The effect of fishmeal supplementation of a straw-based diet on growth and calorimetric efficiency of growth in heifers

BY ISABELLE ORTIGUES[1]*, T. SMITH[1]†, M. GILL[2]‡, S. B. CAMMELL[2] AND N. W. YARROW[1]

[1] *AFRC Institute for Grassland and Animal Production, Shinfield, Reading, Berkshire RG2 9AQ and* [2] *AFRC Institute for Grassland and Animal Production, Hurley, Maidenhead, Berkshire SL6 5LR*

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Thirty-two 160 kg dairy heifers were used to measure the effects of increasing dietary protein content on growth and heat production. A basal diet containing (g/kg) 550 sodium hydroxide-treated straw, 220 barley, 220 sugarbeet pulp and 10 urea was offered with 0, 76 and 152 g fishmeal/kg dry matter of the basal diet (F0, F1 and F2 levels respectively). The three diets were each given at two levels of feeding (low, L; high, H): 57·6 g/d per kg metabolic body-weight ($W^{0.75}$) for the LF0 diet and 74·7 g/d per kg $W^{0.75}$ for the HF0 diet. Apparent digestibility of the diets increased in response to the addition of fishmeal. Mean dry matter digestibility values were 0·67, 0·67, 0·69, 0·66, 0·68 and 0·69 and those for acid-detergent fibre digestibility were 0·60, 0·63, 0·66, 0·58, 0·60 and 0·65 for diets LF0, LF1, LF2, HF0, HF1 and HF2 respectively. Nitrogen retention increased in response to both fishmeal and feeding level. Live-weight gains were 170, 296, 434 g/d for the LF0, LF1 and LF2 diets and 468, 651 and 710 g/d for the HF0, HF1 and HF2 diets respectively. There were significant effects of increasing the plane of feeding and the level of fishmeal in the diet on live-weight gain. Dietary effects on live-weight gains were accompanied by increases in mean energy retention of 23, 45, 82, 94, 160 and 152 kJ/d per kg $W^{0.75}$ for diets LF0, LF1, LF2, HF0, HF1 and HF2 respectively, but no definite evidence was obtained that dietary supplementation with fishmeal modified the efficiency of utilization of metabolizable energy for growth.

Fishmeal: Straw: Energy utilization: Growth: Heifer

Increased growth in cattle in response to fishmeal supplementation has been recorded and responses are consistently larger than those obtained with more degradable nitrogen supplements (Smith *et al.* 1980*a*, *b*; Oldham & Smith, 1981). The magnitude of the response to fishmeal, however, depends on the quality of the basal diet. Thus, with high-concentrate diets (Smith *et al.* 1980*b*) or with high-quality forage diets supplemented with concentrate (Steen, 1985), the responses obtained have been small. On the other hand, with a poorer-quality forage (straw), a marked increase in the weight gain of cattle was noted with a small increment of fishmeal, but a second increment did not elicit any further significant response, even though the highest live-weight gains remained lower than 700 g/d (Smith *et al.* 1980*a*). Presumably in this latter case, growth was limited by the availability of energy.

The efficiency with which energy is utilized for growth is known to be low on forage diets (Agricultural Research Council, 1980), but the results discussed previously suggest that efficiency can be modified by manipulating the balance between absorbed nutrients. One such manipulation is to increase the supply of amino acids to the tissues through supplementation with undegradable protein.

The specific objective of the experiment reported here was, therefore, to determine

Present addresses: * INRA – CRZV Theix, 63122 Ceyrat, France.
† Grassland Research Station, Marondera, Zimbabwe.
‡ ODNRI, Central Avenue, Chatham Maritime, Chatham, Kent ME4 4TB.

simultaneously the effect of different levels of fishmeal supplementation on diet digestibility, live-weight gain and the calorimetric efficiency of this gain (k_f). A straw-based diet was offered to growing heifers at two planes of feeding, either alone or supplemented with two different levels of fishmeal. Preliminary results of this work have been presented (Ortigues *et al.* 1988).

MATERIALS AND METHODS

Experimental plan

The feeding trial lasted 104 d and for the major part of this time, the heifers were housed at the Institute of Grassland and Animal Production's (IGAP) Shinfield facility, in yards, with four animals per yard and with animals being yoked for individual feeding, as described by Smith *et al.* (1980*b*). However, after a minimum of 10 d of adaptation to diet, groups of heifers (four at a time) from the main trial were taken to digestion standings where they remained for 7 d for measurement of diet digestibility and N retention. Thereafter, animals were transported to IGAP's Hurley facility for 2 weeks for measurement of the exchange of respiratory gases by open-circuit calorimetry. Heifers were then brought back to the main yard, where they remained, until completion of the experiment.

