 12, and spent females: 780 + 59 x 10^{-5} , n = 14. So the condition of ripening females seems not to be different. The condition factor of the spent females of REIBISCH (1899) is lower than the present value (865 x 10^{-5}, suggests that the decline in condition around 1900 might have been larger than at present. However, the number of observations is very small. This implies that the summer production could be underestimated. The energy partitioning will not be seriously influenced. DE VEEN (1978) showed that for North Sea sole the condition factors changed in course of the time due to an increased gonad weight.

The feature that plaice does not feed during the spawning period is widely cited but has only a small emperical base (TODD, 1911). The low winter temperature makes it unlikely that plaice will have a significant rate of food intake. From our samples for energy measurement only in the last week of March some of the fish had remainings of food in their intestines.

The values for the summer production and the energy partitioning calculated for the two historic periods should be taken as a crude estimate. The differences found with the present situation are, however, so large that we believe the differences to reflect real changes in these parameters.

References.

Anonymus, 1983 - Report of the North Sea Flatfish Working Group. ICES C.M. 1983/Assessm.: 11.

Bagenal, T.B., 1966 - The ecological and geographical aspects of the fecundity of the plaice. J. Mar. Biol. Ass., 46: 161-186.

Bannister, R.C.A., 1978 - Changes in plaice stocks and plaice fisheries in the North Sea. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 86-101.

Barr, W.A., 1963 - The endocrine control of the sexual cycle in the plaice.*(Pleuronectes platessa L.)*. I. Cyclial changes in the normal ovary. Gen. Comp. Endocrinol., 3: 197-204.

Beukema, J.J. & W. de Bruin, 1979 - Calorific values of the soft parts of the rellinid bivalve *Macoma baltica L.*, as determined by two methods. J. Exp. Mar. Biol. Ecol., 37: 19-30.

Brafield, A.E. & M.J. Llewellyn, 1982 - Animal Energetics. Blackie, Glasgow.

Burd, A.C., 1962 - Growth and recruitment in the herring of the southern North Sea. Fish. Invest., Lond., 28: 1-42.

Clerck, R. de & K. Reyssens, 1982 - The seasonal growth in weight of plaice in the southern North Sea. ICES C.M. 1982/G: 57.

Dunn, R.S. & A.V. Tyler, 1969 - Aspects of the anatomy of the winter flounder ovary with hypotheses on oocyte maturation time. J. Fish Res. Board Ca., 26: 1943-1947.

Franz, V., 1909a - Die Eiproduction der Scholle *(Pleuronectes platessa L.)*. Wiss. Meeresunters., Helgoland, N.F. 9: 58-141.

Franz, V., 1909b - Zur Eiproduction der Scholle *(Pleuronectes platessa L.)*. Wiss. Meeresunters., Helgoland, N.F. 9: 217-224.

Jones, R., 1976 - Growth of fishes. In: Cushing and Walsh. The ecology of the sea: 251-279.

Leeuwen, P.I. van, 1971 - A new method for treating plaice *(Pleuronectes platessa L.)* gonads in order to facilitate the estimation of the egg production. Aquaculture.

MacKinnon, J.C., 1972 - Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice.

(Hippoglossoides plassoides). J. Fish Res. Bd. Canada, 29: 1749-1759.

Mann, R.H.K. & C.A. Mills, 1979 - Demographic aspects of fish fecundity. In: Miller P.J. (edit.) Fish Phenology. Symp. Sool. Sec. Lond., 44: 161-177.

Oosthuizen, E. & N. Daan, 1974 - Egg fecundity and maturity of North Sea cod, *Gadus morhua*. Neth. J. Sea Res., 8: 378-397.

Osae, R.O.A. & J.F. de Veen, 1972 - Changes in growth of two plaice sub-populations in the North Sea. ICES C.M./F: 9: 1-9 (mimeo).

Reibisch, J., 1899 - Veber die Eizahl bei *Pleuronectes platessa* und die Alter bestimmung dieser Form aus den Otolithen. Wiss. Meeresunters., Kiel, 4: 231-248.

Ricker, W.E., 1973 - Linear regressions in fishery research. J. Fish. Res. Board Can., 30: 409-434.

Simpson, A.C., 1951 - The fecundity of plaice. Fish. Invest., Ser. 2, 17 (5).

Snedecor, G.W., 1946 - Statistical Methods. Iowa State College Press.

Todd, R.A., 191. - Report on the food of palice. Fish Invest. Ser. II, Vol. II, No. 3.

Tomlinson, P.K. & N.J. Abramson, 1961 - Fitting a Von Bertalanffy growth curve by least squares. Fish. Bull. Calif., 116: 1-69.

Tyler, A.V. & R.S. Dunn, 1976 - Ration, growth, and mesures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americans*, with hypothesis regarding population homeostasis. J. Fish. Res. Board, Can., 33: 63-75.

Veen, J.F. de, 1978 - Changes in North Sea sole stocks *(Solea solea L.)*. Rapp. P.v.Réun. Cons. int. Explor. Mer, 172: 124-136.

Wallace, W., 1907 - Report on the Age and Growth Rate of Plaice in the southern North Sea. Intern. Invest., Mar. Biol. Assoc., Report II, Part I (Cd 3837).

Wallace, W., 1964 - Report on the Age, Growth and Sexual maturity of the plaice in certain parts of the North Sea. Fish. Invest. Ser. II, Vol. II.

Winberg, G.G., 1956 - Rate of metabolism and food requirement of Fishes. Fish. Res. Bd. Can., Trans. Series, 194: 1-202.

Wootton, R.J., 1979 - Energy costs of egg production and environmental determinants of fecundity in teleost fish. In: Miller, P.J. (edit.) Fish Phenology. Symp. Zool. Soc. London, 44: 139-159.

Yamamoto, K., 1956 - Studies on the formation of fish eggs. I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fish. Sci. Hokkaido Univ. (Ser. 6), 12: 362-373.

Figure 1 - Sampling positions for fecundity in 1982 and 1983, and energy contents of the body and eggs in 1983.

