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**ON THE MECHANISM OF ENERGY ALLOCATION OVER REPRODUCTION AND SOMATIC
GROWTH WITH PARTICULAR REFERENCE TO FEMALE PLAICE**

by

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ON THE MECHANISM OF ENERGY ALLOCATION OVER REPRODUCTION AND
SOMATIC GROWTH WITH PARTICULAR REFERENCE TO FEMALE PLAICE:
A HYPOTHESIS.

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Abstract

The allocation of energy over reproduction and somatic growth was studied on an annual and seasonal basis in female North Sea plaice using samples from commercial landings. On an annual basis the relative amount of energy allocated into eggproduction was not related with that allocated into somatic growth. Fecundity is only indirectly affected by the amount of surplus energy because of the significant correlation with somatic condition and the increased fecundity due to somatic growth. From this it was concluded that the amount of surplus energy did not affect the pattern of allocation of energy over reproduction and somatic growth.

In the seasonal cycle four periods can be distinguished:

- 1) a spawning period from January till March during which a mature 5-year old female loses about 40% of the total energy content.
- 2) a growing period from March till May in which surplus energy is used for the restoration of the depleted body reserves;
- 3) a growing period from May till November in which surplus energy (100%) is used for both somatic growth (23%) and the building up of energy reserves (77%);
- 4) a growing period from November till January in which the surplus energy is mainly used for maturation of the gonad.

From these results a hypothetical model about the mechanism of energy allocation is inferred that is based in physiology and can be tested against field observations and tankexperiments. The model assumes that the surplus energy is used to maintain the body condition at a threshold level that increases during the growing period. Surplus energy exceeding the demands for maintaining body condition at the threshold level is channeled into somatic growth. Implications of the mechanism when studying changes in growth and fecundity are being discussed.

Introduction

The changes in biological parameters as growth, fecundity and age or length at first maturity as observed in several commercially important fish species can be explained by a response to the heavy exploitation. By increasing the growth rate, the number of eggs produced per unit body weight or by shortening the generation time through early maturation, the fish are thought to counteract increased mortality and reduced life span. The causal factors behind these changes however are still unresolved. To tackle this problem Rijnsdorp et al. (1983) suggested to study the interplay of the three parameters within the reproductive strategy. This concept stems from evolutionary ecology and assumes a trade-off between the energy invested in reproduction and in somatic growth in such a way that the individual fitness is maximized (Calow 1981, Ware 1982). The reproductive strategy of a species is thought to be a life history character that was moulded during evolution and adapted to the environmental conditions. The question arises whether intensive exploitation act as a selection force that can change the genetical basis of the reproductive strategy towards an increased reproductive effort at a younger age. Alternative hypotheses explain the observed changes in the biological parameters with increased availability of food due to strongly reduced fishstocks or increased productivity of the ecosystem (May 1984). Before we can discriminate between these alternative hypotheses it is essential to know the mechanism that determines the allocation of energy over reproduction and somatic growth. Once the mechanism is known the response to changes in the environmental conditions for growth can be predicted and compared with the observed changes in the reproductive strategy.

In this paper a hypothesis about the mechanism of energy allocation in female plaice will be derived from a study of the seasonal and the annual pattern of energy allocation. Special attention is given to the question how the conditions for growth - determining the amount of surplus energy available for reproduction and somatic growth - affect the pattern of allocation.

In the North Sea the annual cycle of plaice consists of a growing season from March untill December and a spawning season from December untill March. In the spawning season the mature plaice do not feed and have to rely on energy stores present in the body for their 'winter metabolism' and reproduction. After spawning plaice again start feeding (Rijnsdorp et al. 1983, unpublished RIVO data).

The mechanism of energy allocation proposed in this paper is complementary to the model of Roff (1983). Roff's aim was to develop a simple model that could be used to analyse the fitness of an allocation pattern. The model assumed a fixed amount of surplus energy available and an allocation into reproduction determined by the gonadosomatic index and length or age at first

maturity. The present paper aims to develop a simple model of the mechanism behind the allocation of surplus energy, that is based in physiology and can be tested against field observations and experiments.