Feeds and feeding

The composition of feed constituents offered is presented in Table 1. Chopped winter barley straw was treated with 4·5 g sodium hydroxide/100 g fresh straw, using a sodium hydroxide solution (280 g/l). The unmolassed sugarbeet pulp was purchased from British Sugar plc and the fishmeal (Provimi 66®) from British White Fishmeal Ltd. A mineral supplement (40 g Super Mindif®) was added to each ration daily.

The basal diet consisted of straw, barley, sugarbeet pulp, and a urea–sulphur (95·5:4·5, w/w) mixture in the following proportions 54·7:21·7:22·6:1·0 (by wt, dry matter (DM) basis). Treatment diets differed in the amounts of fishmeal added to the straw-rich basal diet. Levels of fishmeal addition were 0 (F0 diet), 76 (F1) and 152 (F2) g fishmeal DM/kg basal diet DM. These three diets were offered to the animals at two planes of feeding in a 2×3 factorial design. The planes of feeding were calculated for the F0 diet to supply 1·1 and 1·5 times the estimated (from Agricultural Research Council, 1980) maintenance requirements at 160 kg initial live weight for the low (L) and high (H) levels of feeding respectively. The amounts of feed offered to each animal were calculated on the basis of individual metabolic live weights ($W^{0.75}$). Allowances were adjusted weekly using the average of weekly weighings. In case of weight loss from one week to the next, feed allowances were kept unchanged for the following week. The feeds were offered in two equal daily meals, 7 h apart.

Fasting heat production (FHP) was measured on two extra heifers, which were maintained on the F1 diet (low fishmeal), at a daily DM allowance of 71·44 g/kg $W^{0.75}$. Before measurements, the level of feeding was reduced to maintenance over 5 d and kept at maintenance for 7 d. Feeds were then withdrawn for 90 h; water was available at all times. Realimentation was done progressively.

Animals

Thirty-two heifers, aged from 4 to 6 months, and averaging 160 (SEM 1·1) kg initial live weight were used in the experiment. Two were selected on the basis of live weight (one heavy and one light) for measurement of FHP, while the remainder were blocked by weight on the basis of three previous weighings and randomized across six treatment groups with five animals per treatment. The succession of animals through the various measurements

was based on the randomization of an incomplete block design (Cochran & Cox, 1957) to allow for the constraint that only four measurements of digestibility and two of respiratory exchange could be made simultaneously.

Measurements

Intake. Feeds were sampled twice weekly for DM determination at 50° for 48 h. Separate samples were taken each time the rations were weighed out and bulked on a weekly basis. They were then ground through a 1 mm screen to be analysed for ash, total N, acid-detergent fibre (ADF) and gross energy (GE). Refusals were collected daily and were either bulked weekly for the feeding trial, bulked over 5 d but 1 d in advance of the faecal and urine collection, or kept as individual samples during the calorimetric measurements. All refusals were dried (50°, 48 h), ground through a 1 mm screen and analysed for ash, total N and ADF.

Live weight. All yarded animals were weighed twice weekly, 3·5 h after the morning meal. They were also weighed at the end of the balance trial and on the first and last days of calorimetric measurements. Gut fill was estimated from a shrunk body-weight taken on day 105 after 25 and 12 h withdrawal of food and water respectively.

Rumen fluid and blood samples. Rumen fluid was sampled with a tracheal tube 2·5 and 7 h postprandially on days 97 and 98 of the experiment; pH was determined immediately and subsamples were stored at −20° for volatile fatty acid (VFA) analysis. Ammonia-N concentrations were determined on the 2·5 h postprandial samples only, after acidification with a few drops of concentrated sulphuric acid.

Blood was sampled also on days 97 and 98, by jugular puncture 4 h postprandially using EDTA-K_2 as anticoagulant, centrifuged and stored at −20° for analysis of plasma urea-N, glucose and non-esterified fatty acids (NEFA).

Faeces and urine collection. After a minimum of 10 d adaptation to the diets, heifers were moved, in groups of four animals, to digestion standings, for a 5 d total collection of faeces and urine after a 2 d adaptation to the standings (Smith, 1979). Faeces were weighed daily and two subsamples were taken, one (30 g/kg) to be preserved in sulphuric acid (1·5 M) for N determination and the other one (50 g/kg) to be dried at 50° for 48 h and ground through a 1 mm screen for DM, ash, ADF and GE analysis. Subsamples were bulked on a 5 d basis.