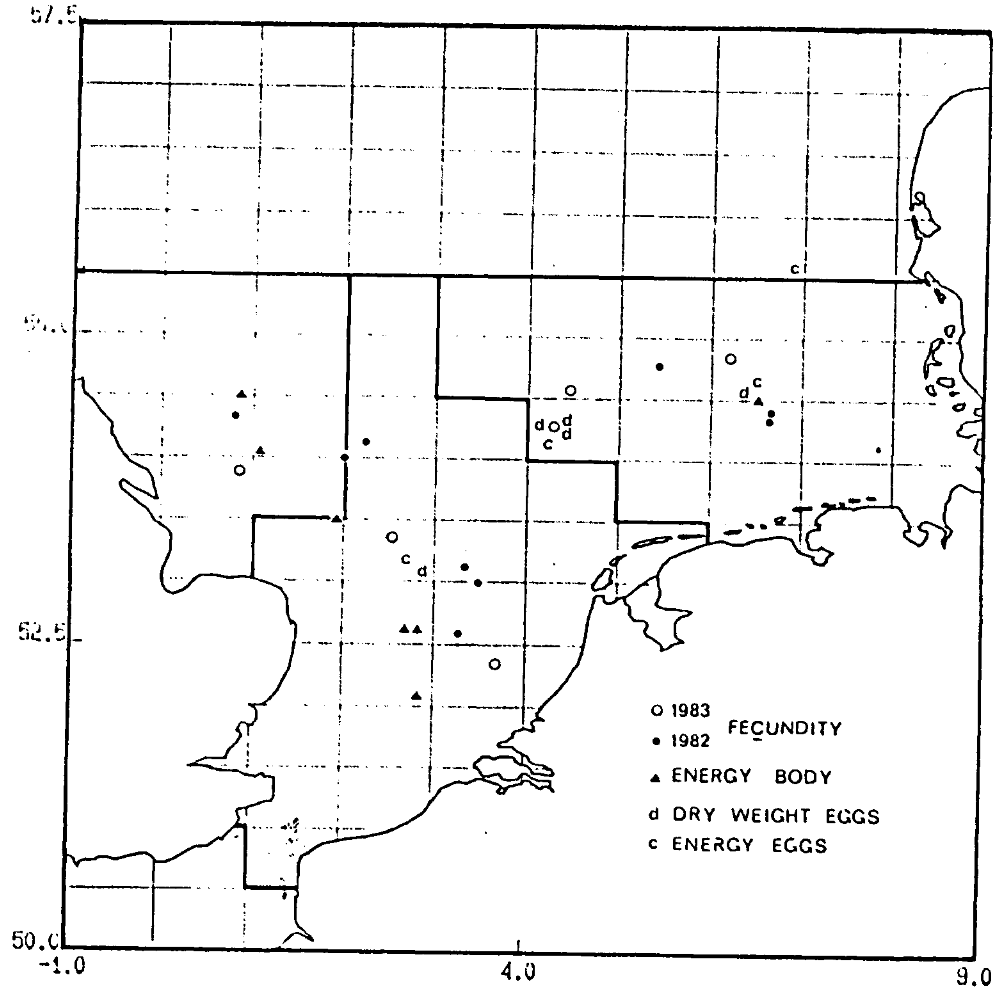

Figure 2 - Growth in length of female plaice in three periods: 1980-1982, 1947-1949 (SIMPSON, 1951) and around 1900 (WALLACE, 1907).

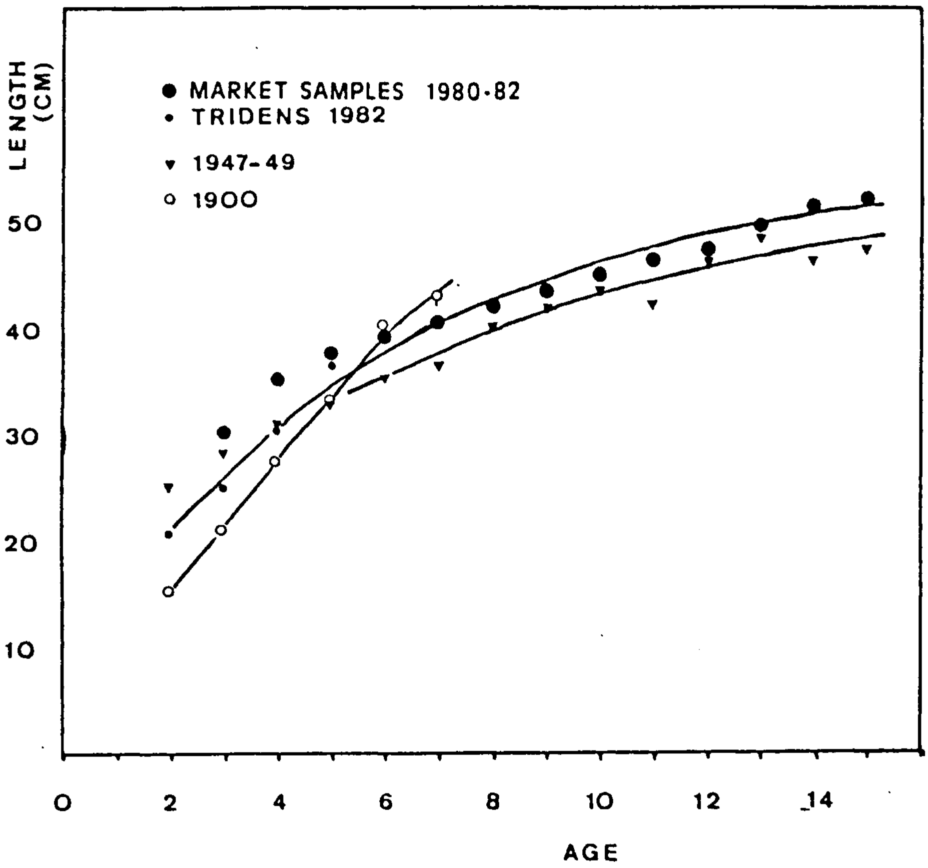

Figure 3 - Maturity - length relations:
a. Southern Bight in 1982, 1979-1980 and 1911 (WALLACE, 1914),
b. North Sea (IV b+c) in 1982.