Material and methods

Definitions and symbols used

The following definitions and symbols will be used:

X^{**2} = square of X,
 X^{**3} = cube of X,
 L_t = length of the fish at time t,
 W_t = gutted weight of the fish at time t,
 E_t = energy content of the fish at time t,
 GW = gonad weight of ripening fish,
 CF_{tot} = gutted condition factor calculated as
 $CF_{tot} = 100 (W_t/L_t^{**3})$,
 CF_{som} = somatic condition factor calculated as
 $CF_{som} = ((W_t-GW)/L_t^{**3})$,
 GSI = gonadosomatic index calculated as $GSI = W_t/L_t^{**3}$,
 E_{ft} = energy factor of the fish at time t calculated as
 $E_{ft} = E_t/L_t^{**3}$,
 E_{fpre} = energy factor of mature females prior to spawning,
 E_{fpost} = energy factor of mature spent females after spawning,
 E_{fgon} = energy per gram fresh weight of gonad,
 SG = somatic growth calculated as the volume increase from year t-1 to year t according $SG = (L_t)^{**3} - (L_{t-1})^{**3}$,
 E_{som} = energy allocated into somatic growth calculated as
 $E_{som} = SG \cdot E_{fspent}$,
 E_{rep} = energy allocated into reproduction calculated as
 $E_{rep} = GSI \cdot W_t \cdot E_{fgon}$.

Energy allocation between reproduction and somatic growth

The problem of how individual female plaice allocate their energy over reproduction and somatic growth has been approached by estimating both the fecundity and the somatic growth during the last year.

From 1982 to 1985 samples have been taken from ripening female plaice landed by Dutch fishermen from the southern North Sea during the spawning season between December and March. For each fish fecundity is estimated as described in Rijnsdorp et al. (1983). In addition length, weight, gonad weight, age and maturity stage were determined. From a total of 487 females, a random sample of 258 fish was taken from the 1982, 1983 and 1984 data. For these 258 females the somatic growth was estimated by backcalculating the length in the previous spawning period. For this purpose the symmetrical otolith was cut through the nucleus along the short axis and burned above a gas flame to brighten the

pattern of annual rings. Under a microscope with a drawing mirror, the pattern of the dark annual rings was drawn on paper and measured with a ruler (magnification 15). The length in the last year (L_{t-1}) was estimated according:

$$L_{t-1} = \frac{OL_{t-1}}{OL_t} * L_t$$

where OL_t is the otolith length at time (t) of sampling and OL_{t-1} is the diameter of the last annulus.

The details of the backcalculation technique of plaice otoliths will be given elsewhere.

Seasonal pattern of allocation

To get a preliminary estimate of the seasonal pattern of allocation the average quarterly growth of 5 year old female plaice was analysed from the Dutch market sampling data. The 5 year olds were selected because these fish are distributed over the fishing grounds of the Dutch fleet throughout the year, so that any bias in the mean quarterly length will be negligible. The data used in the calculation of the seasonal allocation are given in Table 1. Spent fish were chosen as starting point in the calculations because this stage represents the start of the growing period.

For each individual female the surplus production (SP) was calculated from the somatic growth and the total condition at the end of the growing season according to:

$$SP = (CF_2 - CF_1) \cdot L_{t-1}^{*3} + CF_2 \cdot SG$$

with

CF_2 = condition factor including the gonads at the end of the growing season,

CF_1 = condition factor including the gonads at the beginning of the growing season,

The parameters CF_2 , L^{*3} and SG are estimated for each individual, CF_1 is only known from the population average (0.820).

In the two terms of the equation we can recognize the energy needed to rebuild the condition of the body after the spawning season and the energy allocated to somatic growth.

Statistical methods

Analyses of Variance (ANOVA) were carried out with the NAG statistical package GLIM (Baker and Nelder 1978). The model used was a partly factorial nonorthogonal analysis of variance model -

$Y = aF1 + bX1 + cX2 + e$ - in which Y is the dependent variable (fecundity, somatic growth ect); F1 a factor such as year; X1, X2 covariables as length and somatic condition; a, b, c are constants and e is a normally distributed error term. With the parameter estimates from the ANOVA the dependent variable was standardized by calculating the residuals of the observed values and the fitted values.

Results

Annual pattern of allocation

Before studying the relation between the energy channeled annually into reproduction and somatic growth the factors affecting the fecundity and somatic growth separately were analysed. When these factors are known the standardized fecundity and somatic growth can be compared.

An ANOVA was carried out on the fish sampled for fecundity and backcalculated length. Present fish size explained most of the variance in fecundity although somatic condition, year and age made a significant but minor contribution. The somatic growth was not correlated with fecundity (Table 2). Somatic growth was also not correlated with the somatic condition factor at the end of the growing season (Table 3).