Attempts to separate urine and faeces by the introduction and maintenance of urinary catheters proved unsuccessful in these young heifers, and hence for 15 h daily the urine was left to drain down slanted metal trays ('contaminated urine'). During the remaining 9 h, urine was collected manually, directly on urination to obtain a 'pure sample'. Both types of samples were collected in a 2 M-H_2SO_4 solution and bulked over the 5 d. Both urine samples served to give a measure of total urine output, whereas N and GE urinary excretion was determined on the basis of the N and GE contents of the 'pure urine' samples only. Of the total urine output, 318 (SE 15·6) ml/l was collected as 'pure urine'. This technique may partition N and GE excretion between faeces and urine slightly inaccurately but should not affect the results of N balance and energy retention.

Standings and metal trays were washed daily with tap water. Washings were collected, stored in H_2SO_4 (2 M), and analysed for DM and N.

Indirect calorimetric measurement. Respiratory exchanges were measured on two animals at a time with each animal spending 3 d in one of the two calorimetry chambers, the measurements being made on the last 2 d. Flow-rates and gaseous composition (oxygen, carbon dioxide, methane) of air flowing in and out of the chambers were measured as described by Cammell *et al.* (1981) with the modifications according to Cammell *et al.* (1986). A deadspace correction was made but never exceeded 1% of total gas production. Gravimetric calibration of the system showed an average recovery of 95·5% from one of

the chambers. Results pertaining to this chamber were corrected correspondingly. FHP was measured in the middle of the experiment using the two additional heifers. Measurements were made for the last 24 h of a 90 h fast.

Analytical methods

Organic matter (OM) content of the samples was determined by overnight ashing at 550°. ADF was analysed according to Van Soest (1963) after removal of starch as described by Terry & Outen (1973) for the samples which contained starch. GE of all samples was measured in an adiabatic bomb calorimeter. Before this analysis, urine samples were neutralized with NaOH to a pH of 7·5–8·5 followed by freeze-drying. Rumen fluid VFA were analysed by gas–liquid chromatography (Sutton & Johnson, 1969) with isocaproic acid as internal standard. Automated methods were used for rumen NH_3-N (Technicon Instruments), plasma urea (Boehringer Mannheim), plasma glucose (Boehringer Mannheim) and plasma NEFA (Wako Chemicals).

Calculations

Heat production was calculated according to Brouwer (1965) from the observed values for CH_4, O_2 and CO_2 exchange and from the urinary N excretion calculated from the intakes measured on the days of respiratory exchange measurements for each animal and the previously measured proportion of N excreted in the urine.

Efficiency of metabolizable energy (ME) utilization for growth (k_f) at each level of fishmeal was obtained from two methods of analysis. Relationships were fitted between ME intake (MEI) and retained energy (RE) both scaled on the basis of $W^{0.75}$ according to both a linear regression line and the exponential Mitscherlich equation as described by Cammell *et al.* (1986):

$$RE\,(MJ/d) = P3\,(1 - \exp(-P1\,(MEI - P2))), \quad (1)$$

where P1 is the curvature (rate of decrease in efficiency of energy retention with increasing MEI), P2 the estimated ME requirements for maintenance and P3 the asymptote (maximum potential energy retention). At any particular level of MEI, the efficiency of ME utilization (k_f) can be obtained by differentiation of equation 1 with respect to MEI thus:

$$k_f = P1\,P3 \exp(-P1\,(MEI - P2)). \quad (2)$$

Statistical analysis

Data were analysed according to a randomized block design with a 2×3 factorial arrangement of treatments (two planes of feeding × three levels of fishmeal). The linear and quadratic trends of the effects of fishmeal supplements were tested statistically. Missing values due to the unexplained death of one animal and a large refusal during calorimetry were estimated using the GENSTAT computer package and degrees of freedom were modified as appropriate. As the gaseous exchange and derived criteria were calculated separately for each day of measurement (two per animal), all relevant data were analysed according to a split plot design using days as subplots. Parameters derived from the exponential equation were compared by the Student's t test.

RESULTS

Feed composition and intake

The chemical composition of the diet constituents and the average daily intakes for each treatment, expressed on a $W^{0.75}$ basis, are presented in Tables 1 and 2. Within each plane of feeding, the intake of the basal diet (F0) remained similar across treatment groups as

Table 1. *Chemical composition (dry matter basis) of individual feedstuffs and daily amounts of individual feedstuffs offered in each diet (g dry matter/kg metabolic live weight ($W^{0.75}$))*

	Sodium hydroxide-treated straw	Barley	Sugarbeet pulp	Fishmeal	Urea
Chemical composition					
Organic matter (g/kg)	879	974	900	802	ND
Acid-detergent fibre (g/kg)	504	91	174	36	ND
Gross energy (MJ/kg)	17·26	18·48	16·51	20·13	ND
Nitrogen (g/kg)	7·4	21·5	16·7	113	ND
Diet					
LF0	30·6	12·9	12·9	0	0·6
LF1	30·6	12·9	12·9	4·4	0·6
LF2	30·6	12·9	12·9	8·8	0·6
HF0	40·0	17·3	17·3	0	0·7
HF1	40·0	17·3	17·3	6·0	0·7
HF2	40·0	17·3	17·3	12·0	0·7

ND, not determined; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/kg respectively; L, H – low and high levels of feeding respectively.