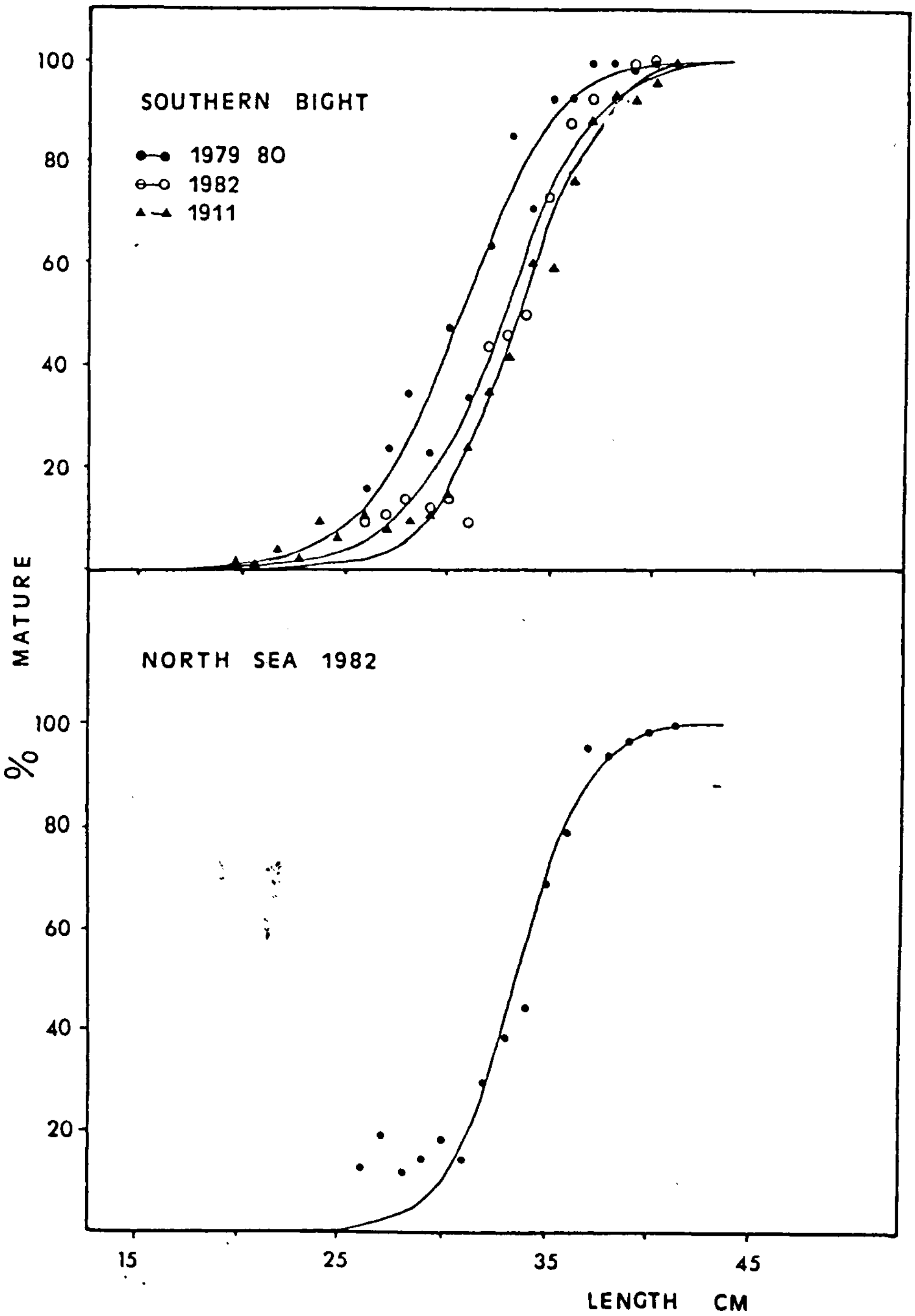

Figure 4 - Maturity - age relations:
a. Southern Bight 1982 and 1911 (WALLACE, 1914),
b. North Sea (IV b+c) in 1982.
The ageing of WALLACE differed slightly from the present study. See text.

