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METABOLISM, FOOD CONSUMPTION, GROWTH AND FOOD CONVERSION OF SHORTHORN SCULPIN (MYOXOCEPHALUS SCORPIUS) AND EELPOUT (ZOARCES VIVIPARUS).

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ABSTRACT.

The seasonal variation in numbers and the length distribution of Bull-rout or shorthorn sculpin (Myoxocephalus scorpius) and Eelpout (Zoarces viviparus) were investigated in the dutch Wadden Sea. Body composition and energy content of the fish were estimated in relation to condition factor K. Metabolism, weight loss of fasting fish, and maximum growth rate with excess food were estimated in the laboratory at different constant temperatures, with groups of fish differing in mean length. Daily weight increment of maximally growing fish and the daily weight loss of fasting fish are both correlated with the metabolic weight of the fish : $W^{0.8}$. Growth rate in length of Bull-rout was maximal at 12-13 ^{0}C (0.3 mm/day), growth of Eelpout was maximal at 15 ^{0}C (0.5 mm/day). The effect of temperature on growth and the energy budget is described. Food consumption of the populations in the Wadden Sea is estimated from the "metabolic biomass" of the fish. Annual food consumption, in gram ash-free dry weight per m^2, is approximately : Bull-rout 1.5-3.0, Eelpout 1.0-1.5 g AFD/m^2/yr.

INTRODUCTION.

The common eelpout or viviparous blenny (Zoarces viviparous L.) and the Bull-rout or short spined sea scorpion (Myoxocephalus scorpius L.) are characteristic resident fish species in the Dutch Wadden Sea. They are found particularly in the tidal channels on mussel beds. Eelpout eat mainly small crustaceans (copepods, amphipods, cypris larvae, very young shore crabs (5 mm), young shrimp (1-2 cm) and small molluscs such as young Mytilus and Hydrobia. Bull-rout eat mainly shrimp, shore crabs, and small fish such as gobies and young clupeoids (KUHL 1961, BAGGE 1977).

Eelpout are viviparous (KORSGAARD 1986) : internal fertilization takes place in July and August (GOETTING 1976, KRISTOFFERSSON & OIKARI 1975) and young of 4 cm length are born in January and February. Bull-rout spawn in November and December (LAMP, 1966). The orange coloured eggs of 2.4 mm diameter are attached in clumps between stones and mussels, and they are guarded by the male until they hatch in March (ENNIS, 1970a).

Both species are common and locally abundant in coastal waters of northern Europe, particularly in brackish waters, and their general biology and physiology are fairly well studied (ENNIS 1970b, HJORT 1975, OIKARI 1978, HEW 1980, KING 1983). Eelpout have been used particularly for studies on genetic and geographic variation and the effect of environmental pollution on fish (HJORT 1975, CHRISTIANSEN et al.1981, ESSINK 1985). Bull-rout have been used particularly for studies on adaptation to low temperatures (FLETCHER et al.1982, O'GRADY et al.1982). The question rises whether these fish are of any importance in the benthic food chain as secondary consumer (Eelpout) or top predator (Bull-rout). In the past numbers and length distribution of both species have been estimated by regular trawling surveys in the dutch Wadden Sea (FONDS,1978). In order to estimate food consumption of the populations in the Wadden Sea from the available data on growth and biomass, growth was measured in the laboratory in relation to fish size, temperature and food consumption.

METHODS.

FIELD DATA. Regular trawling surveys were carried out with fine-mesh trawl (1 cm mesh size in the cod end) on about 30 stations with depths of 2 to 20 m in the western part of the dutch Wadden Sea. All fish were measured and speed of the ship was measured during trawling to estimate the bottom area covered by each haul and numbers of fish per 1000 m^2.

LABORATORY MEASUREMENTS. Live fish were collected and transferred to the laboratory, where they were adapted to different constant temperatures of 2, 5-6, 10, 14-15, 18, 20 and 22 ^{0}C in large polyester tanks of 2.5 x 0.5 x 0.5 m, with seawater of 30 %. salinity. After an acclimatization period of about one month measurements of oxygen consumption, food consumption and growth were carried out over periods of 2 to 4 weeks with groups of fish of equal length and weight. At the start and at the end of growth experiments the fish were measured after light narcotization with MS-222 (Sandoz). Total length was measured to the nearest mm and wet weight was measured to the nearest 0.01 g after the fish had been dried carefully between damp towels. During recovery from narcosis the fish were given a prophylactic dose of 50 mg Streptomycine and 50000 I.U. Penicilline per liter sea water for one hour. At the start and at the end of the experiments some fish were killed with a lethal dose of MS-222 in order to estimate dry weight, body composition and energy content. Small fish were analyzed in groups of 5 to 10 fish of equal length and weight, large fish were analyzed individually.

BODY COMPOSITION AND ENERGY CONTENT. For analysis of body composition the fish were dried at 80 ^{0}C in previously weighed glass pots of 200 to 600 ml to estimate dry weight. Dried fish were stored about 3-4 weeks in chloroform, changed every week, and dried again to estimate lipid content from the decrease in dry weight after chloroform extraction. Finally, dried lipid-free fish were burned 2 hours at 580 ^{0}C to estimate ash content. Protein content was estimated as dry weight minus lipid and ash, ignoring smal amounts of carbohydrates. Energy content of the fish was estimated by multiplying lipid content with the commonly used calorific value of 39.5 Joules per mg and protein content by a "physiologically useful" value of 19.8 Joules per mg or by the maximum energy value of 23.6 Joules per mg for proteins at complete combustion. The sum of lipid and protein energy is given either as "physiologically useful energy" per gram wet weight of fish (Ep,J/g wet) to be used in growth studies, or as "total energy" per gram dry weight (Et,J/g dry) for comparison with estimates of energy content by calorimetry.

RESPIRATION MEASUREMENTS. For measurements of daily oxygen consumption fish were kept in closed respiration tanks of 55 x 50 x 40 cm (110 liter) covered with glass plates with two feeding holes. Seawater was pumped through one hole by way of a plastic tube to the bottom of the tank, flowing out again at the top through the other hole. Oxygen consumption of the fish was estimated by the decline in oxygen content of the water, measured by Winkler titration, when seawater flow was stopped and the tanks completely closed without air bubles for periods of 12-20 hours. The tanks were partly covered against light, to avoid algal production, and BOD was measured in seperate Winkler samples to correct for bacterial respiration (usually less than 1 % of the measured values). Nine respiration tanks were used for measurements with three different fish sizes (small; medium and large fish) kept at three different feeding regimes : weighed rations every day, once per week, and no food (fasting fish).

GROWTH MEASUREMENTS. Maximum growth rates were measured in the large tanks at different constant temperatures, with groups of fish fed daily excess amounts of shrimp (Crangon crangon) and chopped fresh mussel meat (Mytilus edulis). Growth was also measured in smaller tanks (50-100 liter) with groups of fish fed weighed food rations at different time intervals : every day, once per three days or once per week. Dry weight and energy content of food was estimated in the same way as for fish. Growth in length (L) was calculated in mm per day as dL = (Lend - Lstart) / time (days). Growth in weight (W,g) was calculated by the growth constant G = (ln Wend - ln Wstart) / time (days). Mean weight of the fish in the midle of the time period was calculated as (ln Wstart + ln Wend) / 2 or : mean W = √Wst.Wend . Daily growth rate is than given in % per day as (e expG - 1).100, and daily weight increment in the middle of the time period as :
dW = (e expG - 1).√Ws.We. Daily weight increment was estimated in ash-free dry weight and in physiologically useful energy .