Table 2. *Average intakes (g/d per kg metabolic live weight ($W^{0.75}$))of heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Diet	Dry matter (g/kg $W^{0.75}$ per d)	Organic matter (g/kg $W^{0.75}$ per d)	Acid-detergent fibre (g/kg $W^{0.75}$ per d)	Gross energy (MJ/kg $W^{0.75}$ per d)	Nitrogen (g/kg $W^{0.75}$ per d)
LF0	57·6	52·1	19·1	0·990	0·964
LF1	61·6	55·3	19·0	1·072	1·456
LF2	65·7	58·6	19·1	1·156	1·936
HF0	74·7	67·9	24·6	1·287	1·263
HF1	80·5	72·4	24·7	1·406	1·917
HF2	85·5	76·4	25·0	1·505	2·536
SEM†	0·40	0·32	0·15	0·0090	0·0140
Statistical significance of treatment effects	PF × F(l)***	PF × F(l)***	PF***	PF × F(l)***	PF × F(l)***

PF, effect of the plane of feeding; F(l), linear effect of fishmeal; PF × F, interaction term; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/kg respectively; L, H – low and high planes of feeding respectively.

*** $P < 0·01$.

† Standard error of treatment means.

indicated by the relatively constant intakes of ADF. Therefore, as planned, differences in DM and N intake within feeding level (L and H) could be attributed mostly to the addition of fishmeal to the diets.

Rumen and blood variables

Rumen fermentation pattern was little influenced by dietary treatments, as indicated by the lack of variation in the (acetate + n-butyrate):propionate ratio (Table 3). Fishmeal supplementation increased rumen NH_3-N concentration linearly with no apparent effect of plane of feeding. Parallel changes in plasma urea concentrations were also observed (Table 3).

On the low plane of feeding, plasma glucose concentrations were increased at the high

Table 3. *Average rumen volatile fatty acid (VFA) concentrations (mM) and molar proportions, molar ratios, acetate+n-butyrate:propionate, and average concentrations of rumen ammonia-nitrogen (mM), plasma urea, glucose and non-esterified fatty acids (mM) in heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Diet...	LF0	LF1	LF2	HF0	HF1	HF2	SEM†	Statistical significance of treatment effects
Total VFA concentrations	78·0	89·5	85·5	71·0	92·0	79·4	7·88	—
VFA molar proportions								
Acetate	0·722	0·718	0·715	0·724	0·728	0·718	0·0064	—
Propionate	0·178	0·171	0·164	0·184	0·170	0·177	0·0057	—
n-butyrate	0·080	0·089	0·098	0·071	0·082	0·084	0·0052	PF**, F(l)***
Acetate+n-butyrate: propionate	4·6	4·8	5·0	4·3	4·8	4·5	0·17	
Rumen NH_3-N	4·53	8·81	12·39	4·72	10·11	13·35	0·644	F(l)***
Plasma urea	3·28	4·77	5·92	2·55	4·60	6·23	0·268	F(l)***
Plasma glucose	4·50	4·53	4·89	4·70	5·53	5·21	0·121	PF × F(q)***
Plasma non-esterified fatty acids	93·6	87·0	109·8	97·4	113·4	113·4	12·57	—

PF, effect of the plane of feeding; F(l), linear effect of fishmeal; F(q), quadratic effect of fishmeal; PF × F, interaction term; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/Kg respectively; L, H – low and high planes of feeding respectively.

** $0{\cdot}01 < P < 0{\cdot}05$, *** $P < 0{\cdot}01$.

† Standard error of treatment means.

fishmeal level only, whereas at the high plane of feeding glucose concentrations were significantly elevated only at the low fishmeal level (HF1). Plasma NEFA were not significantly affected by dietary treatment (Table 3).

Apparent digestibility and N balance

Apparent digestibility of DM in the basal diet averaged 0·66 (Table 4). Fishmeal additions significantly increased DM digestibility of the whole diet but there were no significant effects of plane of feeding. ADF, GE and N digestibilities were all linearly increased by fishmeal supplementation, but there was little effect of elevating the plane of feeding. N balance was linearly increased by fishmeal addition to the diet, as well as by the increase in the plane of feeding.