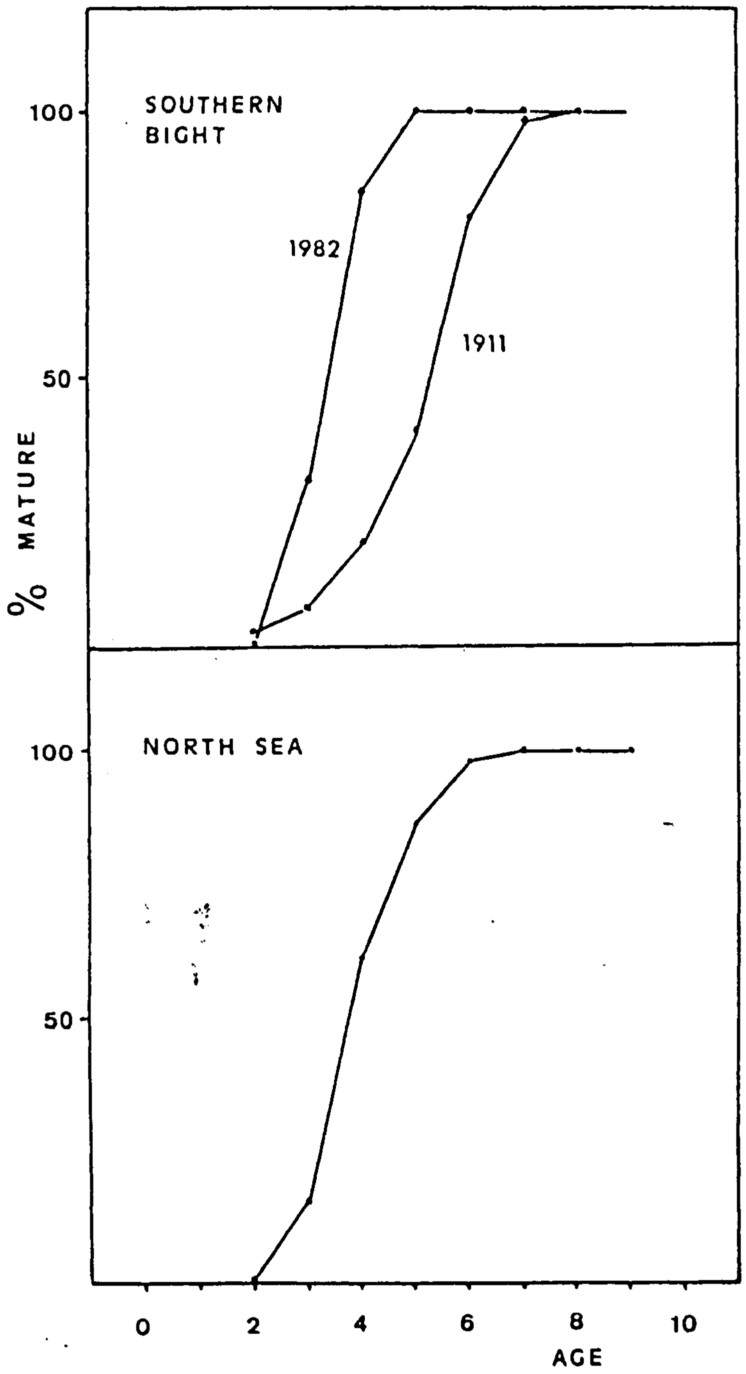

Figure 5 - Seasonal pattern of (a) gonad weight as a percentage of the gutted body weight, (b) condition factor (☆ 10^{-5}) of ripening and spent females in the southern North Sea. Data points based on > 10 observations per month.

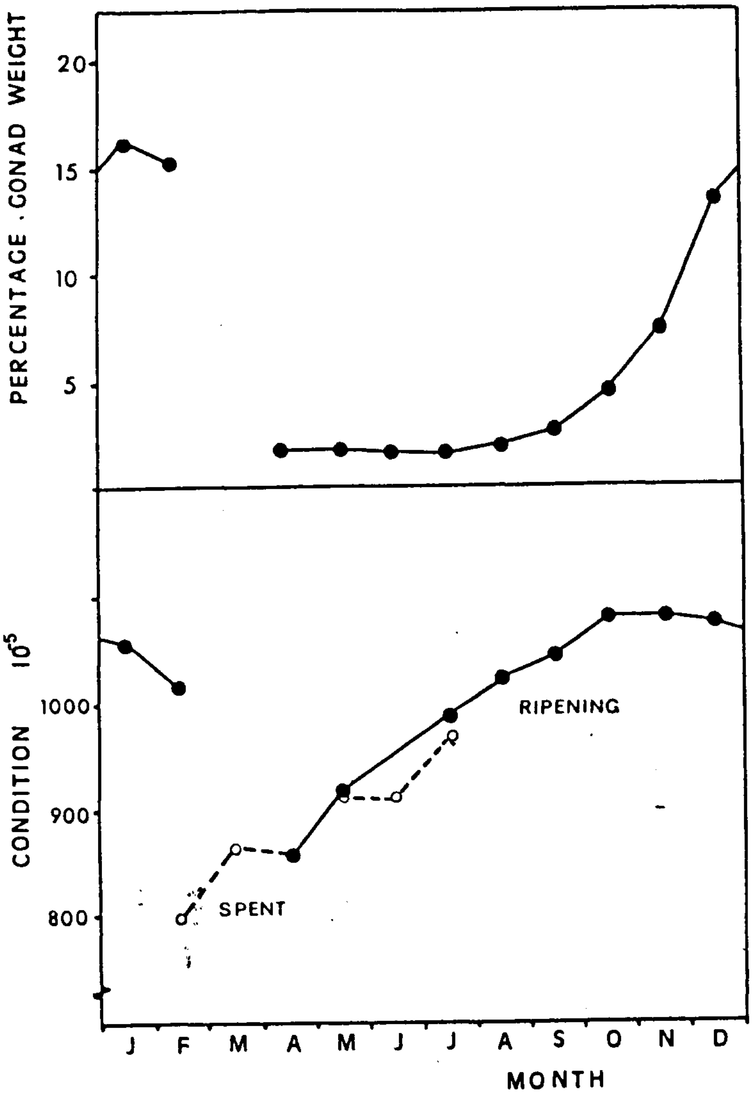

Figure 6 - Relation between the condition factor (☆ 10^{-5}) and the age of ripening (upper line) and spent (bottom line) females in the first quarter of 1982.
Figures indicate the number of observations for each age group.

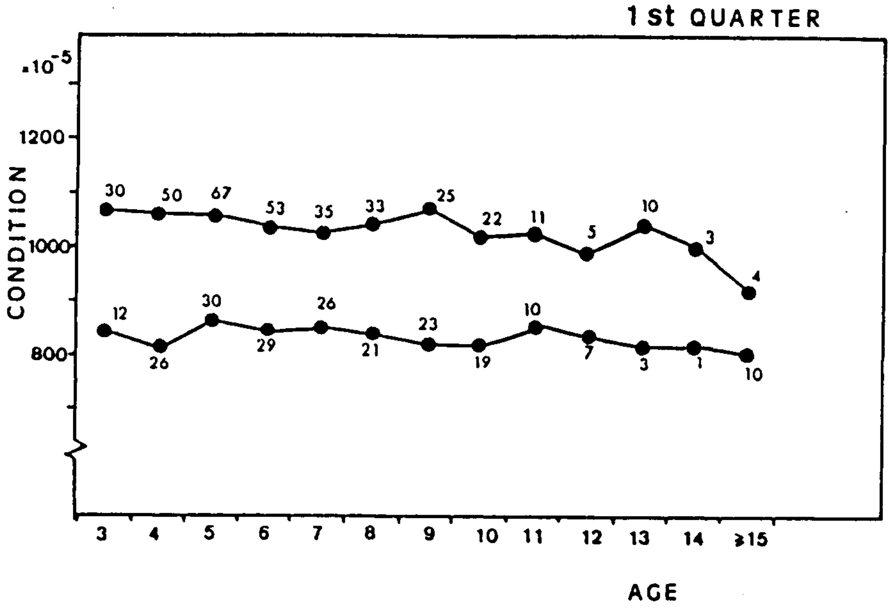

Figure 7 - Relation between the fecundity and the gutted weight in 1982 and 1983.
GM regression lines are drawn for both years.