RESULTS

POPULATION DENSITY AND LENGTH DISTRIBUTION.
The length distribution of Eelpout and Bull-rout caught in monthly trawling surveys on 30 stations from September 1963 to October 1964, is shown in Figure 1 a and b. Similar trawling surveys carried out from January to December 1986 in a more limited area, showed a similar picture. Mean numbers of fish per 1000 m^2 (N) and standard deviations of means (S.D.) are shown at the right hand side. Since standard deviations were often about twice the value of means, the geometric mean number of fish (GN) was calculated by way of log transformation as : e exp(mean lnN).
Numbers of fish per 1000 m^2 were maximal in Autumn (Sep-Dec) and lower in Winter and Summer. Increasing numbers in the catches are partly due to recruitment, when the 0-group fish become large enough (> 7-8 cm) to be retained by the nets. However, changes in abundance probably also reflect changes in activity and dispersion of the fish from their natural habitat of mussel beds, where fishing was not feasible.
In the length frequency distribution four age classes can be distinguished : 0-group, I-group, II-group and older fish. For both species the catches are dominated by 0-group and I-group fish. II-group fish are already scarce and older fish larger than 25 cm are very rare. Both species become mature at the end of their second Summer. Table 1 shows the length at age of males and females of Bull-rout and Eelpout, from otolith readings of fish caught in standing nets (files Netherlands Institute for Sea Research, H.WITTE, pers.comm.). Females growth faster and reach a larger size (Bull-rout 27 cm, Eelpout 29 cm) as compared to males (Bull-rout 20 cm, Eelpout 23 cm).
Shifts of peaks in the length distribution indicate that both species grow mainly during Summer, from about April to October-November. During Winter the length distribution does not show a consistent increase in fish size. Growth rate in length (dL,mm/day) of

Bull-rout and Eelpout in the Wadden Sea in Summer was estimated by connecting peaks in the length distribution, and by the difference in mean length between 0-group and I-group fish assuming that growth takes place over a period of about 6 months (Table 2).

CONDITION FACTOR, BODY COMPOSITION AND ENERGY CONTENT.

Total numbers of fish analyzed were:

Bull-rout : 98 samples containing 446 fish of 7 to 23 cm length,
Eelpout :132 samples containing 520 fish of 10 to 26 cm length.

The weight (W,g wet) to length (L,cm) relationship appeared to be for Bull-rout $W = A.L^{-3.10}$ and Eelpout $W = A.L^{-3.25}$. Therefore condition of the fish was estimated by a condition factor (K) based on the coefficient A : Bulrout $K = 100.W.L^{-3.10}$ and Eelpout $K = 100.W.L^{-3.25}$. Condition factor was calculated both for wet weight (Kwet) and for dry weight (Kdry). The relationship between wet weight condition factor (Kwet) and the parameters of body composition and energy content were calculated and equations giving the best fit are presented in Table 3, together with the correlation coefficient r.

The data on body composition were sorted according to condition factor of the fish from low to high condition (Bull-rout: Kwet 0.78-1.14, Eelpout: Kwet 0.14-0.24) and grouped into condition groups. Mean values of percentage body composition and energy content of fish in the different condition groups are presented in Table 4.

Percentage dry weight and percentage lipid increase with the condition factor while percentages water, ash and protein decrease (c.f.PEKKARINEN 190).This results in an increase of percentage ash-free dry weight and energy content of fish with increasing condition factor (Fig. 2).

Fasting fish hardly change in length while the decrease in weight results in a decrease of condition factor. With the values in Table 4 the actual weight of ash, lipid and protein can be calculated for a standard fish, for example of 15 cm length. (Bull-rout W,g wet = $0.01.Kwet.Lcm^{3.1}$, Eelpout $W = 0.01.K.L^{3.25}$). From these values the relative losses of lipid energy and protein energy can be estimated for a fasting fish, decreasing in weight and condition (Table 5). Fasting fish utilized lipid- and protein energy in about equal proportions, only fasting Eelpout in very good condition show a higher loss of lipid energy.

LABORATORY MEASUREMENTS.

Measurements of maximum growth rate with groups of fish fed daily excess food rations were carried out with both species at different constant temperatures over periods of about one month in April 1987 (5,10,15 & 20 °C), in September 1987 (14,18 °C), and only with Eelpout in June-July 1988 (2,6,10,14,18,22 °C). Daily weight or energy loss of fasting fish was measured in the same periods at the same temperatures.

FOOD. Bull-rout were fed with frozen shrimp (Crangon crangon), Eelpout were fed with chopped shrimp and/or with fresh mussel meat (Mytilus edulis). Dried shrimp contained about 20-24 % ash, 3-5 % lipid, 64-70 % protein, 1% glycogen and 4-6 % chitine. Faeces of fish fed with shrimp contained many remains of shrimp skins, indicating that chitin was not properly digested by the fish. Energy value of shrimps as food was therefore calculated without the energy value of chitin as : 15 kJ per gram dry weight or 19.5 kJ per gram ash-free.

Dried mussel meat contained about 10 % ash, 6-7 % lipid, 58 % protein and 25 % glycogen (c.f.DARE & EDWARDS, 1975). Energy value of mussel meat was estimated to be approximately 18.5 kJ per gram dry weight or 20.5 kJ per gram ash-free dry.

RELATIONS WITH FISH SIZE. Values of daily change in mg ash-free dry weight or energy (J) were plotted against the geometric mean wet weight (W,g wet) of fish, fasting or growing maximally. A linear relationship was obtained when log weight change or energy change (dW or dE) was plotted against log mean weight : log dW = log A + B.log W, or : $dW = A\ W^B$. Values of A and B for Bull-rout and Eelpout, fasting or growing at different constant temperatures, are given in Table 6 together with the correlation coefficient (r), the number of groups (N), and the total numbers (n) and size range of fish at each temperature.

The weight exponent B for maximum daily growth is similar to the weight exponent for daily weightloss of fasting fish, varying between 0.7 and 0.9 for both Bull-rout (n=7) and Eelpout (n=11). The mean value of the weight exponent appears to be similar to the mean metabolic weight exponent for fish estimated by WINBERG (1956). In order to get a size independant parameter for growth all estimated values of metabolism and weight or energy change were divided by the mean "metabolic" wet weight of the fish : W,g $wet^{0.8}$. Mean values of maximum daily growth are presented in Table 7, mean values of daily weight loss of fasting fish in Table 8.

Daily weight increment divided by metabolic weight appears to be more or less linearly related with daily growth in length, irrespective of fish size or water temperature. Figure 3 shows a plot of all growth measurements with different groups of fish at different temperatures.