Animal performance

The initial live weight of the heifers (Table 5) showed some statistically significant differences across treatments which were unexpected on the basis of the live weights used to create blocks. Blocking live weights, obtained the week before the actual start of the trial averaged 154 (SEM 3·1), 155 (SEM 2·5), 155 (SEM 3·0), 156 (SEM 2·7), 156 (SEM 2·8) and 155 (SEM 3·0) kg for diets LF0, LF1, LF2 and HF0, HF1 and HF2 respectively. Adjustment of live-weight gain data using covariance analysis was investigated; however, it did not improve the responses measured and it was not used in the final analysis.

Live-weight gains, calculated by linear regression, were significantly higher at the higher plane of feeding (170 g/d on LF0 and 468 g/d on HF0) (Table 5). Addition of fishmeal to the diets had a positive linear effect ($P < 0{\cdot}01$) on live-weight gains, although the second

Table 4. *Coefficients of apparent digestibility of dry matter, organic matter, acid-detergent fibre, gross energy and nitrogen and N balance (in g/d or g/kg N intake per d) in heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Diet...	LF0	LF1	LF2	HF0	HF1	HF2	SEM†	Statistical significance of treatment effects
Digestibility								
Dry matter	0·672	0·668	0·688	0·655	0·682	0·688	0·0066	F(l)***
Organic matter	0·689	0·694	0·714	0·647	0·702	0·710	0·0095	PF × F(1, q)**
Acid-detergent fibre	0·602	0·634	0·657	0·577	0·601	0·653	0·0176	F(l)***
Gross energy	0·632	0·643	0·669	0·617	0·656	0·669	0·0083	F(l)***
N	0·446	0·519	0·621	0·411	0·569	0·586	0·0196	F(l)***, PF × F(q)*
N balance								
g/d	3·8	10·1	17·4	11·7	24·4	33·5	1·79	F(l)***, PF***
g/kg N intake per d	0·94	1·49	1·85	1·81	2·51	2·60	1·98	F(l)***, PF***

PF, effect of the plane of feeding; F(l), linear effect of fishmeal; F(q), quadratic effect of fishmeal; PF × F, interaction term; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/kg respectively; L, H – low and high planes of feeding respectively.

* $0{\cdot}05 < P < 0{\cdot}10$, ** $0{\cdot}01 < P < 0{\cdot}05$, *** $P < 0{\cdot}01$.

† Standard error of treatment means.

Table 5. *Initial and final live weights (kg), live-weight gains (g/d), gut fill (as a proportion of final live weight) and body scores of heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Diets...	LF0	LF1	LF2	HF0	HF1	HF2	SEM†	Statistical significance of treatment effects
Live weight								
Initial	156	159	159	164	162	161	0·8	PF × F(l)***
Final	175	190	209	212	229	235	2·7	PF***, F(l)***
Live-weight gain	170	296	434	468	651	710	29·0	PF***, F(l)***
Gut fill	0·068	0·063	0·071	0·073	0·067	0·077	0·0069	

PF, effect of the plane of feeding; F(l), linear effect of fishmeal; F(q), quadratic effect of fishmeal; PF × F, interaction term; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/kg respectively; L, H – low and high planes of feeding respectively.

* $0{\cdot}05 < P < 0{\cdot}10$, ** $0{\cdot}01 < P < 0{\cdot}05$, *** $P < 0{\cdot}01$.

† Standard error of treatment means.

increment of fishmeal at the high plane of feeding (HF2 diet) appeared to elicit a smaller response than the first increment (HF1 diet). Results for the HF2 diet, however, were associated with a large standard error. Since gut fill represented a relatively constant proportion of live weight the differences in live-weight gain among treatment groups were not artefacts due to differences in gut fill (Table 5).

Table 6. *Mean live-weights of the animals over the balance period (kg), gross energy intake and partition of energy utilization (kJ/d per kg metabolic live weight ($W^{0.75}$)) during the measurements of respiratory exchanges in heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Diets...	LF0	LF1	LF2	HF0	HF1	HF2	SEM†	Statistical significance of treatment effects
Live weight	161	169	178	189	188	193	3·6	PF***, F(l)**
Gross energy intake	1033	1116	1180	1343	1430	1481	24·0	PF***, F(l)***
Energy losses								
Faeces	382	398	390	505	493	491	14·3	PF***
Urine	24	30	36	24	32	36	1·6	F(l)***
Methane	92	88	90	106	108	108	24·5	PF***
Heat	512	555	580	615	636	693	10·3	PF***, F(l)***
Energy retention	23	45	82	94	160	152	13·5	PF***, F(l)***

PF, effect of the plane of feeding; F(l), linear effect of fishmeal; F(q), quadratic effect of fishmeal; F0, F1, F2 – 0, 76 and 152 g fishmeal DM/kg respectively; L, H – low and high planes of feeding respectively.
* $0{\cdot}05 < P < 0{\cdot}10$, ** $0{\cdot}01 < P < 0{\cdot}05$, *** $P < 0{\cdot}01$.
† Standard error of treatment means.