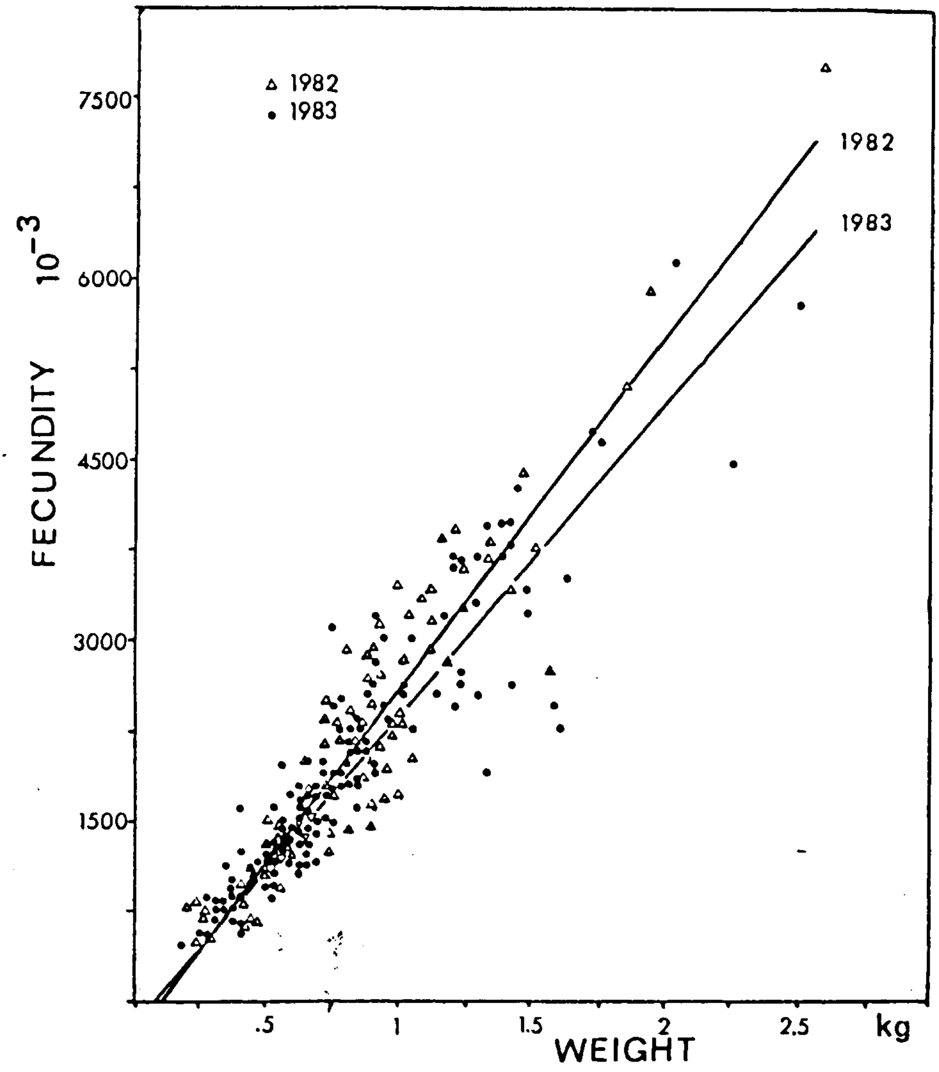

Figure 8 - GM regression lines of the fecundity against the cube of the length for three periods: 1982 - 1983, 1947 - 1949 (SIMPSON, 1951) and around 1900 (REIBISCH, 1899; FRANZ, 1909 a+b).

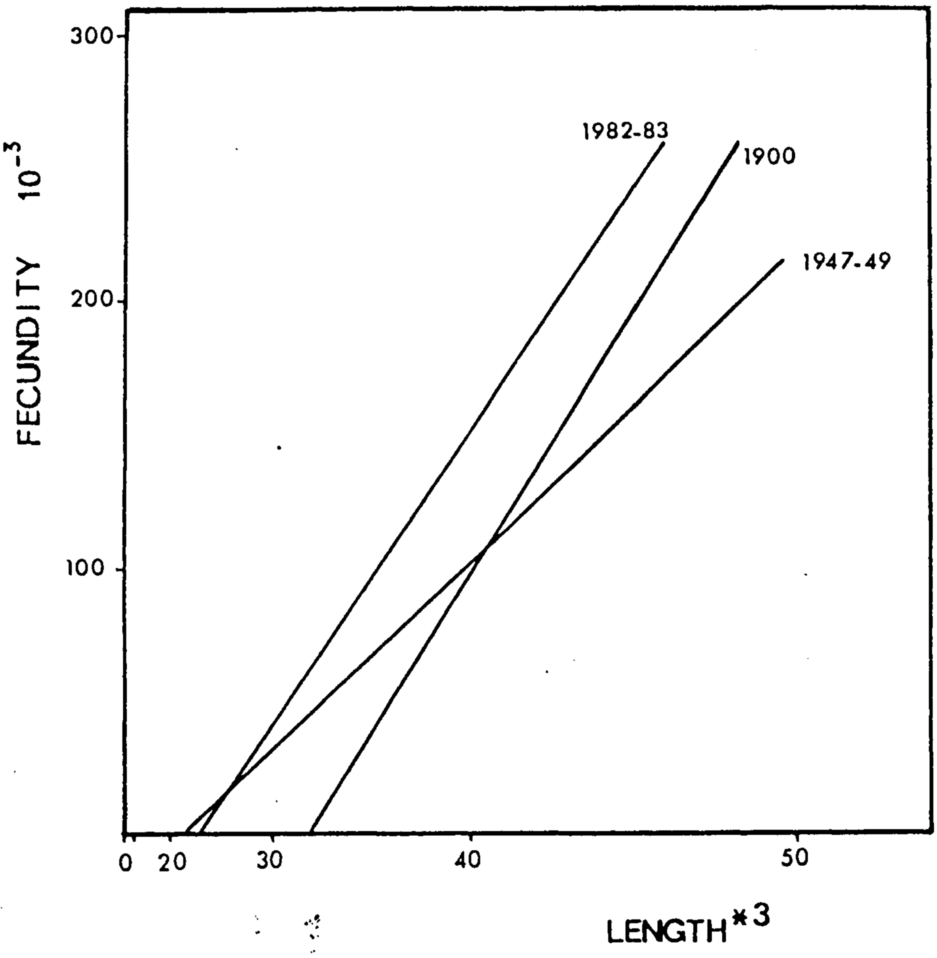

Figure 9 - Calorific contents of ripening and spent females in relation with time. The figures indicate the number of individuals samples. Crosses indicate the mean values for mixed samples. Bars show the standard deviations.

