Journal of Fish Biology (1998) **52,** 962–972

Energy allocation in larval and juvenile *Coregonus lavaretus*: validation of a bioenergetics model

H. HUUSKONEN*, J. KARJALAINEN*, N. MEDGYESY† AND W. WIESER†

**Karelian Institute, Department of Ecology, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland and †Institut für Zoologie, Universität Innsbruck, Technikerstrasse 25, A-6020 Innsbruck, Austria*

(*Received 7 July 1997, Accepted 8 January 1998*)

Food consumption and energy allocation of larval and juvenile whitefish *Coregonus lavaretus* L. were studied by conducting respirometry experiments at 10, 12 and 15° C. Results from these experiments were compared with those predicted by a bioenergetics model that used observed growth as the major input. The data were used to assess the performance of the model, and evaluate its suitability for estimation of food consumption by whitefish. The mean absolute % error (ε) between observed and predicted food consumption was 16·3%, and the modelling efficiency (M_E) was 0·90, indicating that the model was reasonably robust. Linear regression analysis of predicted *v.* observed food consumption values gave a slope slightly above unity, indicating a tendency for the model to overestimate consumption at higher values. ε and M_E were also calculated for total metabolic rate (R_T), and they equalled 13·0% and 0·85, respectively. Despite some deficiencies, it is concluded that the model can be used for prediction of food consumption by highly active, planktivorous fish such as whitefish.

Key words: food consumption; bioenergetics; respirometry; *Coregonus lavaretus*; whitefish; energy partitioning.

INTRODUCTION

Predator–prey relationships are the main interactions between different components of aquatic ecosystems. The effects of fish on their prey are determined by abundance and species composition, and by the intensity of predation. Thus, an important aspect in ecological studies is the ability to estimate accurately the food consumption of fish. The two most common methods for estimating food consumption have a basis in stomach content analysis and gastric evacuation rates (Eggers, 1977; Elliott & Persson, 1978; Olson & Mullen, 1986; Boisclair & Leggett, 1988; Héroux & Magnan, 1996) or estimation of the energy budgets of individual fish (Kitchell *et al.*, 1977; Hewett & Johnson, 1992). Both methods have weaknesses; stomach content analyses and evacuation studies are laborious and time consuming, whereas the construction of bioenergetics models requires intensive laboratory studies for parameter estimation. Once constructed, however, bioenergetics models are easy to run on modern computers (Hewett & Johnson, 1992; Ney, 1993).

Several bioenergetics models have been constructed for estimating food consumption or growth in fish species (e.g. Hewett & Johnson, 1992). The majority of models have been developed for adult fish, and, due to differences in mass-specific parameters and energy densities, they are not directly applicable to

‡Tel.: +358-13-2513480; fax: +358-13-2513449; email: hannu.huuskonen@joensuu.fi

0022–1112/98/050962+11 $25.00/0/jb980644

early life-history stages (Hewett & Johnson, 1992). In recent years, however, bioenergetics models have also been constructed for larval and juvenile fish (e.g. Post, 1990; Karjalainen *et al.*, 1997*a*,*b*). The models have also become more elaborate as attempts are made to describe the dynamic processes affecting the fate of ingested energy (Ney, 1993). As the number of model parameters increases however, the potential for errors in model output may also rise (Ney, 1993). In spite of that, models are often applied uncritically, and seldom has the accuracy of predictions been evaluated (Ney, 1993).

During the past few years, we have studied metabolism and energy allocation in young coregonids to collect data for bioenergetics modelling (Karjalainen *et al.*, 1995, 1996, 1997*a*,*b*; Hanel *et al.*, 1996; Huuskonen & Karjalainen, 1997). The present study applied a bioenergetics model based on that developed by Hewett & Johnson (1992) to larval and juvenile whitefish *Coregonus lavaretus* L. It was then determined how well model predictions for food consumption derived from observed growth coincided with food consumption observed under experimental conditions. In addition, with simultaneous recording of oxygen consumption it was possible to compare observed and simulated energy allocation. The experiments were independent of those used for parameter development, thereby allowing the assessment model performance and its suitability for estimation of food consumption in an active, planktivorous fish species, the whitefish.