TEMPERATURE EFFECT ON GROWTH. Mean growth rate in length is plotted against temperature in Figure 4. In the lower temperature range growth rate increases exponentially to a maximum at 13 °C (Bull-rout, 0.3 mm/day) and 15 °C (Eelpout, 0.5 mm/day), decreasing rapidly again at higher temperatures. At temperatures above 20 °C mortality of the fish was high, the upper lethal temperature limit lies probably close to 22-23 °C. Growth rate of Eelpout was still fairly high at 2 °C, indicating that the lower temperature limit for growth is probably below 0 °C. The effect of temperature (T,°C) on maximum growth rate in length (dL,mm/day) can be described by a polynomial :

$$\text{Bull-rout: } dL = -0.01 + 0.019\ T + 0.0023\ T^2 - 0.00016\ T^3 \quad (r=0.95),$$
$$\text{Eelpout : } dL = 0.05 + 0.013\ T + 0.0051\ T^2 - 0.00025\ T^3 \quad (r=0.98).$$

The relation between temperature and maximum growth rate of Bull-rout appears to be rather symmetric. A good fit is also obtained with the parabola equation :

$$\text{(Bull-rout): } dL = 0.3\ e^{-0.025(T-11.9)^2} \quad (r=0.98,\ n=6).$$

In this equation 11.9 is the optimum temperature at the top of the parabola where dL = 0.3 . Similarly growth rate in weight can be described by :

$$dW,\text{mgAFD}.W^{-0.8} = 5.9\ e^{-0.016\ (T-12.4)^2} \quad (r=0.96,\ n=4).$$
$$dE,J.W^{-0.8} = 148\ e^{-0.015\ (T-12.5)^2} \quad (r=0.96,\ n=4).$$

The effect of temperature on daily weight loss (dW,mg AFD/$W^{0.8}$) or energy loss (dE,J/$W^{0.8}$) can be described for temperatures of 5-15 °C (Bull-rout) or 2-20 °C (Eelpout) by :

$$\text{Bull-rout : } dW = -\ 0.88\ e^{0.1T} \quad \text{and } dE = -\ 23\ e^{0.1T} \quad (r=0.97,\ n=4).$$

Eelpout : $dW = -1.53 - 0.13\,T$ and $dE = -39 - 3.7\,T$ ($r=0.99$, $n=6$).

METABOLISM. Measurements of daily oxygen consumption and growth of fish given different weighed food rations are presented in Table 9. Oxygen consumption of Eelpout was twice as high during the night as compared to daytime measurements, the fish were apparently more active during the night (cf.WESTIN & ANEER, 1987).

Oxygen consumption was multiplied with an oxycalorific coefficient of 13.55 J per mg oxygen, to estimate metabolic heat loss of the fish (BRAFIELD,1985). Metabolic heat losses of fasting fish (Table 9) are fairly similar to energy losses estimated from weight loss (Table 8).

At full feed respiration of Bull-rout reaches a maximum of 15 mg $Ox/day/W^{0.8}$ at 15 ^0C, maximum oxygen consumption of Eelpout at the same temperature is 11 mg $Ox/day/W^{0.8}$.

Oxygen consumption (heat loss) increases with increasing temperature. Metabolism also increases exponentially with increasing ration size. When values of metabolic heat loss of fasting fish in Table 9 are subtracted from the values of metabolic heat loss of fish fed different rations, the remaining extra metabolic heat loss for food digestion (SDA) is about 31-43 % of the energy of food rations consumed. Heat loss is also correlated with growth in energy (c.f.JOBLING,1985). When metabolic heat loss (QR) is plotted against the growth in energy (QG) according to $QR = A + B.QG$, the following relations are found :

Bull-rout :	5 ^0C : $QR = 56 + 0.55\,QG$	(n=3)
	10 ^0C : $QR = 64 + 0.60\,QG$	(n=3)
	15 ^0C : $QR = 127 + 0.70\,QG$	(n=3)
	20 ^0C : $QR = 116 + 0.83\,QG$	(n=2)
Eelpout :	15 ^0C : $QR = 149 + 0.48\,QG$	(n=3)

In these equations A is the maintenance heat loss when G=0, while B represents the metabolic costs of growth (JOBLING,1983b).

In the respiration tanks with Bull-rout fed weighed rations once per week at four different temperatures, faeces was collected and its ash-free dry weight estimated as 9.3 % of food ration (s.d. 2.9 , n=4). Figure 5 shows the energy budget of maximally feeding Bull-rout in relation to temperature. The relative metabolic costs increase at temperatures over 13 ^0C, while growth decreases.

FOOD CONVERSION. Growth (G) and food consumption (C) show a linear relationship : $G = -A + B.C$. In this equation - A is the weight (or energy) loss of a fasting fish (C=0) and B is the net proportion of food converted into growth. Maintenance food requirements (Cmaint, when G=0) can be calculated as A/B , and net food conversion efficiency as 1/B. Values of A, B, 1/B and Cmaint are presented in Table 10. The net food conversion factor B is similar in the two species. When the exeptionally low value for Bull-rout at 20 ^0C is omitted the mean conversion factor becomes 0.465 (s.d.:0.020) for food and growth in ash-free dry, or 0.601 (s.d.:0.030) for energy conversion.

FOOD CONSUMPTION IN THE SEA. With the available information on growth rate and food conversion an attempt can be made to estimate food consumption of the fish in the Wadden Sea. Seasonal variations in numbers are probably mainly due to changes in catchability of the fish. Maximum numbers caught in Autumn may give the best impression of population numbers and biomass. Total biomass of Bull-rout an Elpout was estimated from the length distribution (Fig.1) and the known length-weight relationship for fish with a mean condition (Bull-rout: $W,g\ wet = 0.0093\ Lcm^{3.10}$, Eelpout: $W,g\ wet = 0.0019\ Lcm^{3.25}$).

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Numbers of fish per 1000 m^2 , biomass (ΣW,g wet) and metabolic biomass ($\Sigma W^{0.8}$), calculated for months with maximum catches, are presented in Table 11.

Daily weight increment of the fish (G), as proportion of metabolic weight, is correlated with food consumption (C) but also with growth rate in length (dL). From estimates of growth rate in length of fish in the sea (Table 2) their daily food consumption can be estimated. For growth (G) and food consumption (C) in mg ash-free dry weight divided by metabolic wet weight (mg AFD/W,$g^{0.8}$) G = 0.465 C - A for both species, where A/0.465 is maintenance food. When a mean water temperature of 15 °C is taken for the Summer and 5 °C for the Winter, daily food intake can be calculated as follows :

Bull-rout: $G = 0.465\ C - A = 18.4\ dL + 1$;
$C = (18.4\ dL + A + 1) / 0.465 = 39.6\ dL + 2.15\ (A+1)$.
$A = 0.9\ e^{0.1T}$; 5 °C : A = 1.46 , 15 °C : A = 4.03
Summer 1963 : dL = 0.40 mm/day, 15 °C : $C = (15.84 + 10.81).W^{0.8}$
Summer 1964 : dL = 0.25 ,, , ,, $C = (9.90 + 10.81).W^{0.8}$
Winter 63/64: dL = 0 ,, 5 °C : Cmaint. = $3.19\ W^{0.8}$.

Eelpout : $G = 0.465\ C - A = 12.8\ dL$;
$C = (12.8\ dL + A) / 0.465 = 27.5\ dL + 2.15\ A$.
$A = 1.54 + 0.13\ T$; 5 °C : A = 2.2, 15 °C : A = 3.5
Summer 1963 : dL = 0.40 mm/day, 15 °C : $C = (11.00 + 7.53).W^{0.8}$
Summer 1964 : dL = 0.30 ,, , ,, $C = (8.25 + 7.53).W^{0.8}$
Winter 63/64: dL = 0 ,, 5 °C : Cmaint. = $4.73\ W^{0.8}$.

With the values of "metabolic biomass" ($\Sigma W^{0.8}$) in gram per 1000 m^2 from Table 11, daily food consumption for growth and maintenance in Summer and Winter can be estimated. When these values are multiplied with 182 days for Summer and Winter annual food consumption in ash-free dry weight becomes 1.5 - 3.0 gram ashfree dry per m^2 per year for Bull-rout, and 1.0-1.5 g AFD/m^2/year for Eelpout.

DISCUSSION.

POPULATION IN THE WADDEN SEA. Variations in catches of Bull-rout and Eelpout during the year are probably mainly due to catchability of the fish. Increasing numbers together with decreasing size of Bull-rout in December indicate that young fish migrate from shallower areas or from the mussel beds into the tidal channels, possibly following shrimp and crab migrating from the tidal flats into deeper water.