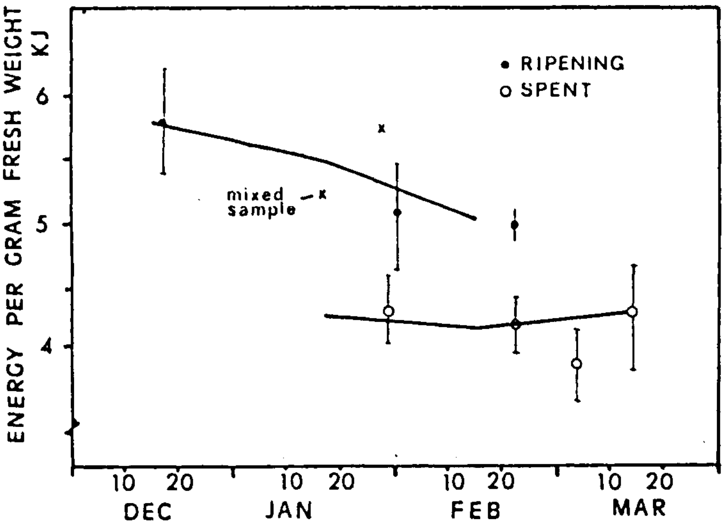

Figure 10 - Energy budget for mature female North Sea plaice. The total summer production is partitioned in somatic growth, egg production and winter metabolism.

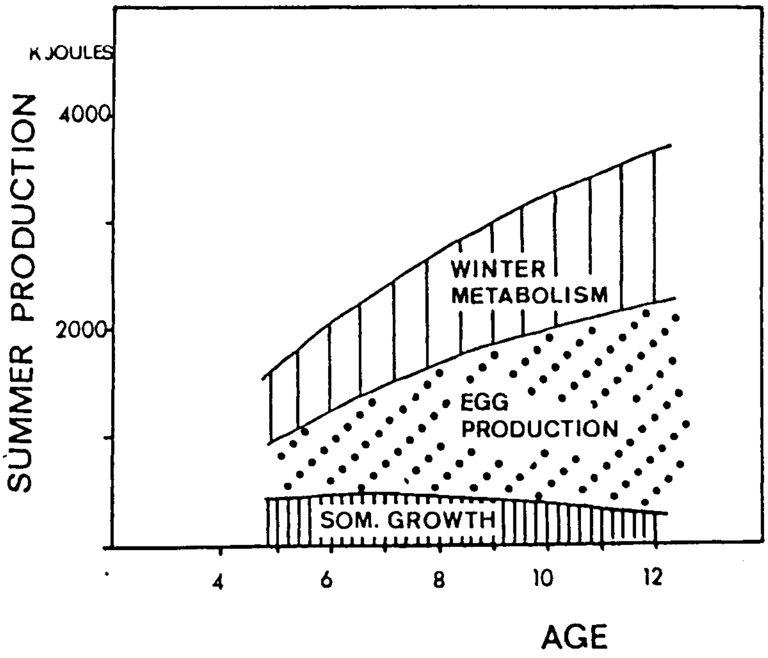

Figure 11 - Relation between summer production and weight of the fish at the beginning of the feeding period in 1980 - 1982, in comparison with 1947 - 1949 and 1900.

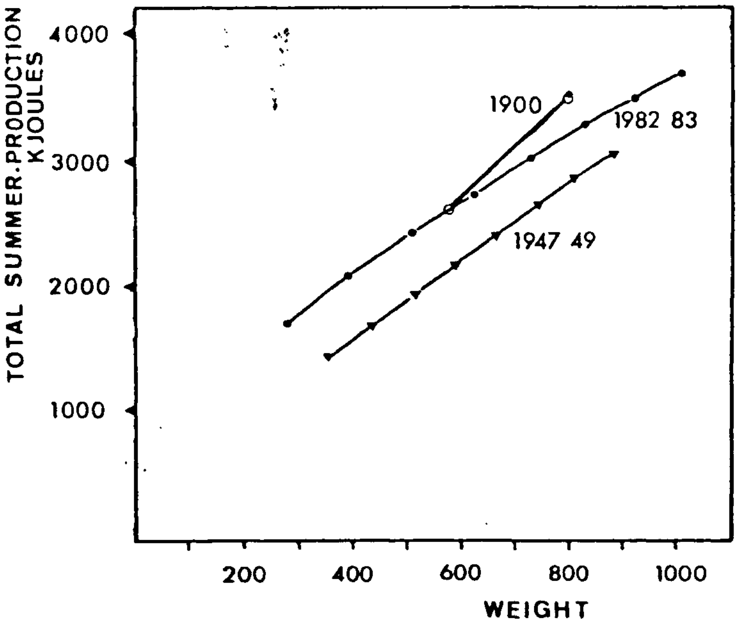

Figure 12 - Ratio of the energy partitioned in egg production and somatic growth in relation with age (A) and weight (B) of the fish for three periods.