A plot of somatic growth of female plaice, as obtained by backcalculation of the individual growth curves, against the length at the beginning of the growing period shows that individual somatic growth is rather variable (Fig 1). Somatic growth increases up to a size of about 20 cm and decreases at larger fishsizes. The coefficient of variation of the somatic growth estimates is about 50% for each of the 2 cm length groups in the range of 20 to 50 cm. In order to compare the somatic growth with the fecundity of the same individual fish, only the estimates from the last year can be used after standardization for the effect of length and age of the fish. Somatic growth was correlated with age and with size of the fish at the beginning of the growing period (Table 4). To normalize the error term somatic growth was logtransformed. Because only mature individual females were included in the analysis of variance and it is known that the growth rate affects the age and length at first maturity, within the young age groups (3 and 4) mainly fast growing females will be present. Because of this bias, the results of the ANOVA should not been given a further biological interpretation.

The total amount of energy available for somatic growth and eggproduction (surplus production) was correlated with fish-length, age and year (Table 5). Because the surplus production depends on both total condition and somatic growth a statistical comparison between surplus production and standardized fecundity or somatic growth will lead to spurious

correlations and therefore has no meaning. So only standardized fecundity can be compared with standardized somatic growth. In figure 2 it is shown that these do not show a correlation, so above average somatic growth does not result in above or below average fecundity.

Seasonal pattern of allocation

The energy loss of a 5 year old female plaice during the spawning period amounts to 80% of the energy produced during the previous growing period and is about 40% of the total energy content of the body (Fig 3). The production of surplus energy during the growing season mainly takes place from the 1st to the 2nd and from the 2nd to the 3rd quarter with respectively 27% and 44% of the total annual energy production. In the first month of the growing season the fish uses the energy primarily to restore the depleted body reserves. Growth in length is insignificant at 3% of the quarterly surplus. Hereafter the proportion of surplus energy used for growth in length is on average 23% (range 21% - 25%). Only in the last months prior to spawning energy is primarily channeled into gonad maturation.

Gonad development starts in September-October (Fig 4). The gonadal growth in the following months exceeds the total growth. Apparently energy already stored in the body is reallocated from the body to the gonad. From the 3rd to the 4th quarter gonad growth exceeds the total growth minus somatic growth by 15% and from the 4th to the 1st quarter even 55% of the gonad growth is supported by the energy reserves in the body.

During the growing season the condition factor of female plaice continuously increases towards a maximum in November (Fig 4). In December and January the condition of the ripening fish slightly decreases. After spawning the condition factor is severely reduced.

Discussion

In the seasonal cycle of energy allocation of mature female plaice the following 4 periods can be distinguished:

- 1) a spawning period from December to March in which the fish loses the energy stored in the gonad (eggproduction) and energy reserves (winter metabolism),
- 2) a period of restoration of the depleted body condition after the spawning season from March till May,
- 3) a period of growth from May till November in which both somatic growth and energy storage for reproduction occurs,
- 4) a short period from November till November prior to the spawning period in which growth continues and energy reserves are reallocated from carcass to gonad.

In the period between March and June the difference between the condition factors of spent fish and ripening fish (Fig-4) is

partly due to the recruitment of juvenile females to the adult population, but may also result from differences in the exact timing of the seasonal cycle in different subpopulations. The reallocation of energy from carcass to gonads was also observed in winter flounder (MacKinnon 1972) and Irish Sea plaice (Dawson and Grimm 1982).

The amount of surplus energy is determined by both the somatic growth and the pre-spawning condition of the fish. The variability in somatic growth is much greater than in pre-spawning body condition (coefficients of variations about 50% and 10% respectively). We therefore can conclude that the amount of surplus energy is mainly related with somatic growth. The amount of surplus energy therefore mainly affects somatic growth. Fecundity is only indirectly affected by the amount of surplus energy because of the significant correlation with somatic condition (Table 2) and the increased fecundity due to somatic growth.

These results can be summarized in the following hypothetical model. The surplus energy is assumed to be allocated over energy reserves and somatic growth in such a way that at the end of the growing period an optimal body condition will be reached. This optimum body condition reflects the sum of three different components: the minimum energy content of the body required to survive after spawning, an adequate energy reserve for winter metabolism and an optimum amount of energy for reproduction (eggproduction). To achieve this target condition at the end of the growing season, the average fish follows the pattern observed in the condition factor (Fig 3). These population averages are supposed to indicate the threshold condition in each month. When the condition factor happens to fall below the threshold the surplus energy will be channeled into body reserves; when the condition factor exceeds the threshold the fish will use the surplus energy for somatic growth until the condition again falls below the threshold (Fig 5).