The length to weight relationship of Bull-rout in our measurements was different from the relationship estimated by RACIBORSKI (1984): $W = 0.0316\ L^{2.75}$, using fresh, frozen and alcohol preserved fish. KRISTOFFERSSON & OIKARI (1975) estimated length-weight relationship of Eelpout from the Baltic as : $W = 0.01\ L^{2.8}$, the length exponent being also lower than in our measurements.

The population of Bull-rout in the Wadden Sea in 1963-1964 was dominated by the yearclass 1963. This may have been due to an exeptionally high survival of larvae and good recruitment after the severe winter of 1962-63. Myoxocephalus scorpius is considered to be an arctic species (COWAN 1971), adapted to low water temperatures (FLETCHER et al.1982, O'GRADY et al.1982).

SIZE EFFECT. Maximum daily growth in weight or energy appears to be correlated with the metabolic weight of the fish. According to JOBLING (1983) growth rate of fish in % per day (G %) is exponentially correlated with fish weight : $\ln G = \ln a - 0.4 \ln W$ or $G\ \% = a\ W^{-0.4}$. This implies that the actual daily weight increment dW is correlated with fish weight to the exponent 0.6 :
from $G\ \% = dW.100.W^{-1} = a\ W^{-0.4}$ follows : $dW = 0.01\ a\ W^{1-0.4}$

According to ELLIOTT (1975) maximum daily food consumption of Salmo trutta is correlated with fish weight$^{0.75}$, while maximum daily weight increment is correlated with fish weight$^{0.68}$. Such a difference between weight exponents for feeding and growth has not been observed in measurements with plaice, flounder and sole (FONDS et al. 1985, 1989) and is also not evident in the measurements with Myoxocephalus scorpius and Zoarces viviparus presented here. Demersal fish are possibly different from pelagic fish in this respect.

METABOLISM. Metabolism and daily weight loss of fasting fish decrease with decreasing condition factor. Since weight loss is proportional to the metabolic weight ($W^{0.8}$), a small fish will lose weight more rapidly than a large fish and the effect of decreasing condition on rate of weight loss will be more pronounced in small fish. For comparison of weight loss of small and large fish, weight loss should be measured over the same range of (decreasing) condition factor, which takes much more time in the bigger fish.

FOOD CONSUMPTION. The food conversion factor is estimated as 0.465 in ash-free dry weight and 0.601 in energy. Feeding fish usually store particularly lipids from the food, with the result that they grow more in energy than in ash-free dry weight.

Annual food consumption of Bull-rout and Eelpout populations in the Wadden Sea is estimated to be approximately 1.5-3.0 and 1.0-1.5 gram ash-free dry weight per m^2, that is 2.5-4.5 g AFD/m^2 for both species together. Annual food consumption of young plaice and flounder, feeding on tidal flats in the Wadden Sea, is approximately 1.5 - 6 gram ash-free dry per m^2 (KUIPERS 1977, DE VLAS 1979). Annual food consumption of Bull-rout and Eelpout together in the subtidal area is comparable to the annual food consumption of plaice and flounder on the tidal flats.

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TABLE 1.

Length at age of fish caught in fyke nets, from reading of otoliths.

Age Years	MYOXOCEPHALUS SCORPIUS males	(n)	females	(n)	ZOARCES VIVIPARUS males	(n)	females	(n)
1	12.5	(6)	12.4	(8)				
2	16.4	(11)	19.1	(11)	15.2	(6)	16.2	(5)
3	17.9	(15)	21.9	(15)	19.6	(13)	21.7	(12)
4	20.4	(5)	24.0	(5)	20.9	(8)	22.7	(6)
5	19.1	(21)	23.7	(8)	21.5	(11)	25.5	(14)
6	-		27.0	(1)	23.0	(4)	29.0	(3)
7-8	-		-		-		27-31	(2)

TABLE 2.

Mean length in cm of different age classes of Myoxocephalus scorpius and Zoarces viviparus in the Wadden Sea in Autumn, and the estimated daily length increment (dL,mm/day) during Summer.

Year classes :	O	I	II	Older
MYOXOCEPHALUS				
L,cm Oct-Nov.:	10-13	16-17	20-23	25-32
dL, mm/day :	0.35-0.45	0.20-0.30	0.10-0.15	<0.10
ZOARCES				
L,cm Sep-Oct.:	10-12	15-17	18-21	22-25
dL, mm/day :	0.40-0.45	0.25-0.35	0.10-0.25	<0.10

TABLE 3.

Percentage body composition and energy content of Bull-rout and Eelpout in relation to condition factor Kwet (K), where W is wet weight in gram and L is total length in cm. Bullrout 98 samples with a total number of 446 fish of 7-23 cm length and Kwet varying from 0.79 to 1.14, Eelpout 132 samples with 520 fish of 10-26 cm and Kwet from 0.14 to 0.24.

	MYOXOCEPHALUS $Kwet = 100.W.L^{-3.10}$	r (n=98)	ZOARCES $Kwet = 100.W.L^{-3.25}$	r (n=132)
% Dry weight	$= 44.6 - 21.6\ K^{-1}$	-0.743	% Dry = $13.6 + 47.0\ K$	0.676
% Ashfree dry	$= 42.9 - 23.7\ K^{-1}$	-0.778	% AFD = $9.3 + 53.4\ K$	0.700
% Ash in dry W	$= (0.1\ K - 0.04)^{-1}$	0.825	% Ash $= (0.31\ K - 0.016)^{-1}$	0.625
% Lipid ,,	$= 33.6 + 47.4\ K$	0.738	% Lip = $165\ K - 21.0$	0.750
% Prot. ,,	$= 78.5 - 8.9\ K$	-0.377	% Prot= $96.0 - 107\ K$	-0.624
Ep, $J.mgwetW^{-1}$	$= 11.5 - 7.1\ K^{-1}$	-0.778	Ep,J = $0.7 + 19.1\ K$	0.735
Et, $J.mgdryW^{-1}$	$= 35.9 - 14.0\ K^{-1}$	-0.787	Et,J = $14.5 + 39.4\ K$	0.755

TABLE 4.

Body composition and energy content of Myoxocephalus scorpius and Zoarces viviparus, in relation to condition factor $K=100.W.L^{-B}$, where W is in gram and L in cm. Mean values with standard deviations for condition groups. For each condition group are given number of samples N, total numbers of fish (n) and size range of the fish : total length L(cm) and wet weight (gram). Energy content is given as "physiologically useful" energy in Joules per gram wet weight (Ep KJ/gw) and as "total" energy per gram dry weight (Et KJ/gd). kilo