MATERIALS AND METHODS

FISH

Whitefish used in this study originated from two populations: Lake Pyhäselkä in eastern Finland and Lake Constance on the border between Austria, Germany and Switzerland. Although these whitefish differ in origin, no differences in muscle morphology or respiration rate have been detected between fish of the two populations (Hanel *et al.*, 1996). Larvae and juveniles were reared from artificially fertilized eggs at the University of Joensuu, Finland, and at the University of Innsbruck, Austria. In Joensuu the fish were maintained at 12° C in 45-l flow-through glass aquaria. They were fed on *Artemia* nauplii once every hour during the light phase (from 0900 to 0300 hours) *via* an automatic feeding system. In Innsbruck the rearing temperatures were 5 and 15° C. The volume of flow-through aquaria was 60 l, and the photoperiod was 16L : 8D. In both places, the aquaria were cleaned once a day by siphoning faeces and uneaten *Artemia* from the bottom.

RESPIROMETRY

Oxygen consumption was measured in the feeding respirometer described in detail by Wieser & Medgyesy (1990*a*). Briefly, the flow of water through the fish chamber is closed at intervals and the mass-specific oxygen consumption (μmol g^{-1} h^{-1}) is calculated from oxygen depletion measured by a YSI 5750 polarographic oxygen sensor (POS). When the chamber is not in a measurement phase, the POS and chamber are flushed with aerated water.

Each experiment lasted for 3–5 days (Table I). The experiments at 10 and 15° C were carried out in Innsbruck in 1991 and those at 12° C in Joensuu in 1995–1996. For experiments conducted in Joensuu the day was divided into eight feeding periods, nine non-feeding periods in the light and six non-feeding periods in the dark. At the beginning of each feeding period, a known number of *Artemia* nauplii was introduced into the fish chamber of the respirometer, and the oxygen consumption of the feeding fish (three to seven fish depending on size) was recorded for 40 min. The remaining nauplii and fish

TABLE I. Summary of feeding respirometer experiments

T (° C)	M_F (mg)	n	Duration (days)	G (%M_F day^{-1})	C (J ind^{-1})	Q (J ind^{-1})	R_S (J ind^{-1})	R_F (J ind^{-1})	A_E (%)
10	19	53	4	4·7	63 (15)	13 (21)	12 (19)	7 (11)	51
	21	55	4	8·2	74 (16)	31 (42)	14 (19)	9 (12)	73
	29	39	4	5·6	114 (22)	36 (32)	17 (15)	10 (9)	55
	42	34	4	6·2	141 (24)	58 (41)	25 (18)	17 (12)	71
	43	34	4	7·5	136 (22)	52 (38)	24 (18)	21 (15)	71
	65	31	4	5·5	178 (26)	103 (58)	33 (19)	32 (18)	94
	70	29	4	3·6	197 (25)	38 (19)	41 (21)	24 (12)	65
	82	29	4	4·1	186 (25)	54 (29)	43 (23)	28 (15)	67
	88	23	4	2·9	272 (36)	48 (18)	43 (16)	35 (13)	46
12	25	17	4	6·6	87 (15)	31 (36)	18 (21)	11 (13)	69
	150	3	3	1·3	159 (20)	33 (21)	56 (35)	17 (11)	67
	421	4	4	5·8	945 (46)	494 (52)	256 (27)	69 (7)	87
	755	3	3	1·2	819 (61)	128 (16)	284 (35)	59 (7)	58
15	7	68	5	16·1	55 (8)	26 (47)	9 (16)	8 (15)	78
	9	63	4	16·0	77 (14)	27 (35)	10 (13)	7 (9)	57
	10	66	5	13·8	65 (8)	26 (40)	11 (17)	12 (18)	75
	19	49	3	11·1	68 (14)	26 (38)	14 (21)	8 (12)	71
	21	49	3	10·4	73 (21)	25 (34)	16 (22)	7 (10)	66
	25	40	4	12·8	149 (19)	78 (52)	30 (20)	18 (12)	85
	25	40	4	11·0	141 (18)	65 (46)	26 (18)	16 (11)	76
	59	23	4	12·0	252 (23)	145 (58)	68 (27)	34 (13)	98
	67	24	4	8·3	260 (24)	142 (55)	62 (24)	32 (12)	91