The effect of the amount of surplus energy on the annual pattern of allocation resulting from the above mechanism is illustrated in figure 6. When surplus energy is insufficient to achieve the optimal condition at the end of the growing season ($SP < b$ in Fig 6), reproductive output will be reduced to prevent post spawning condition to drop too low. In case the surplus production decreases below some minimum level ($SP < a$) the fish may not reproduce at all.

With increasing fish size the part of the surplus energy allocated into reproduction increases (see Fig 10 in Rijnsdorp et al. 1983). Therefore, variability in the energy surplus of individual females will be more likely to result in variability in fecundity or gonad weights at larger fish sizes. In small and medium sized fish fecundity and gonad weight is buffered against variations in surplus energy through reduced or increased somatic growth.

So far we have assumed that the conditions for growth for an individual fish are constant throughout the growing period. In the real world this is unlikely to be true. Bad conditions early in the growing period might temporarily result in a below average condition and no somatic growth. When later in the year the conditions improve the fish will first have to raise its condition to the seasonal threshold value before surplus energy can be used for somatic growth. At the end of the growing season the fish will then have the optimal body condition and the expected fecundity, but a relatively low somatic growth. In the reversed situation where bad conditions for growth occur at the end of the growing season things will be different. In this situation the fish will not be able to maintain its condition at the threshold level. The pre-spawning condition will be lower than normal and so are the energy reserves for winter metabolism and egg production. The fish will not be able to produce the expected amount of eggs although the growth in length has been normal or even above normal. The small but significant influence of somatic condition on fecundity (Table 2) might indicate that bad conditions at the end of the growing period can lower the reproductive output.

The assumption of the present model that body condition gets priority in the allocation of surplus energy over reproduction and growth is supported by the observation that the pre-spawning condition in different years only shows small variations whereas the length increment is much more variable. Also the constancy of the pre-spawning condition in respect to the length or age of the fish and the strong dependence of somatic growth of fish-length indicates that a fish firstly regulates its body condition and only in secondly the somatic growth.

The present analysis depends heavily on backcalculated lengths. If this technique involves a high variance on the estimated length, any relation between somatic growth and some other parameter could be masked. At present the variances involved are not well known. However, three considerations indicate that the present findings will not be confounded by inaccuracies in backcalculation. Firstly, the estimate of somatic growth could be expected to become less accurate for older fish due to decreases in the absolute length increment. A repetition of the present analysis on a subset of observations including only fish of age 3, 4 and 5 ($n=129$) gave essentially the same results. Secondly, recent work on the backcalculation technique in several flatfish species shows that in brill both symmetrical and assymetrical otoliths give comparable estimates of the individual growth curve (Lucio 1986). Also the mean backcalculated length at age 1 and 2 correspond closely to mean lengths as observed in young fish surveys (Lucio 1986, van Leeuwen and Rijnsdorp 1986). Thirdly, a comparison of the length of five male plaice tagged in the spawning season (length between 22 and 33 cm) and recaptured in the next spawning season showed that the estimated somatic growth was on average 1.03 times the observed increase ($SD = 0.24$; range between -0.18 and + 0.43).

In North Sea plaice long term changes in surplus production and fecundity have been observed (Rijnsdorp et al. 1983). The observed increase in fecundity is reflected in the increase in gonadosomatic index from about 0.10 in 1947-1949 (Simpson 1951) to 0.15 in 1982-1983 (Fig 4b), although artificial effects of differences in methods can not be ruled out and should be critically evaluated.

According to the mechanism proposed in this paper an increase in the surplus energy can not be fully responsible for any increasing trend in fecundity or gonadosomatic index and might indicate that genetical changes have occurred, increasing the energy allocated into reproduction. The observed increase in fecundity in North Sea plaice after the second world war and the decline in mean length at age of the older fish during the same period (Bannister 1978), is in line with the increase in allocation of energy into reproduction. If the mechanism of energy allocation is also applicable in North Sea sole, the observed increase in the gonadosomatic index (de Veen 1976) tentatively suggests that genetical changes have also occurred in this species.