N (n)	Fish size Length, cm Weight, g	Condition factor K-wet	Condition factor K-dry	% of wet W. % Dry	% of wet W. % Wat	% of wet W. % AFD	% of dry weight % Ash	% of dry weight % Lip	% of dry weight % Prot	Energy content Ef/gw	Energy content Et/gd
MYOXOCEPHALUS		$K=100.W.L^{-3.10}$									
17	8- 23 cm	0.864	0.167	19.29	80.71	15.03	22.16	6.64	71.19	3.219	19.45
(64)	5-156 g	0.029	0.012	0.87	0.87	0.93	1.47	1.40	1.39	0.236	0.50
34	7- 22 cm	0.910	0.191	21.03	78.97	16.91	19.61	9.55	70.85	3.744	20.52
(184)	4-135 g	0.029	0.006	0.73	0.73	0.74	1.14	1.83	1.52	0.217	0.50
27	8- 23 cm	0.952	0.212	22.29	77.71	18.25	18.11	12.26	69.55	4.152	21.29
(116)	5-165 g	0.042	0.011	0.93	0.93	0.97	1.58	2.39	1.83	0.310	0.69
20	8- 22 cm	1.076	0.262	24.35	75.65	20.67	14.87	16.53	68.37	4.881	22.68
(82)	8-151 g	0.041	0.010	0.66	0.66	0.70	0.95	1.62	1.44	0.209	0[illegible]
ZOARCES		$K=100.W.L^{-3.25}$									
16	10-22 cm	0.158	0.0326	20.69	79.31	17.24	16.75	4.90	78.35	3.62	20.46
(55)	3-37 g	0.009	0.0015	0.64	0.64	0.79	1.58	1.84	1.10	0.23	0.63
28	10-24 cm	0.175	0.0377	21.54	78.46	18.33	14.91	7.43	77.66	3.94	21.28
(131)	4-50 g	0.007	0.0013	0.72	0.72	0.84	1.58	2.40	2.19	0.25	0.65
40	11-25 cm	0.188	0.0421	22.37	77.63	19.30	13.73	10.15	76.12	4.27	21.98
(153)	6-61 g	0.007	0.0014	0.82	0.82	0.90	1.21	2.52	2.17	0.28	0.59
25	10-23 cm	0.204	0.0475	23.25	76.75	20.37	12.39	12.19	75.42	4.60	22.63
(115)	3-48 g	0.006	0.0014	0.79	0.79	0.86	1.36	2.53	2.13	0.30	0.64
19	13-26 cm	0.222	0.0535	24.09	75.91	21.21	11.94	16.88	71.18	5.00	23.47
(54)	9-99 g	0.013	0.0040	1.03	1.03	0.94	1.55	3.27	4.33	0.30	0.43

TABLE 5.

Weight and energy content of a 15 cm fish at different levels of condition factor and the relative changes in lipid - and protein energy.

Kwet	wet weight g	dry weight g	Ash weight g	E lip. KJ	E prot. KJ	E tot. KJ	Change in energy: Total KJ	Lip. %	Prot. %
MYOXOCEPHALUS									
0.864	38.2	7.38	1.634	19.4	103.9	123.3			
							> 27.4	46	54
0.910	40.3	8.46	1.661	31.9	118.8	150.7			
							> 24.1	56	44
0.952	42.1	9.38	1.700	45.5	129.3	174.8			
							> 57.8	52	48
1.076	47.6	11.59	1.724	75.7	156.9	232.6			
ZOARCES									
0.158	10.5	2.17	0.364	4.2	33.7	37.9			
							> 8.0	40	60
0.175	11.6	2.50	0.373	7.3	38.5	45.8			
							> 7.5	51	49
0.188	12.5	2.79	0.384	11.2	42.1	53.3			
							> 8.9	45	55
0.204	13.5	3.15	0.390	15.2	47.0	62.2			
							> 11.5	74	26
0.222	14.7	3.55	0.424	23.7	50.0	73.7			

TABLE 6.

The correlation between daily change in weight (dW,mg ashfree dry) or energy (dE, Joules) and the mean wet weight (W,gram) of Bull-rout and Eelpout. Measuremts with groups of fish (N) growing maximally with unlimited food or fasting at different constant temperatures. For each temperature are shown the total number (n) and size range of fish (length L,cm and wet weight W,g), and the parameters of A and B from the equation dW (or dE) = $A.W^B$ with the correlation coefficient r for N groups.

Temp. °C	Days	Numbers N (n)	Size range: L cm	Ww,g	Weight increment dW = A . W ^{B} A	B	corr. coef.	Growth in energy dE = A . W ^{B} A	B	corr. coef.
MYOXOCEPHALUS ,			MAXIMUM DAILY GROWTH WITH EXCESS FOOD :							
5	27	5 (23)	9-15	7-46	1.77	0.775	0.988	44	0.789	0.979
10	28	4 (16)	9-15	7-46	2.01	0.823	0.968	53	0.814	0.958
14.5	28	6 (32)	9-18	9-85	3.44	0.862	0.989	90	0.859	0.990
18	30	4 (21)	13-18	26-90	3.23	0.857	0.965	110	0.783	0.966
			DAILY WEIGHTLOSS DURING FASTING :							
5	28	4 (13)	8-14	7-37	1.90	0.905	0.973	48	0.893	0.949
10	29	5 (29)	9-16	8-57	8.37	0.717	0.988	187	0.750	0.988
14.5	29	8 (35)	8-18	6-85	4.18	0.854	0.926	105	0.855	0.929
18	29	3 (8)	13-18	27-90						
ZOARCES ,			MAXIMUM DAILY GROWTH WITH EXCESS FOOD :							
2	36	5 (18)	12-23	6-51	1.60	0.783	0.945	40	0.783	0.933
5-6	27-36	6 (31)	12-19	7-28	3.46	0.826	0.955	80	0.859	0.996
10	30	5 (16)	12-19	6-26	7.00	0.812	0.957	178	0.809	0.959
14.5	30	9 (37)	12-23	7-48	6.76	0.739	0.938	167	0.730	0.934
18	30	4 (19)	11-18	6-26	3.40	0.914	0.961	77	0.960	0.959
20	30	3 (17)	13-18	6-26	6.22	0.806	0.999	171	0.771	0.999
			DAILY WEIGHTLOSS DURING FASTING :							
2	32	5 (17)	12-23	6-48	-1.15	0.835	0.984	-29	0.847	0.980
5-6	30	7 (22)	11-20	5-27	-0.83	0.963	0.960	-20	1.009	0.939
10	30	6 (24)	11-20	4-32	-2.17	0.796	0.980	-53	0.827	0.965
14.4	15	12 (53)	12-21	7-39	-2.90	0.795	0.920	-81	0.779	0.909
18	13	7 (14)	12-18	6-29	-3.43	0.817	0.904	-93	0.833	0.893

TABLE 7

Maximum growth rate of Bull-rout and Eelpout at different constant temperatures. Measurements with groups of fish (N) over periods of 28 to 36 days in Apr & Sep,1987 and in Jun-Jul,1988. Mean values with standard deviations of daily growth in length (dL,mm/day), daily weight increment in ash-free dry (dW,mg AFD) and in energy (dE,Joules) Daily growth in weight and energy is divided by the mean metabolic wet weight of the fish : W,g wet$^{0.8}$.

Temp ^0C	Numbers N	(fish)	Size range: L,cm	Ww,g	dL, mm / day Mean	S.D.	dW,mgAFD/$W^{0.8}$ Mean	S.D.	dE,J/$W^{0.8}$ Mean	S.D.
MYOXOCEPHALUS										
5	4	(13)	8-14	8-33	0.089	0.038	2.43	0.33	60	10
10	5	(29)	9-16	11-44	0.297	0.028	6.17	0.49	152	11
14	4	(19)	12-18	26-72	0.291	0.083	5.01	1.37	125	34
15	4	(16)	8-16	8-48	0.261	0.034	4.61	0.86	117	19
18	3	(8)	13-18	32-78	0.101	0.048	3.14	0.38	80	10
20	3	(11)	10-13	12-27	0.064	0.016	3.10	0.09	80	3
ZOARCES										
2	5	(18)	12-24	5-24	0.085	0.007	1.56	0.34	38	13
5	3	(22)	12-20	5-34	0.241	0.017	4.15	0.74	103	24
6	4	(16)	12-20	7-37	0.243	0.059	3.68	0.23	94	40
10	5	(16)	11-21	4-39	0.434	0.083	7.32	1.26	184	40
14	7	(18)	11-24	5-55	0.541	0.091	5.55	1.16	134	49
15	3	(23)	11-20	5-38	0.546	0.055	7.89	0.10	195	8
18	3	(17)	10-18	4-29	0.428	0.067	4.74	1.13	119	32
20	3	(17)	12-20	6-31	0.421	0.057	5.85	1.86	147	58
22	3	(3)	12-20	6-34	0.104	0.018	1.81	0.84	47	39

TABLE 8.