T, Temperature; M_F, mean fresh mass of fish at the beginning of the experiment; n, number of fish; G, specific growth rate; C, food consumption [percentage of maximum consumption (C_{max}) in parentheses]; Q, growth [percentage of C ($=K_1$) in parentheses]; R_S, standard metabolic rate (percentage of C in parentheses); R_F, feeding-induced thermogenesis (percentage of C in parentheses); A_E, assimilation efficiency.

faeces were then flushed into the collecting chamber over an interval of 20 min. During the following non-feeding period oxygen consumption of the fish was measured in the absence of food. The last feeding took place at midnight. This was followed by eight non-feeding periods, of which the last six were in the dark. Each morning at 0900 hours the fish were removed from the respirometer and placed in an aquarium, the collecting chamber was emptied and the bacterial oxygen consumption of the empty respirometer system was determined. Experiments in Innsbruck followed a similar protocol to those in Joensuu, with the following exceptions. For bacterial measurement the fish (23–68 individuals) were removed from the respirometer, and when the fish were replaced into the respirometer at 0800–0900 hours the light was switched off. At 1600 hours, light intensity was increased and full brightness was reached within the 20-min flushing period of the respirometer. Meanwhile known numbers of *Artemia* were put into the feeding reservoir ready for the experiment. Eight feeding periods followed by seven non-feeding periods, were run until the following morning.

Two methods were used for investigating fish growth. For small fish (fresh mass under about 70 mg), the initial fresh mass (M_F) and dry mass (M_D) were estimated from data collected for aliquots of fish from same group as those used in the experiments. M_D was determined after drying the fish at 80° C for 24 h. For larger fish, the growth of the fish used in the experiments was determined directly. On the day preceding each experiment, the fish, which had been fasted for 12–18 h, were anaesthetized with tricaine, dried gently on blotting paper and M_F was measured by transferring the fish to a container with a small amount of water. After weighing, the fish were allowed to recover, without feeding, overnight. After the experiments the fish were narcotized and M_F (all fish) and M_D (small fish) determined.

Food consumption was calculated as the difference between the number of *Artemia* added to the fish chamber and the number found uneaten in the collecting chamber. The volume of water collected was determined first, and by subsequent counting of the numbers of *Artemia* in four to five samples under a binocular microscope, an estimate of the total number of *Artemia* was obtained. The fish were fed in excess, and a substantial proportion of the *Artemia* remained uneaten during a feeding period.

CALCULATIONS

Three components of the energy budget could be determined directly: food consumption (C), total metabolism (R_T) and growth (Q). Further, it was possible to separate total metabolic rate (R_T) into standard metabolic rate (R_S) and feeding-induced thermogenesis (R_F), i.e. the energy used for maintenance was distinguished from costs related to activity and the digestion, absorption and processing of food (Wieser & Medgyesy, 1990*b*). Metabolic rates were calculated as in Wieser & Medgyesy (1990*b*): (1) R_T = sum of all oxygen consumption measurements recorded hourly; (2) R_S = the average of the three lowest values during the dark period multiplied by the number of hours during an experiment; and (3) $R_F = R_T - R_S$. The following calculations were used to convert oxygen consumption and somatic growth into energy units: 1 µmol O_2 = 0·45 J and 1 mg M_D = 22·7 J (Wieser & Medgyesy, 1990*b*). For the large fish, M_F was converted directly into joules according to the following equation:

$$E = 4{\cdot}484\ M_F^{1{\cdot}107}$$

where E is the energy content (kJ) and M_F the fresh mass (g) of the fish (P. Muje, pers. comm.; $n = 353$, $r^2 = 0{\cdot}991$).

The efficiencies with which food was assimilated (assimilation efficiency, A_E) and utilized for growth (gross conversion efficiency, K_1) were calculated according to the following equations:

$$A_E = 100(Q + R_T)/C$$

$$K_1 = 100(Q/C)$$

where Q is growth, R_T is total metabolic rate, and C is food consumption, all expressed in terms of energy (J).