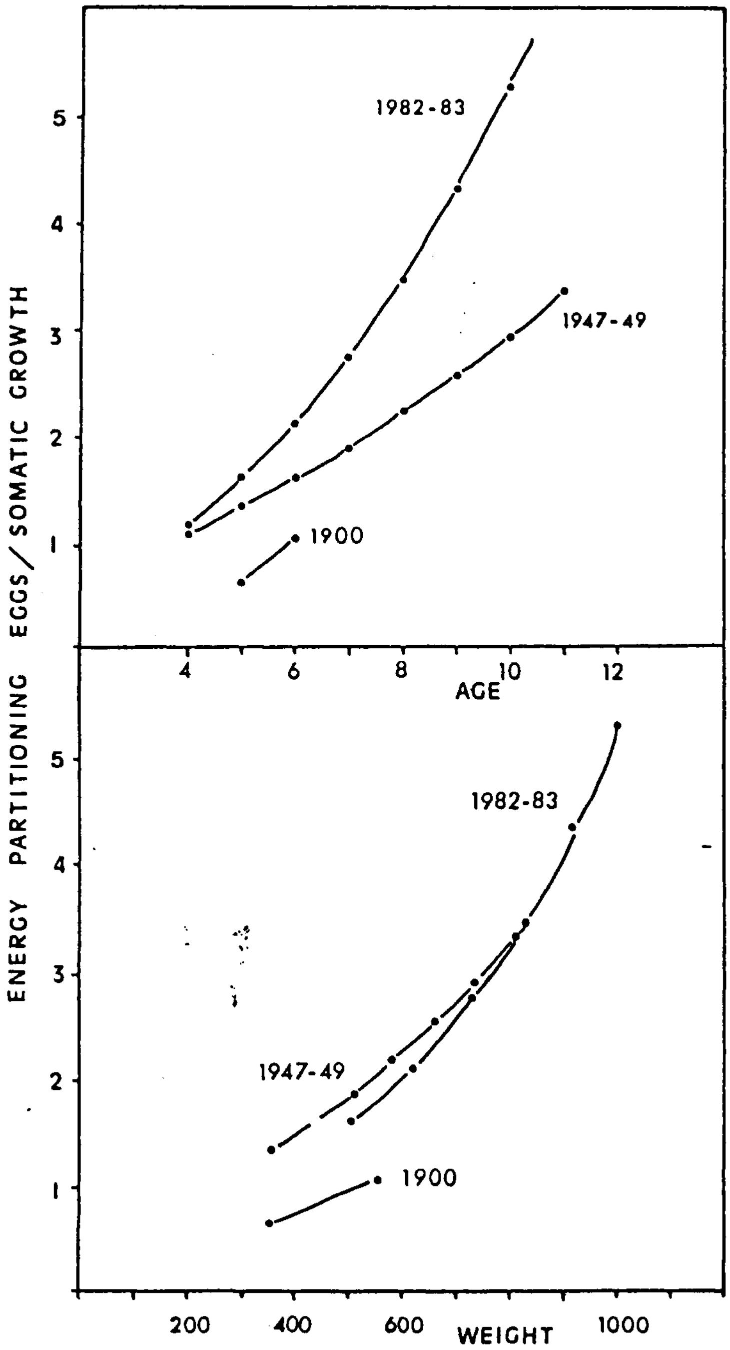

Table I - Summary of the sampling for fecundity estimates (A), and calorific measurements (B)

A: FECUNDITY ESTIMATES	SEASON 1982		SEASON 1983		
DATE	POSITION	NUMBER OF FEMALES	DATE	POSITION	NUMBER OF FEMALES
21.12.81	5300N 330E	14	13.12.82	5320N 230E	33
07.01.82	5235N 250E	17	13.12.82	5415N 415E	20
11.01.82	5420N 640E	8	10.01.83	5355N 050E	39
11.01.82	5400N 200E	11	14.01.83	5450N 610E	20
18.01.82	5403N 215E	13	14.01.83	5430N 420E	25
25.01.82	5310N 320E	10	24.01.83	5245N 345E	18
01.02.82	5440N 530E	12			
08.02.82	5420N 050E	11			
22.02.82	5420N 640E	6			

B: CALORIFIC MEASUREMENTS TOTAL BODY:		NUMBER OF FEMALES			NUMBER OF MALES		
DATA	POSITION	stage 2	stage 7	stage 1	stage 3-4	stage 6	stage 1
17.12.82	5235N 250E	-	-	-	(1*)	-	-
17.12.82	5210N 250E	11	-	6	3	-	-
17.01.83	5430N 055E	(2*)	-	-	3*	-	-
28.01.83	5240N 250E	(2*)	4	-	4 (4*)	-	(1*)
31.01.83	5430N 630E	17	-	4 (3*)	(1*)	-	
21.02.83	5330N 200E	2	9	(3*)	-	(3*)	
04.03.83	5240N 250E	-	10	(4*)	-	(6*)	
14.03.83	5400N 100E	-	10	(1*)	-	(2*)	

(n*) number of measurements of mixed samples

Table II - Relative number of oocytes per unit ovary weight (x) for different positions in the ovary and its standard deviation (SD) and number of observations (n)
1, caudal, 2, middle, 3, anterior

	Positions		
	1	2	3
x	0,984	1,007	1,006
SD	0,057	0,034	0,045
n	8	8	11

Table III - Maturity staging of female plaice in the Dutch research

code	stage	description
1	juvenile	lumen transparent, grey colour
2	ripening	orange coloured oocytes visible
3		as 2, with a few ripe transparent eggs
4	ripe	ovary completely filled with ripe transparent eggs
5	spawning	ripe eggs partly shed
6	nearly spent	ovary contains only a small amount of ripe eggs
7	spent	back to stage 2

Table IV - 1st quarter mean length at age of female plaice in the Southern North Sea at present and in the past.

	Present		Past	
Age	Tridens 1982	Market sampling 1980-82	Simpson (1951)	Wallace (1907)
2	20.8		25.7	15.7
3	25.3	30.8	28.9	21.3
4	31.6	35.7	31.1	27.4
5	36.9	37.9	33.4	33.8
6		39.6	35.6	40.7
7		40.9	36.9	43.4
8		42.1	40.7	
9		43.4	42.8	
10		45.3	43.8	
11		46.9	42.5	
12		47.1	47.0	
13		49.9	49.2	
14		51.8	46.6	
15		52.5	47.7	

Bertalanffy growth curves:	Linf	k	t0
1980-82)1	54.45	.1769	-0.777
1947-49	57.01	.1029	-3.745
1900	121.05	.0642	-0.097

)1 data from Tridens up to age 5, and from market sampling for age >=6

Table V – Regression coefficients of logit transformed proportions mature females (P) against length (L)
model: logit P = a + b (L-0.5)

Data	Source	a	b	r	L 50%
North Sea 1982	this study	-10.73	.320	.982	34.1
Southern Bight 1982	this study	-10.09	.303	.964	33.8
Southern Bight 1979-80	this study	-7.20	.237	.957	30.8
Southern Bight 1911	Wallace(1914)	-8.84	.266	.989	33.7

Table VI – Regression coefficients of the log - log transformed weight (W) length (L) relationship for different maturity stages in the 1st quarter market sampling data of 1982
model: log W = a + b log L

Maturity stage	a	b	95% c.l.	r	n
juvenile	-4.62	2.987	2.907-3.067	.96	375
ripening	-4.80	3.063	2.989-3.137	.98	322
spent	-4.74	2.991	2.919-3.063	.98	218

Table VII – Correlation and regression coefficients of fecundity (Fec) in relation with the weight (W) and length (L)

Relation	a	b	r	N	p
Fec = a + bW	-16.60	0.2579	0.917	257	<0.001
Log Fec = a + blogL	-6.690	3.174	0.861	257	<0.001
Fec = a + bL**3	-1.745	0.00252	0.844	257	<0.001
Log Fec = a + b log W	-2.101	1.094	0.918	257	<0.001

Table VIII - Correlation and regression coefficients of the relation between fecundity (Fec) and the weight (W) for three different areas in the North Sea in the spawning periods of 1982 and 1983.