The concept of an optimum body conditions stems from the assumption of an optimum allocation of energy over reproduction and growth (reproductive strategy). The post-spawning condition is assumed to be a resultant of the trade-off between reproductive effort and mortality. An increased of the reproductive effort will result in a lower post spawning condition and a higher mortality rate (Roff 1982, 1983, Wootton 1985). The pre-spawning condition is thought to be related with the physical upper limit of reproduction set by the available space in the body to store the gonads (Jones 1974, Roff 1982). However the increase in gonadosomatic index as observed in North Sea sole (de Veen 1976) shows that at least in the past the physical upper limit did not restraint the reproductive effort in this species. A discussion of the fitness aspects of the mechanism of energy allocation is beyond the scope of this paper.

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Table 1. Input data for the calculation of the seasonal energy allocation of a 5 year old female plaice.

[illegible]

Table 2. Results of the ANOVA of plaice FECUNDITY for the model
 $F = a + bL^{**3} + cA + d1Y1 + d2Y2 + d3Y3 + eSC + fSG$
 with L^{**3} = cube of the length at spawning, A = Age,
 Y = Year; SC = Somatic condition (guttled) and
 SG = somatic growth (volume increase).

Parameter estimates

parameter	variable	Parameter estimates	SE
a		- 176.6	27.90
b	L^{**3}	0.319	0.017
c	A	- 4.407	2.280
d1	year 1982	0.0	
d2	year 1983	- 13.07	6.693
d3	year 1984	- 17.76	6.301
e	SC	0.1932	0.026
f	SG	- 0.0227	0.049

Analysis of variance

	df	SS (/100)	MS (/100)	F	
L^{**3}	1	5458	5458	368.37	**
Y	2	118	59	3.98	*
A	1	55	55	3.71	ns
SC	1	808	808	54.53	**
SG	1	3	3	0.20	ns
error	251	3719			
Total	257	21310			

** $P < 0.01$

* $P < 0.05$

ns not significant

Table 3. Results of the ANOVA of the SOMATIC CONDITION of female plaice for the model:

$$SC = a + b_1Y_1 + b_2Y_2 + b_3Y_3 + cA + dL + eSG$$

with Y = year, A = age, L = length in the previous spawning season, SG = somatic growth growing season and A*L = interaction of A and L.

Parameter estimates

parameter	variable	Parameter estimates	SE
a		981.3	84.57
b1	year 1982	0.0	
b2	year 1983	- 69.76	15.53
b3	year 1984	- 53.49	14.82
c	A	- 32.68	19.58
d	L	1.079	2.029
e	SG	0.0080	0.1061

Analysis of variance

	df	SS (/1000)	MS (/1000)	F	
Y	2	183	91.5	10.63	**
A	1	72	72	8.37	**
L	1	23	23	2.67	n.s.
SG	1	1	1	0.12	n.s.
error	252	2169	8.607		
A*L	1	8	8	0.93	n.s.
error	251	2161	8.610		
Total	257	2472			

Table 4. Results of the ANOVA of logtransformed SOMATIC GROWTH for the model:

$SG = a + b_1Y_1 + b_2Y_2 + b_3Y_3 + cA + dL + eL^{**2} + fSC + gA*L$
 with SG = log transformed volume increase, Y = year, A = age, L = length in the previous spawning season, L^{**2} = square of length, SC = somatic condition factor at present spawning season and $A*L$ = interaction of A and L.

Parameter estimates

parameter	variable	Parameter estimates	SE
a		5.849	0.6720
b1	year 1982	0.0	
b2	year 1983	0.0498	0.0745
b3	year 1984	0.0729	0.0697
c	A	- 0.7366	0.1599
d	L	0.0514	0.0510
e	L^{**2}	- 0.001273	0.000935
f	SC	- 0.000012	0.000291
g	$L*A$	0.1346	0.00376

Analysis of variance

	df	SS	MS	F	
Y	2	0.30	0.15	0.79	ns
A	1	9.33	9.33	48.86	**
L	1	1.84	1.84	9.64	**
L^{**2}	1	2.59	2.59	13.56	**
S	1	0.30	0.30	0.78	ns
error	251	47.93	0.19		
$A*L$	1	2.34	2.34	12.83	**
error	250	45.59			
Total	257	63.67			

Table 5. Results of the ANOVA of the SURPLUS PRODUCTION of plaice according to the model

$$SP = a + bL^{**3} + cA + dY + eL*A$$

with L^{**3} = cube of the length at the start of the growing season, A = age, Y = year and

$L*A$ = interaction of L and A.