TABLE II. Parameter values used in a bioenergetics model for whitefish. (sources of data are given as footnotes)

Symbol	Parameter description	Value
Consumption, C_{max} g g^{-1} day^{-1}		
C_A	Intercept for C_{max}	0·07692*
C_B	Coefficient, C_{max} *v.* M_F	−0·61966*
C_Q	Coefficient e^{c*T}	0·08007*
Metabolism, R gO_2 g^{-1} day^{-1}		
R_A	Intercept for routine rate of R	0·00584†
R_B	Coefficient, routine rate of R *v.* M_F	−0·05341†
R_Q	Coefficient, R *v.* temperature	0·05060†
A	Coefficient, activity	1†
S	Coefficient, specific dynamic action	0·17‡
Egestion		
F	Proportion of consumed energy egested	0·19‡§
Excretion		
U	Proportion of absorbed energy excreted	0·07‡§
Energetic content		
Artemia	Energy content J gM_F^{-1}	2625 ¶
Fish	Energy content J gM_F^{-1}	4286 ¶

*Karjalainen *et al.* (1997*a*); †Karjalainen *et al.* (1995); ‡Hewett & Johnson (1992); §Dabrowski *et al.* (1988); ¶Karjalainen *et al.* (1997*b*).

BIOENERGETICS MODEL

The components of the bioenergetics model are those of the balanced energy equation (Kitchell *et al.*, 1977; Hewett & Johnson, 1992):

$$C = C_{max} * p * f(T) = Q + R * f(T) * A + (C - F) * S + U,$$

where C is food consumption rate; C_{max} is maximum consumption rate; p is a proportionality coefficient; $f(T)$ is a function of temperature dependence; Q is growth during the modelling period; R is metabolic rate; A describes the effect of activity on metabolic rate; S is the proportion of energy utilized to process absorbed food; F is egestion; and U is excretion. The computer version of the general bioenergetics model (Hewett & Johnson, 1992) was applied to estimate food consumption. All calculations in the model are based on specific rates (g of food per g of fish per day) based on fresh mass (M_F), and parameter values are presented in Table II.

In modelling simulations, consumption was adjusted by changing the proportionality coefficient (p) until predicted growth matched observed growth (Hewett & Johnson, 1992). The maximum consumption rate (gM_F gM_F^{-1} day^{-1}) was expressed as a power function of mass and temperature ($C_{max} = C_A M_F^{C_B} e^{C_Q T}$, the explanations of the parameters being given in Table II). Data for maximum food consumption by vendace *Coregonus albula* L., were used for fitting the C_{max}-function (Karjalainen *et al.*, 1997*a*). The C_{max}-function assumes no upper temperature limit for food consumption, i.e. it should only be used at temperatures between 6° and 18° C (Karjalainen *et al.*, 1997*a*).

Metabolic rate (R) of larvae was also described as a function of mass and temperature ($R = R_A M_F^{R_B} e^{R_Q T} A$, Table II) according to Karjalainen *et al.* (1995). The temperature

TABLE III. Validation of the bioenergetics model. The difference between predicted and observed values is expressed as mean absolute % error (ε)

Energy budget component	ε	M_E	Linear regression		
			Slope	Intercept	r^2
Food consumption	16·3	0·90	1·13*	− 18·4 NS	0·943
Total metabolic rate	13·0	0·85	1·34***	− 10·9**	0·992

Statistical testing of the model includes modelling efficiency (M_E) and linear regression analysis of predicted *v*. observed data. Statistical deviations of the slope from 1 and the intercept from 0 were tested by *t*-test; NS, Not significant; *$P<0·05$; **$P<0·01$; ***$P<0·001$.

dependence of metabolic rate has been investigated for temperatures between 4 and 24° C (Karjalainen *et al.*, 1995). Specific dynamic action (S), egestion (F) and excretion (U) were set as constant proportions of food consumption (Table II). Coefficient A was 1 and, thus, the activity of fish was assumed to be included in the routine respiration rate.

Constant energy densities (J gM_F^{-1}) of fish and prey were assumed, the energy densities measured by bomb calorimetry being 4286 and 2625 J gM_F^{-1} for whitefish and *Artemia*, respectively (Table II).

The model was tested by the comparison of observed and predicted food consumption. The ability of the model to predict total metabolic rate was also evaluated by comparing observed values (R_S+R_F) with those predicted by the model ($R+S$). Five criteria were used for validation (Mayer & Butler, 1993: mean absolute % error ($\varepsilon=100[\Sigma(|y_o-y_p|/|y_o|)]/n$, where y_o represents observed values, y_p predicted values and n the number of pairs), modelling efficiency [$M_E=1-\Sigma(y_o-y_p)^2/\Sigma(y_o-y_m)^2$, where y_o and y_p are the same as above and y_m is the mean of observed values], regression coefficient (r^2) of linear regression between predicted and observed values and the location of the regression line (slope, intercept).