Daily weightloss (mg ash-free dry) and loss in energy (Joules) of fasting Bull-rout and Eelpout.Mean values with standard deviations (S.D.) of measurements with groups of fish (N), divided by the metabolic wet weight of the fish (W,g wet$^{0.8}$).

Temp. ^0C	Days	Numbers N	fish	Size range: L,cm	Ww,g	dW,mgAFD/$W^{0.8}$ Mean	S.D.	dE,J/$W^{0.8}$ Mean	S.D.
MYOXOCEPHALUS									
5	27	5	23	9-15	7-42	-1.56	0.13	-41	4
10	28	4	16	8-15	6-46	-2.05	0.39	-53	12
14	28	2	7	14-19	30-85	-3.71	0.71	-98	19
15	15	4	25	9-17	9-65	-4.08	0.35	-105	9
18	30	4	21	13-18	23-90	-3.73	0.36	-96	9
20	16	4	29	9-17	7-57	-2.20	0.33	-57	6
ZOARCES									
2	32	5	17	12-23	6-49	-1.87	0.20	-46	10
5	28	3	12	12-20	5-23	-1.33	0.61	-26	2
6	32	6	14	14-24	10-70	-2.20	0.74	-62	22
10	29	6	24	11-20	4-32	-2.86	1.02	-78	35
14	32	9	34	12-24	7-54	-3.35	0.75	-92	23
15	16	5	21	14-21	9-39	-3.35	1.08	-88	36
18	17	9	16	12-22	6-44	-3.94	1.25	-109	37
20	17	1	6	20.3	30-27	-3.12	-	-76	-

TABLE 9.

Measurements of daily food intake, daily growth and oxygen consumption of Bull-rout and Eelpout. All values divided by the metabolic wet weight of the fish : W,g wet$^{0.8}$.

Temp. ^{0}C	Days,	with food	Fish size: Length cm	Weight gwet	n	Food mg AFD/day/Wfish$^{0.8}$	Growth mg AFD/day/Wfish$^{0.8}$	Oxygen mg AFD/day/Wfish$^{0.8}$	Food Joules/day/Wfish$^{0.8}$	Growth Joules/day/Wfish$^{0.8}$	Oxygen Joules/day/Wfish$^{0.8}$
MYOXOCEPHALUS, fed with shrimp:											
5	26	0	9.0	8.1	7	0	-1.60	2.54	0	-40	34
	26	4	8.7	7.7	6	3.37	0.12	3.87	66	- 5	52
	28	26	8.4	6.8	6	4.60	0.74	4.80	90	16	65
	28	26	11.2	16.4	8	4.73	0.50	-	92	12	-
10	27	0	10.1	11.2	5	0	-1.44	3.37	0	-39	46
	27	4	9.9	11.0	6	6.47	1.53	5.63	126	34	76
	29	27	10.2	11.4	6	18.09	6.16	11.57	352	148	156
	29	27	11.6	20.3	7	17.98	6.26	-	350	158	-
15	15	0	9.2	9.2	5	0	-3.78	4.45	0	-98	60
	27	4	9.0	8.5	3	7.07	-0.98	7.62	138	-29	103
	29	27	8.8	8.1	5	17.85	4.06	14.75	348	102	200
	29	26	11.1	16.1	9	12.65	2.60	-	246	64	-
20	16	0	9.2	9.2	5	0	-1.93	5.12	0	-56	69
	28	4	8.8	8.0	5	4.73	-0.53	7.74	92	-14	104
	29	28	8.4	7.4	5	14.07	1.44	15.69	274	37	212
	30	28	11.0	15.4	7	9.92	0.59	-	193	14	-
ZOARCES, fed with shrimp:											
6	29	4	14.2	10.4	5	2.44	0.21	-	48	5	-
	29	9	13.5	8.9	5	5.41	1.11	-	105	26	-
	29	28	12.6	8.2	4	11.67	3.67	-	228	95	-
15	15	0	14.1	10.4	5	0	-4.75	7.88	0	-128	107
	15	0	18.0	23.8	4	0	-3.78	6.85	0	-101	93
	15	0	20.9	39.1	3	0	-4.04	7.13	0	-109	97
	23	3	13.4	9.0	5	2.90	-2.86	8.18	57	-78	111
	23	3	16.7	17.9	4	2.73	-2.54	7.19	53	-69	97
	23	3	20.1	31.1	3	2.19	-3.20	8.34	43	-89	113
	23	21	12.3	7.5	5	10.33	0.60	11.35	201	10	153
	23	21	15.7	15.8	4	9.80	1.35	10.60	191	29	144
	23	21	19.4	33.0	3	8.56	0.75	8.12	167	14	110
ZOARCES, fed with mussel meat:											
6	29	4	13.7	8.9	4	3.19	-0.87	-	65	-24	-
	29	9	13.1	8.9	4	5.33	0.56	-	110	13	-
	29	27	12.9	7.7	5	7.61	0.98	-	156	25	-
14	24	9	13.0	7.9	3	11.48	2.15	-	236	53	-
	24	22	13.1	8.4	4	26.84	9.01	-	551	224	-

TABLE 10.

The correlation between daily food consumption (C) and daily growth (G) of Bull-rout and Eelpout fed different food rations. Parameters of the equation G = - A + B.C, where - A is the weightloss of fasting fish (C=0) and B is the net proportion of food converted into growth. Net food conversion efficiency is calculated as 1/B, maintenance food rations (G=0) as A/B. Food and growth in ash-free dry (AFD) or energy (J), divided by the metabolic wet weight of the fish ($W, g^{0.8}$).