Partition of energy intake

The partition of GE intake as determined by calorimetry is presented in Table 6. Urinary energy represented 1·8–3·0 % of the GE intake, as previously reported for straw diets (Robb *et al.* 1980). CH_4 production by the heifers remained unchanged with fishmeal supplementation and could be considered to be a function of the level of feeding of the basal diet alone. Energy retention was significantly increased with both plane of feeding and fishmeal supplementation.

Metabolizability of the diets (ME:GE) was elevated at the high plane of feeding ($P < 0{\cdot}10$) and increased linearly with fishmeal ($P < 0{\cdot}01$). Values averaged 0·518, 0·538, 0·562 and 0·527, 0·557 and 0·571 (SEM 0·0088) for diets LF0, LF1, LF2 and HF0, HF1 and HF2 respectively. Thus, ME intakes were 535, 600, 662, 709, 797 and 845 (SEM 16·7) kJ/d per kg $W^{0.75}$ for diets LF0, LF1, LF2, HF0, HF1 and HF2 respectively.

FHP

The FHP values were 19·49 and 17·76 MJ/d for each of the two animals. These values corresponded to 0·392 and 0·357 MJ/d per kg $W^{0.75}$.

Efficiency of ME utilization for growth

The calorimetric efficiencies of ME utilization for growth at each of the three levels of fishmeal were first examined by fitting linear regression lines to the data (Table 7). These linear relationships accounted for 76·3, 83·6 and 59·2 % of the total variance for the F0, F1 and F2 diets respectively. Comparison of slopes showed that the efficiency of ME utilization for growth was increased ($P < 0{\cdot}05$) by the first increment of fishmeal but was lower with the second increment of fishmeal to a value not significantly different from that of the basal diet (F0). From these relationships the ME requirements for maintenance were extrapolated to be higher with the F1 diet than with the F0 or F2 diets. However, the Agricultural Research Council (1980) definition of k_f confines its derivation to energy retention values above maintenance. The two daily energy retention values for one heifer on treatment LF1 were markedly negative and when these were excluded from the

Table 7. *Equations relating energy retention and metabolizable energy (ME) intake (MEI) (both in MJ/kg metabolic live weight ($W^{0.75}$) per d) for heifers offered straw-based diets at two planes of feeding and supplemented with different levels of fishmeal*

Fishmeal level...	None		Low				High	
n*...	8		10		9		10	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Linear regression								
Slope	0·413[a]	0·0588	0·636[b]	0·0644	0·525	0·0576	0·377[a]	0·0705
Intercept	−0·192[a]	0·0369	−0·341[b]	0·0454	−0·256	0·0416	−0·167[a]	0·0536
ME_m	0·465	—	0·536	—	0·488	—	0·443	—
r	0·882	—	0·919	—	0·916	—	0·783	—
RSD	0·0210	—	0·0292	—	0·0224	—	0·0312	—
Curvilinear model								
P1	1·591[a]	0·3939	0·285[b]	0·3154	0·773	0·2588	1·308[a]	0·4098
P2	0·479[a]	0·0172	0·535[b]	0·0780	0·501	0·0159	0·493[ab]	0·0291
P3	0·328[a]	0·0996	2·288[a]	2·6299	0·792	0·2858	0·413[a]	0·1413
Predicted efficiency at MEI (MJ/kg $W^{0.75}$ per d) of:								
0·5	0·504[a]	0·0461	0·656[b]	0·0302	0·613	0·0329	0·535[a]	0·0406
0·6	0·430[a]	0·0557	0·638[b]	0·0470	0·567	0·0456	0·470[a]	0·0548
0·7	0·367[a]	0·0616	0·621[b]	0·0631	0·525	0·0574	0·412[a]	0·0651
0·8	0·313[a]	0·0646	0·604[b]	0·0785	0·486	0·0675	0·361[a]	0·0721

ME_m, estimated ME requirements for maintenance (MJ/kg $W^{0.75}$ per d); RSD, residual standard deviation; P1, rate of decrease in k_f with increasing MEI; P2, estimated ME requirements for maintenance; P3, maximum potential energy retention.

[a,b] Mean values in the same horizontal row with different superscript letters were significantly different ($P < 0·05$). When comparisons were made using n 9 for the low-fishmeal diet, differences were not significant.