RESULTS

ENERGY ALLOCATION

The specific growth rate (G) ranged from 2·9 to 8·2% at 10° C, from 1·2 to 6·6% at 12° C and from 8·3 to 16·1% at 15° C (Table I), and the generalized energy budget for young whitefish could be described as (mean ± S.D.):

$$C(100)=F+U(29\pm14)+R_S(21\pm6)+R_F(12\pm3)+Q(38\pm13).$$

Thus, the fish allocated a larger proportion of ingested energy to growth than to metabolism, and Q was the largest component of the energy budget.

BIOENERGETICS MODEL

The M_E of the bioenergetics model was 0·90 and ε 16·3% for food consumption (Table III, Fig. 1). Regression analysis of predicted *v*. observed food consumption gave a regression line with a slope slightly above and significantly different from unity (*t*-test, $P<0·05$), but the intercept did not differ from zero (*t*-test, $P>0·05$). Validation criteria calculated for total metabolic rate indicated a tendency for the model to provide overestimates: the slope and intercept

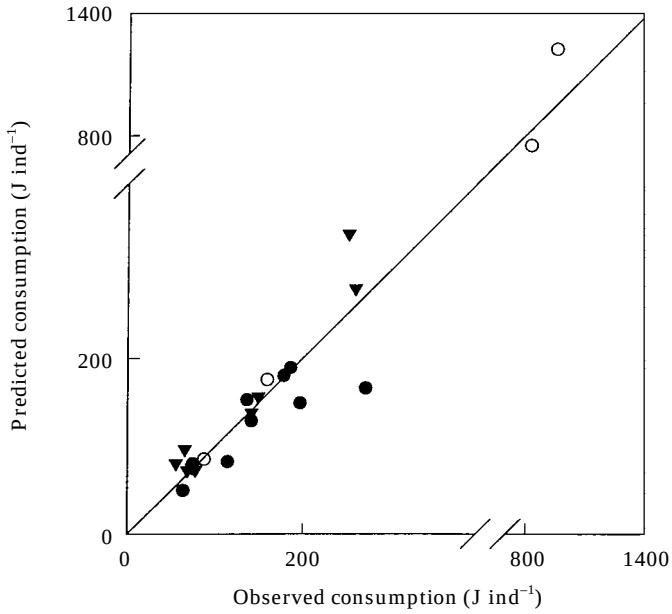

FIG. 1. Predicted *v.* observed food consumption of whitefish. Predicted values have been generated by a bioenergetics model. Experimental temperatures as well as 1 : 1 line are given. ●, 10° C; ○, 12° C; ▼, 15 °C.

differed significantly from one and zero, respectively (Table III, Fig. 2). The M_E for total metabolic rate was 0·85 and ε was 13·0% (Table III).

DISCUSSION

Mayer & Butler (1993) suggested that modelling efficiency (M_E) was measured to assess agreement between observed and simulated values. It is a dimensionless statistic, and values close to one indicate a near-perfect model (Mayer & Butler, 1993). In this study, the M_E for food consumption was 0·90, which can be considered adequate for subsequent application of the model. Note that there are no absolute criteria in model validation, and the decision of acceptance or rejection is ultimately subjective (Mayer & Butler, 1993). The M_E for metabolic rate was 0·85 indicating that parameter values used in the model had been determined relatively successfully. Nevertheless, the high slopes obtained in the regressions of predicted *v.* observed data indicate that there was a tendency for food consumption and total metabolic rate to be overestimated. Food consumption was overestimated mainly in larger fish (Fig. 1), while total metabolic rate was overestimated over the entire range, with the discrepancy becoming more obvious at higher values (Fig. 2). Parameter values for metabolism are among the most critical in influencing prediction errors in fish bioenergetics models (Bartell *et al.*, 1986), so it is not unexpected that somewhat high estimates of metabolism in the model result in overestimation of food consumption.