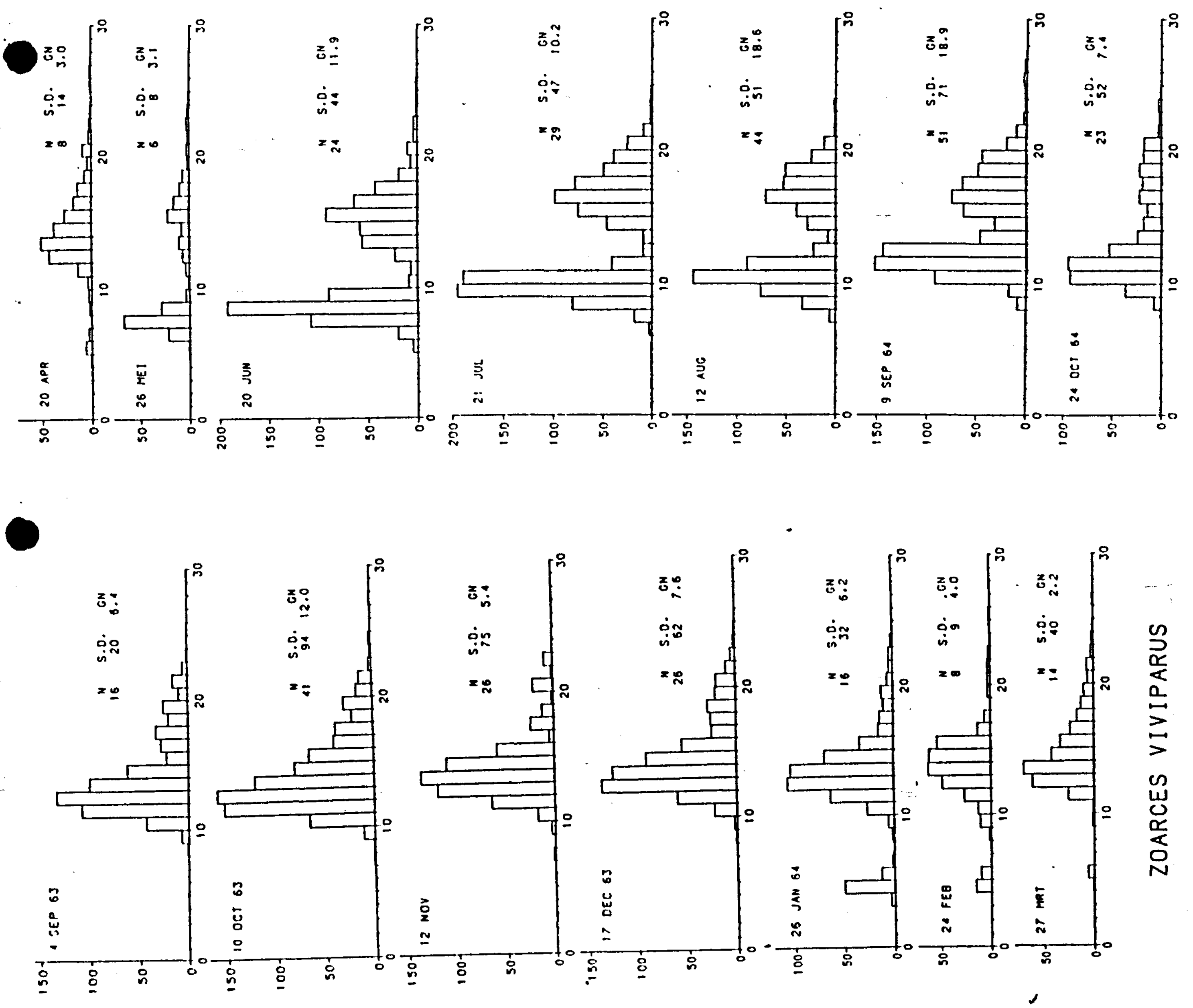
Temp. ^0C	Ash-free dry weight: G = A + B.C A	B	1/B	Cmaint	Energy (Joules): G = A + B.C A	B	1/B	Cmaint	r	n
MYOXOCEPHALUS, fed with shrimp:										
5	-1.58	0.475	2.11	3.30	-41	0.591	1.69	69	0.995	5
10	-1.64	0.438	2.28	3.74	-44	0.564	1.77	78	0.997	5
15	-3.94	0.466	2.15	8.45	-102	0.609	1.64	168	0.994	5
20	-1.97	0.252	3.97	7.83	-54	0.344	2.91	157	0.993	5
ZOARCES, fed with shrimp:										
6	-1.59	0.469	2.13	3.39	-45	0.639	1.57	70	0.975	4
15	-3.87	0.491	2.04	7.89	-103	0.641	1.56	161	0.984	4
ZOARCES, fed with mussel meat:										
6	-2.15	0.440	2.27	4.90	-60	0.583	1.71	103	0.985	4
14	-3.67	0.478	2.09	7.68	-91	0.578	1.73	158	0.999	4

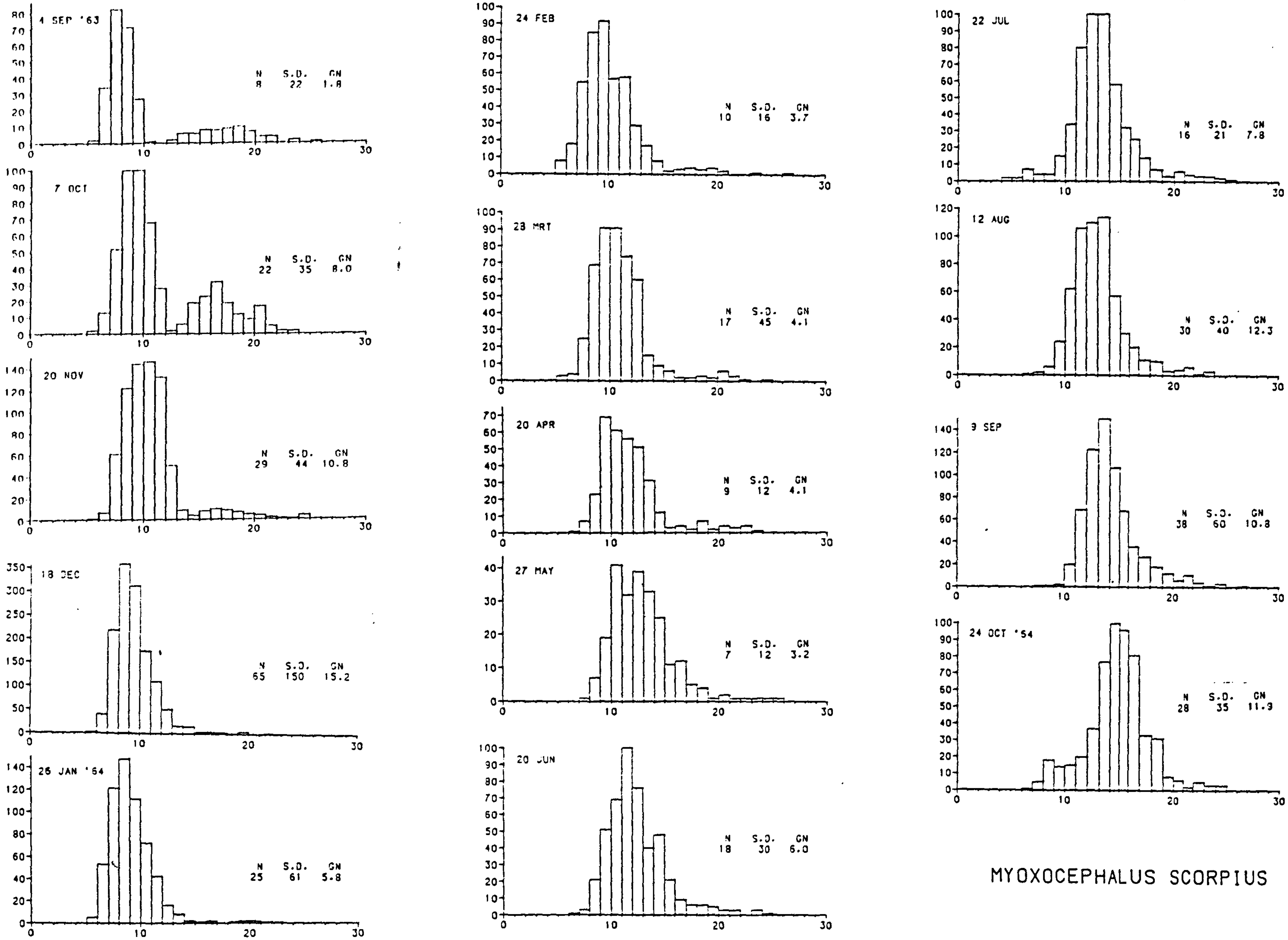
TABLE 11.

Biomass and daily food consumption of Bull-rout and Eelpout in the Wadden Sea in 1963-64. Mean wet weight and metabolic weight (gram) per fish, relative yearclass abundance (%), mean numbers per 1000 m^2 (N), total biomass (ΣW,g wet) and metabolic biomass ($\Sigma W^{0.8}$,g wet) per 1000 m^2. Daily food consumption for maintenance and growth of the fish in Summer (S) and Winter (W) is estimated in gram ash-free dry weight per 1000 m^2.