Parameter estimates

parameter	variable	Parameter estimates	SE
a		290.6	36.74
b	L^{**3}	0.00356	0.00060
c	A	- 41.97	7.776
d1	1982	0.0	
d2	1983	- 44.44	16.32
d3	1984	- 14.33	15.54
e	$L*A$	0.0001043	0.0000737

Analysis of variance

	df	SS (/1000)	MS (/1000)	F	
L^{**3}	1	978	978	102.2	**
A	1	387	387	40.5	**
Y	2	78	39	4.1	*
error	253	2420	9.565		
$L*A$	1	19	19	2.0	n.s.
error	252	2401	9.528		
Total	257	3676			

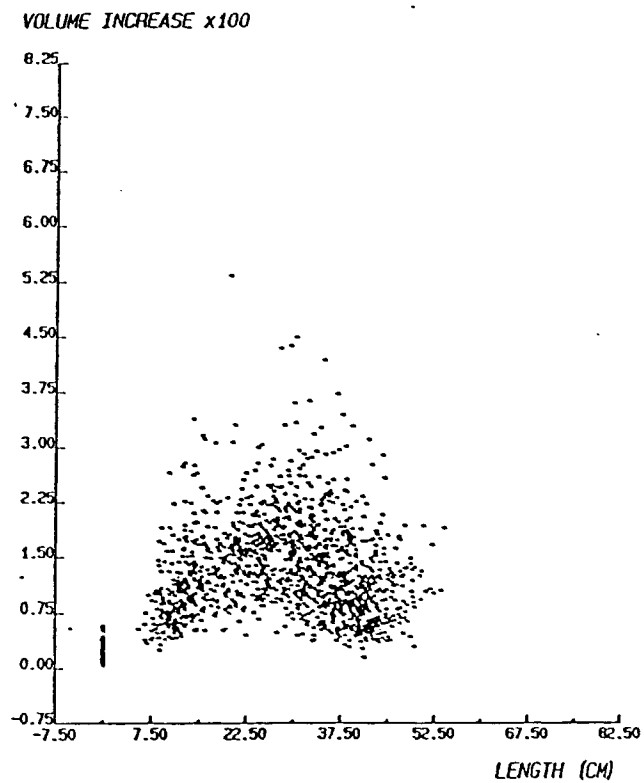


Figure 1. Relation between somatic growth and fish-length at the beginning of the growing period. The somatic growth is expressed as the increase in volume during the growing period.

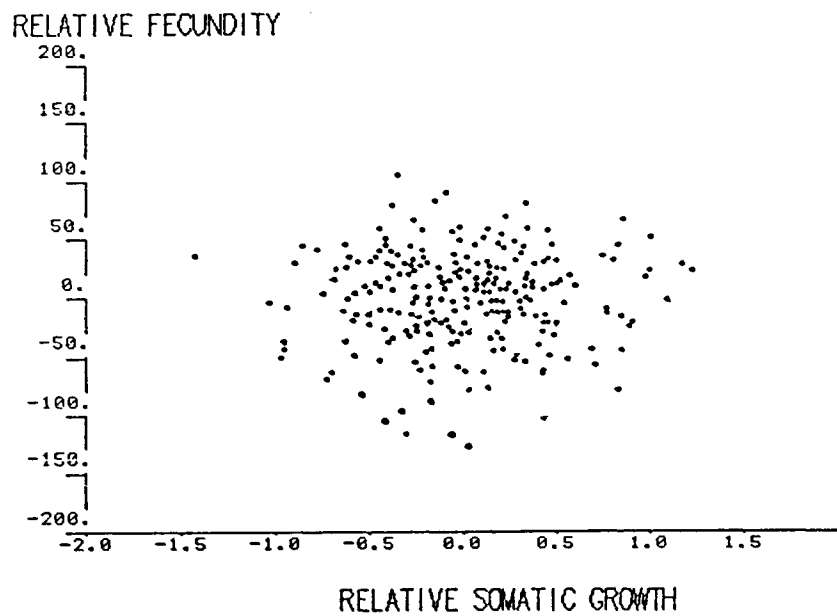


Figure 2. Relation between the fecundity and somatic growth in individual female plaice. To allow a comparison the fecundity and somatic growth were standardized (see text for details).