* No. of animals per treatment; n 9 for the low-fishmeal diet corresponds to the removal of one heifer that presented a negative energy balance.

analysis, the efficiency value for F1 decreased to 0·525 (Table 7), although the percentage of the variation accounted for was little changed (82·8% compared to 83·6%). The efficiency value for F1 no longer differed from that for F0 or F2.

The exponential model was then fitted to the data for each level of fishmeal using the two measured values of FHP as additional data points, although the model was not constrained to pass through these points (Table 7). The derived equations accounted for 97·9, 96·6 and 95·8% of the total variance for the F0, F1 and F2 diets respectively. P1, the rate of decline of k_f with increasing MEI, was significantly decreased with the F1 diet as compared with the F0 or F2 diets. Consequently the calculated efficiencies of ME utilization were significantly elevated with the first increment of fishmeal, but dropped significantly with the F2 diet to values close to the efficiencies obtained with the basal diet. Efficiency values should be compared in the range of ME intakes which was common to any level of fishmeal, i.e. about 0·6–0·7 MJ/d per kg $W^{0.75}$. Table 7 included a larger range of intakes to give the general trends. In a similar manner to the results obtained with the linear relationships, the calculated ME requirements for maintenance (P2) were significantly higher with F1 than with F0 diet, but decreased to intermediate values with F2. The standard error attached to the P3 value of the F1 diet was very large, mostly because of the negative energy retentions from one heifer. Exclusion of these data from the analysis changed the percentage of variance explained to 98·0% and resulted in the differences in

k_f between diets being no longer significant ($P < 0{\cdot}05$). The difference in estimated maintenance requirements was also decreased (Table 7). Thus, the results suggest a tendency for the first increment of fishmeal to increase the efficiency of utilization of ME and the maintenance requirement of the animals but the statistical significance of these results appeared to relate to the data from one particular heifer.

DISCUSSION

Addition of the higher level of fishmeal to a fixed straw basal diet doubled total N intake. It increased the predicted (Agricultural Research Council, 1984) rumen degradable N (RDN) intake from 33 to 54 g/d at the low plane of feeding and from 46 to 74 g/d at the high plane of feeding. It also increased the undegradable N intake from 4 to 33 g/d at the low plane of feeding and from 6 to 46 g/d at the high plane of feeding. These calculations assumed N degradability values of 0·5, 0·8, 0·8 and 0·4 for straw (Smith, 1978), barley, sugarbeet pulp and fishmeal (Agricultural Research Council, 1980) respectively. In addition, the undegradable straw N was considered to be unavailable for absorption (Whitelaw *et al.* 1986).

As a response to these predicted changes, live-weight gains increased by 264 g/d at the low plane of feeding and by 247 g/d at the high plane of feeding. Live-weight gains increased with successive increments of fishmeal, although at the higher plane of feeding the response to the second increment of fishmeal was smaller than that to the first increment. In a previous experiment with equivalent levels of fishmeal supplementation to straw diets, live-weight gains of heifers fed at about 1·5 times maintenance were found to level off significantly at the higher level of fishmeal (Smith *et al.* 1980*a*).

These differences in live-weight gain are discussed in relation to diet digestibility and nutrient supply and to the partition of energy utilization.

Diet digestibility and nutrient supply

Addition of fishmeal to the basal diet enhanced DM, OM and GE digestibilities, mostly through an increase in ADF digestibility. The increased ADF digestion could have taken place in the large intestine, as shown previously (Ortigues *et al.* 1988). The elevated RDN supply to the rumen, as indicated by the higher rumen NH_3 concentrations, could also have caused the elevated diet digestibility. By contrast the higher plane of feeding did not significantly modify the digestibility of the diets. The high level, however, only reached 1·9 times the maintenance requirements, compared with 1·1 times maintenance at the low level. Rate of passage of digesta through the tract may not have been sufficiently modified by such differences to induce changes in digestibility (Vermorel & Bickel, 1980).

An interaction between the plane of feeding and the level of fishmeal supplementation was noted for OM digestibility. It paralleled a similar effect observed for plasma glucose concentration. The smaller response in digestibility to fishmeal between LF0 and LF1 on the one hand and between HF1 and HF2 on the other hand appeared to have been reflected in terms of live-weight gain at the high plane of feeding only. A limited energy supply relative to the N supply (Balch, 1967) could account for the tendency of the live-weight gains to plateau with the HF2 diet only.