Date	Mean weight Wwet	$W^{0.8}$	Total n	% of yearclass 64	63	62	61	per area of 1000 m^2 N	ΣW,g	$\Sigma W^{0.8}$	Food, g AFD/day Maint.	Growth
MYOXOCEPHALUS											Maint.	Growth
1963												
Oct.	23.0	11.2	505	-	72	20	8	22	505	246	S: 2.66	3.90
Dec.	11.1	6.7	1906	-	97	2	1	65	718	432	S: 4.67	6.84
											W: 2.30	
1964												
Aug.	26.6	13.4	780	-	92	6	2	30	780	179	S: 1.93	1.77
Sep.	34.9	16.7	1328	-	96	3	1	38	1328	634	S: 6.86	6.28
											W: 3.38	
ZOARCES											Maint.	Growth
1963												
Oct.	10.3	6.2	815	-	87	12	1	41	422	255	S: 1.92	2.81
											W: 1.20	
1964												
Jul.	9.9	5.8	960	55	39	6	-	29	286	169	S: 1.27	1.86
Sep.	11.8	6.9	833	57	34	8	-	51	603	351	S: 2.64	3.86
											W: 1.65	

FIGURE 1. Length distribution of Bull-rout and Eelpout in the dutch Wadden Sea, estimated from monthly trawling surveys on 30 stations. Vertical axis : numbers of measured fish. Mean numbers of fish per 1000 m^2 (N), standard deviations of means (S.D.) and geometric mean numbers per 1000 m^2 (GN) are presented on the right hand side of the histograms. a.Zoarces viviparus b.Myoxocephalus scorpius (other side)





MYOXOCEPHALUS SCORPIUS

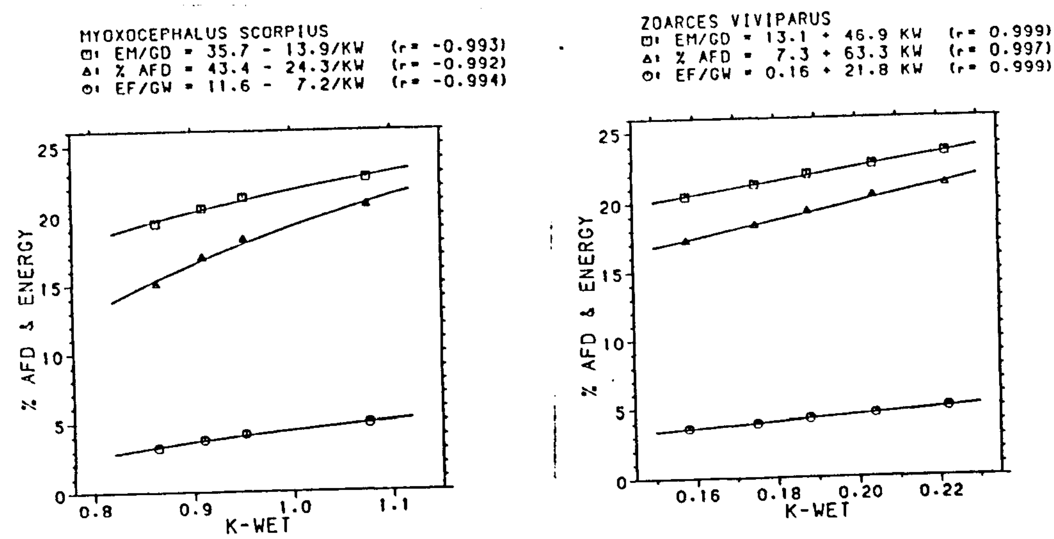


FIGURE 2. Percentage ash-free dry weight (▲)and energy content per gram wet weight (○) or dry weight (□) plotted against condition factor of Bull-rout ($K = 100.W.L^{-3.1}$) and Eelpout ($K = 100.W.L^{-3.25}$)

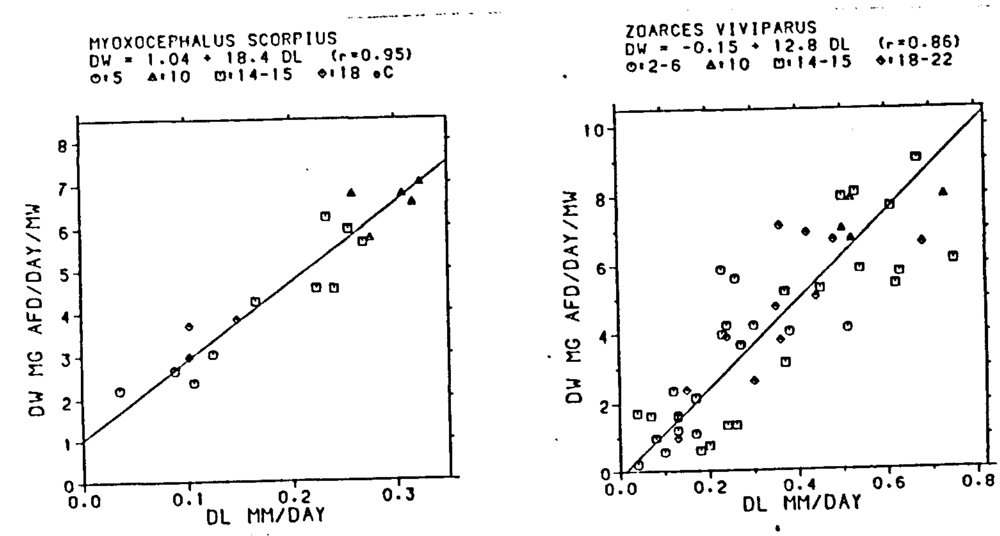


FIGURE 3. A plot of daily weight increment dW, in mg ash-free dry divided by metabolic wet weight of fish (MW = W,g $wet^{0.8}$), against daily growth in length (dL,mm per day) of Bull-rout and Eelpout growing at different temperatures.

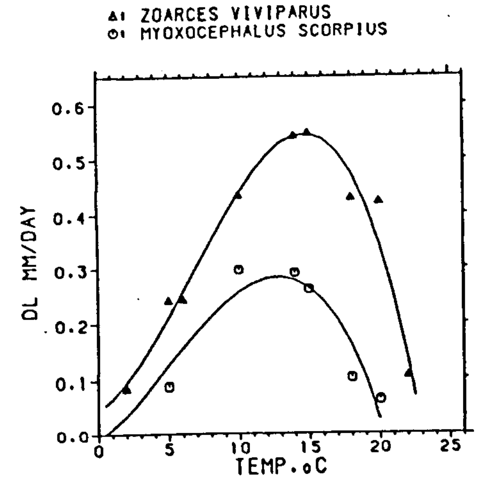


FIGURE 4. Maximum daily growth in length (dL,mm per day) of Bull-rout (○) and Eelpout (▲) growing at different constant temperatures.

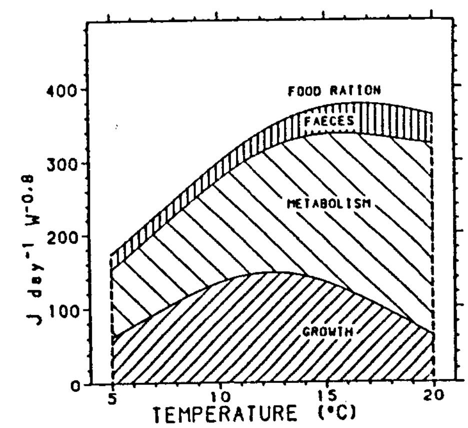


FIGURE 5. Energy budget of maximally fed Bull-rout in relation to water temperature.