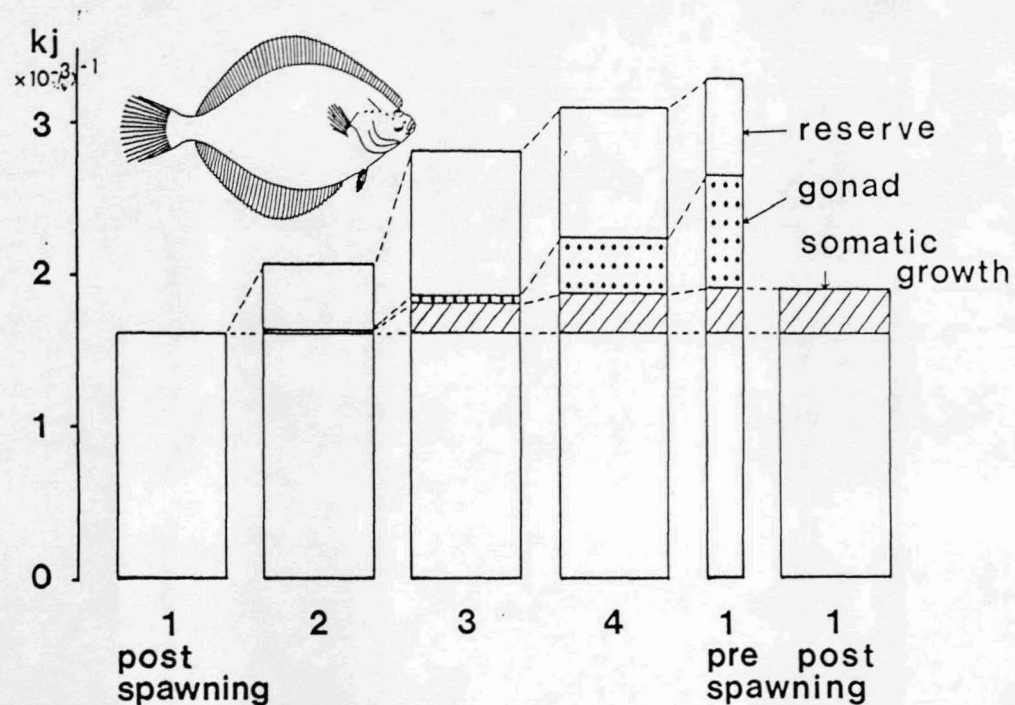


Figure 3. Quarterly pattern of energy allocation over energy reserves, gonad development and somatic growth in 5 year old female plaice. In the 1st quarter the bodycomposition of pre- and post spawning fish is shown.