N digestibility and balance were increased by fishmeal supplementation. In an experiment with similar straw diets, an elevated amino acid supply to the duodenum of steers supplemented with 110–120 g fishmeal/kg dietary DM was observed (Ortigues *et al.* 1988). Other experiments, however, have reported a reduction in the increase in amino acid supply with successive increments of fishmeal added to silage-based diets (Cottrill *et al.* 1982; Gill & Beever, 1982; Rooke & Armstrong, 1987). Thus, the tendency for live-weight gains to plateau with the HF2 diet could also be due to a smaller increment in amino acid supply.

Both the changes in total energy supply and in N supply could explain the responses in live-weight gain obtained. Whether total nutrient supply or the balance of nutrients supplied was responsible for the effects observed remains to be determined. In a previous experiment, supplementation of a straw diet with fishmeal at a level intermediate between F1 and F2 resulted in an increase in the proportion of ME originating from absorbed amino acids (Ortigues *et al.* 1988). Other experimental results would support the hypothesis that the balance of nutrients was a determining factor of the response to fishmeal. For example, it has been shown that growing beef bulls offered a concentrate diet containing 120 g crude protein (N × 6·25; CP)/kg DM had fatter carcasses than bulls offered diets containing 100 or 140 g CP/kg DM and deposited less carcass protein than those offered the 140 g CP/kg DM diet (Anderson *et al.* 1988).

Partition of energy utilization

The efficiency of ME utilization of the basal diet for growth was found to be comparable to that reported previously for straw-based diets (Wainman *et al.* 1975; Robb *et al.* 1980). However, while efficiency appeared to increase (not significantly) in response to the first increment of fishmeal, this increase was apparently lost with the second increment. Contradictions already exist in the literature with respect to the effect of dietary protein content on efficiency of ME utilization for growth. Negative or inconclusive results have been reported by Walker & Norton (1971), Barry (1981) and Thomson *et al.* (1983), while positive relationships were found by Blaxter & Boyne (1978) and Ribeiro *et al.* (1981). A more specific response to increased protein supply was shown by MacRae *et al.* (1985), who infused casein into the abomasum of mature sheep offered an autumn-harvested grass which increased efficiency values from 0·45 to 0·57. Responses to protein supplementation in terms of energy utilization appear to depend on the physiological state of the animal (Ørskov *et al.* 1976) and on the balance of nutrients (Hartsook & Hershberger, 1971; MacRae & Lobley, 1986). Theoretical explanations of these results were presented in a simulation exercise by Black *et al.* (1987) which indicated the importance of considering the overall balance of nutrients available to the tissues. A similar exercise (Ortigues, 1987) was conducted using values from the present experiment and the assumptions collated by Gill *et al.* (1984). The main conclusions reached were that: (1) when ATP formed from acetate oxidation is used for protein deposition, rather than being dissipated, energetic efficiency is increased; (2) energetic efficiency decreases when acetate becomes limiting, as amino acids are then the main carbon and ATP sources; and (3) energetic efficiency is increased when the proportion of amino acids metabolized through gluconeogenesis is increased and when the proportion of glucose metabolized through the pentose phosphate pathway increases. In planning the experiment on this basis, it was hypothesized that an increase in efficiency would be measured with F1 as a result of a reduction in wasteful oxidation of acetate and enhanced tissue deposition, while a lack of response might be obtained with the second increment of fishmeal if maximum protein deposition had been reached with the F1 diet or if acetate (energy) had become limiting or both. The present results do not unequivocally support this hypothesis because of the large between-animal variability. No explanation can be provided for the negative energy balance noted with one heifer on treatment LF1 but obviously such a variation in the data limits the conclusions drawn as to the effect of fishmeal supplementation on k_f.

The exponential nature of energy exchanges in animals offered different planes of nutrition has been shown (Blaxter & Boyne, 1978; Cammell *et al.* 1986) and in the present experiment, the exponential model accounted for a greater proportion of the variance than the linear model. However, the relatively small range of MEI achieved with a straw-rich diet did not permit an adequate description of curvilinearity in the data, such that some of

the parameters of the curves were calculated with a large error term (e.g. potential energy retention). Theoretically the exponential model has the advantage of permitting the efficiency of ME utilization to vary with change in growth rates and the associated changes in body composition, arising from modifying the level of intake (Geay & Robelin, 1979). The present curvilinear relationships were defined using FHP values for animals stabilized on the F1 diet only. A more generalized use of the exponential model would require measurements of heat production in animals fully adapted to sub-maintenance levels of feeding.

In conclusion, no definite evidence could be obtained that the improvement in animal growth performance resulting from dietary supplementation with fishmeal was accompanied by changes in the efficiency of energy utilization. Further work is, therefore, required to measure both body composition and the supply of nutrients in order to achieve a full interpretation of the potential response to supplementation.

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