SPAWNING SEASON

	1982					1983				
Area	a	b	95%cl	r	N	a	b	95%cl	r	N
Southern Bight	-18.15	.2829	.2544-.3114	.964	31	-7.82	.2437	.2215-.2659	.948	51
German Bight	28.05	.2103	.1514-.2692	.745	26	-9.07	.2415	.2111-.2719	.866	65
Flamborough	-51.43	.3004	.2682-.3326	.937	45	-6.08	.2339	.1950-.2728	.866	39
total North Sea	-27.74	.2814	.2603-.3025	.926	102	-9.52	.2425	.2269-.2581	.915	155

1982 + 1983

	a	b	r	n	
Total North Sea	-16.60	.2579	.916	257	predictive regression (AM)
	-35.61	.2815			functional regression (GM)

Table IX-Results of the stepwise multiple regression analysis of the influence of size (L**3), condition factor (CF) and age (A) on the fecundity (Fec) in 1982 and in 1983
model: Fec = a + b1 L**3 + b2 CF + b3 A

CORRELATION MATRIX

	1982				1983			
	L**3	CF	Age	Fec.	L**3	CF	Age	Fec
L**3	1	.12843	.84161	.86540	1	-.04362	.87416	.85280
CF	.12843	1	.01877	.46285	-.04362	1	-.0241	.30049
Age	.84161	.01877	1	.68339	.87416	-.0241	1	.79073
Fec	.86540.	.46285	.68339	1	.85280	.30049	.79073	1

	Regression coefficients:	Standard errors:	t value	Regression coefficients:	Standard errors:	t value
a	-446.064			-368.11		
b1	.002882	.000126	22.87	.001917	.000175	10.95
b2	399.032	40.0301	9.97	353.476	33.38	10.59
b3	not accepted as significant variable			5.7888	2.198	2.63

Table X – Geometric mean regression coefficients of the fecundity (Fec) against the cube of the length (L**3) in three periods.
model: Fec = u + v L**3

Source	u	v	95% c.l.	r	n
Reibisch (1899) Franz (1909 a + b)	-107.4	.00322	.00290-.00353	.861	109
Simpson (1951)	-20.6	.00191	.00178-.00204	.870	197
this study	-37.7	.00298	.00279-.00318	.844	257

Table XI – Calorific measurements of the total body of female plaice of two maturity stages.

DATE	% DRY WEIGHT			ENERGY/GRAM DRY			ENERGY/GRAM FRESH		
	x	SD	n	x	SD	n	x	SD	n
ripening females (stage 2)									
17-12-82	25.8	1.4	11	22.5	1.1	11	5.81	.42	11
17-01-83	24.1	2.1	11	21.8	0.3	2*	5.27	.04	2*
28-01-83	26.2	3.1	8	22.0	0.4	2*	5.77	.10	2*
31-01-83	23.7	1.3	17	21.3	1.1	17	5.06	.46	17
21-02-83	22.6	0.9	2	22.0	0.4	2	4.98	.08	2
spent females (stage 7)									
28-01-83	22.8	1.0	5	18.8	0.9	4	4.31	.29	4
21-02-83	21.5	1.1	9	19.5	0.8	9	4.18	.25	9
04-03-83	20.8	1.2	10	18.8	1.4	10	3.89	.29	10
14-03-83	22.0	2.0	10	19.6	0.9	10	4.31	.42	10

n * mixed samples.

Table XII – Energy and dry weight measurements of ripe plaice eggs in 1983

	Individual samples			Mixed samples		
	x	SD	n	x	SD	n
Energy value per gram dry weight	24.42	.39	9	24.59	.28	3
Dry weight per 1000 eggs	.250	.023	9	—		

Table XIII - Energy budget of mature females North Sea plaice in 1982-1983

AGE	LENGTH cm	WEIGHT DEC gram	WEIGHT MARCH gram	FECUNDITY *10E-3	SUMMER PRODUCTION	SOMATIC GROWTH	EGG PROD.	WINTER METABOLISM
4	31.06	344	277	52.8			322	544
5	34.85	487	391	89.3	1694	469	548	682
6	38.03	632	509	126.7	2071	485	778	812
7	40.69	775	624	163.2	2418	473	1000	950
8	42.92	909	732	197.7	2728	443	1213	1071
9	44.79	1034	831	229.5	3012	406	1410	1196
10	46.35	1145	921	258.2	3250	368	1585	1297
11	47.66	1245	1002	283.8	3464	330	1740	1393
12	48.77	1334	1073	306.6	3648	293	1882	1477

Table XIV - Estimated energy budgets for two historic periods, assuming similar condition factors and energy values to 1982 and 1983

PLAICE NORTH SEA 1947-1949

AGE	LENGTH cm	WEIGHT DEC gram	WEIGHT MARCH gram	FECUNDITY *10E-3	SUMMER PRODUCTION	SOMATIC GROWTH	EGG PROD.	WINTER METABOLISM
4	31.31	353	284	41.4			254	634
5	33.82	445	358	55.4	1423	303	340	780
6	36.09	541	435	69.9	1675	315	429	931
7	38.13	638	513	84.7	1925	320	520	1085
8	39.98	735	591	99.5	2170	320	610	1239
9	41.64	831	668	114.0	2406	316	699	1391
10	43.15	924	743	128.2	2632	307	786	1538
11	44.50	1013	815	141.9	2847	296	871	1680
12	45.72	1100	885	154.9	3050	284	950	1816
PLAICE NORTH SEA 1900								
5	33.77	443	356	16.5			101	1014
6	39.20	693	558	86.4	2568	825	530	1214
7	44.28	999	804	172.0	3522	1009__	1055	1457