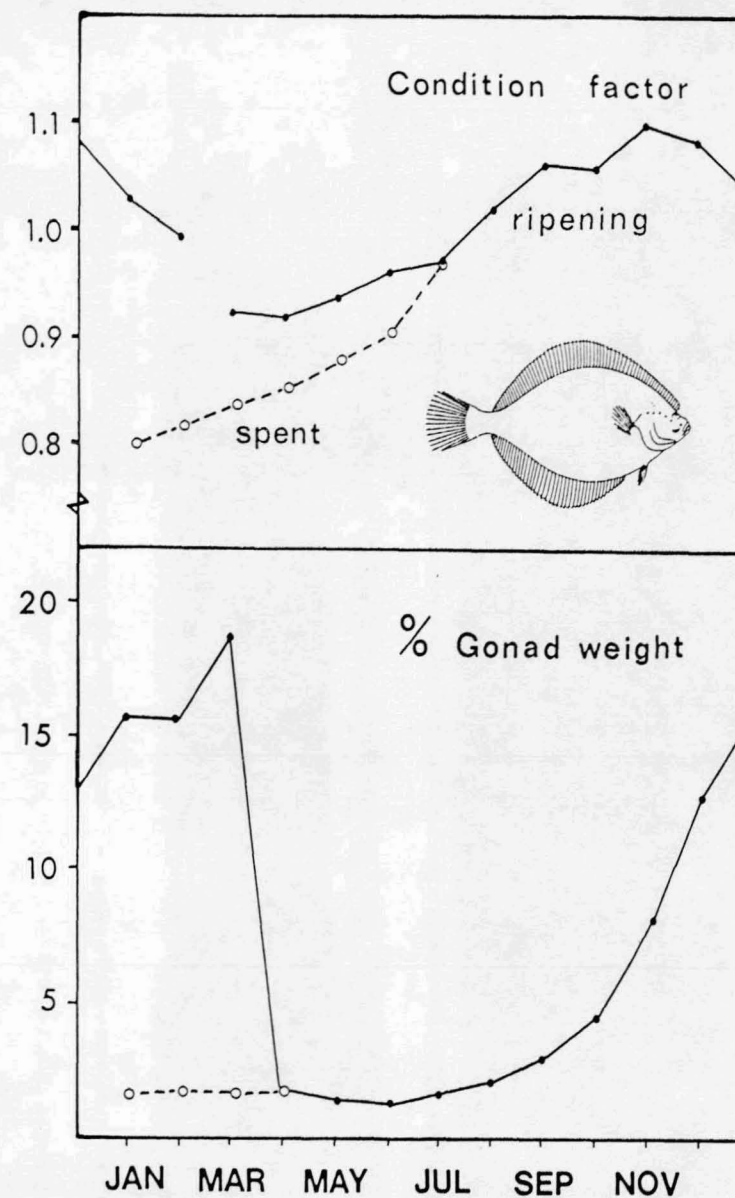


Figure 4. Monthly change in condition factor (upper panel) and gonadosomatic index (lower panel) of mature, spent and ripening, female plaice.

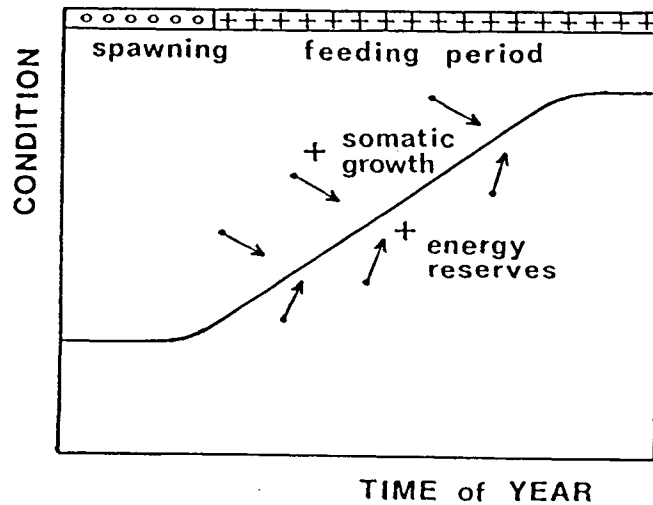


Figure 5. Mechanism of allocation of surplus energy over somatic growth and energy reserves (reproduction). The line indicates the increase of the condition-threshold during the growing period. A fish with a condition below this threshold level will channel its surplus energy into restoration of its bodycondition. A fish with a condition above the threshold level will channel the surplus energy into somatic growth.

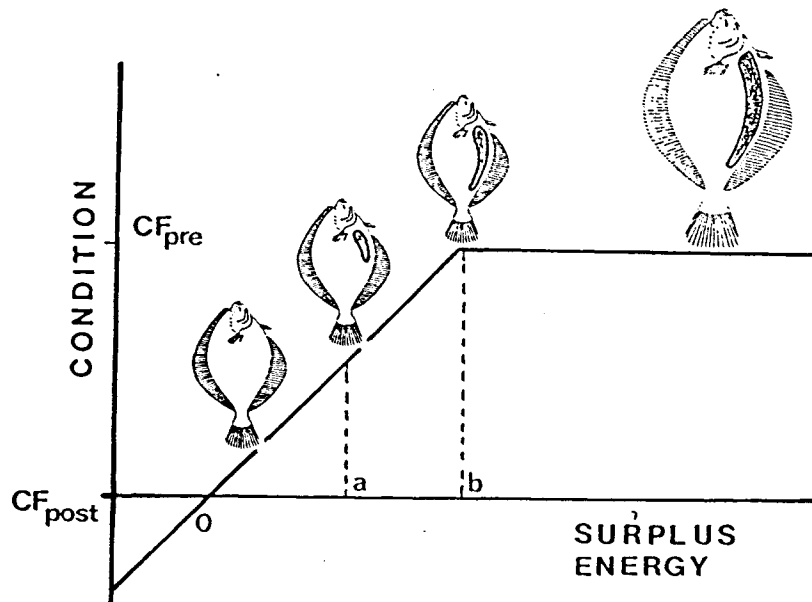


Figure 6. Relation between the amount of surplus energy and the allocation over energy reserves (reproduction) and somatic growth, resulting from the mechanism in Figure 5. At below zero surplus energy the fish will lose condition below the post spawning level (CF_{post}) and will not show any reproduction or somatic growth. With increasing surplus energy up to level a the energy reserves will be build up without somatic growth. Reproduction will start when surplus energy exceeds level a and will take an increasing share of the surplus energy. When surplus energy exceeds () the fish will show both reproduction and somatic growth, while reproduction will take a constant share of the surplus energy.