R_F refers to the energy used by fish in excess of maintenance (Wieser & Medgyesy, 1990*b*), i.e. it includes specific dynamic action (the term S in the

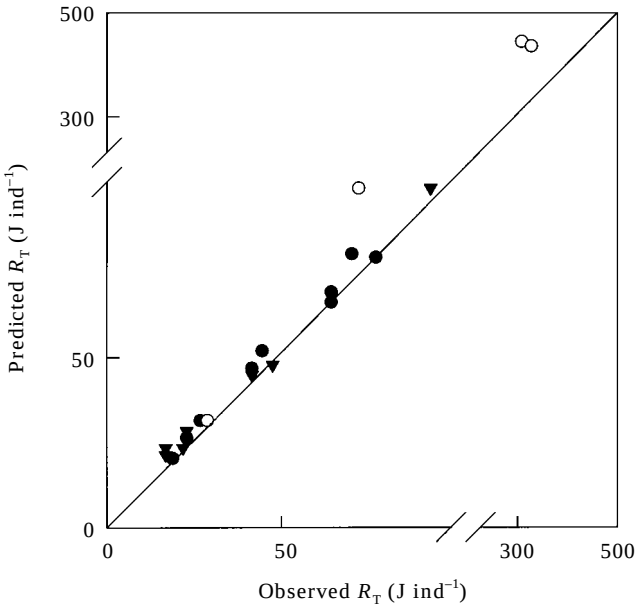

FIG. 2. Predicted *v.* observed total metabolic rate (R_T) of whitefish. Predicted values have been generated by a bioenergetics model. Experimental temperatures as well as 1 : 1 line are given. ●, 10° C; ○, 12° C; ▼, 15° C.

model) and costs of locomotory activity. Hence, R_F is equal to or larger than specific dynamic action. In constructing the model it was assumed that 17% of absorbed energy (corresponding to 13·8% of ingested energy) would be dissipated as specific dynamic action. R_F was, however, usually less than that (Table I: 12% of ingested energy on average), so it is clear that the model value for specific dynamic action was an overestimate. This was especially true for the two experiments conducted on the largest fish, where R_F was only 7% of ingested energy (Table I). These discrepancies account for the high model estimates of total metabolic rate in large fish. However, because the significance of specific dynamic action as a source of error in bioenergetics models is limited (Bartell *et al.*, 1986), its effect on estimates of food consumption was not pronounced. Although the coefficient of specific dynamic action is usually assigned a value representing a constant proportion of absorbed or ingested energy, this is not an ideal practice (Beamish & Trippel, 1990). The major component of specific dynamic action is the metabolic cost of growth (Wieser, 1994), so specific dynamic action may be better represented as a growth multiplier appended to metabolic rate.

Locomotory activity is an important component of the energy budget, but costs are difficult to estimate. Boisclair & Leggett (1989) stated that bioenergetics models may provide better estimates of food consumption for piscivorous than for planktivorous or benthivorous fish because the activity costs of the former may be lower. The effect of activity on metabolic rate can be modelled either by determining resting metabolic rate and using an activity multiplier, or by applying metabolic rate which itself contains the activity component (Hewett & Johnson, 1992). In our model no additional

activity multiplier was employed (activity coefficient = 1) but the activity was included in R as routine activity (Karjalainen *et al.*, 1995). Whether the routine metabolic rate corresponds to the activity level in field conditions is not known but when the model was applied for vendace and smelt *Osmerus eperlanus* L. reared in 45-l flow-through glass aquaria, reliable estimates of food consumption were obtained (Karjalainen *et al.*, 1997*a*). It is feasible that the activity pattern of larval fish reared under laboratory conditions resembles that of wild fish because they need to utilize a large fraction of their swimming capacity also in the laboratory.

The bioenergetics model used here is based on the assumption that energy lost via faeces and nitrogenous excretion represents fixed proportions of 19% of ingested and 7% of absorbed food energy, respectively (Table II). Consequently, assimilation efficiency (A_E) is assumed to be a constant 75·3% of ingested energy. This greatly simplifies calculations, although assimilation may have a dynamic nature characterized by size-, ration- and temperature-dependent effects (e.g. Elliott, 1976; Keckeis & Schiemer, 1990; Jobling, 1994). The average observed assimilation efficiency (71%) corresponded well to the model assumptions, but there was considerable variation (range from 46 to 98%). It is possible to model egestion and excretion as functions of temperature and ration (e.g. Elliott, 1976; Cui & Wootton, 1988) but egestion and excretion have been observed to contribute only slightly to prediction errors in sensitivity analyses of bioenergetics models (Bartell *et al.*, 1986).

This paper has tested the accuracy of predictions given by a bioenergetics model at different, constant temperatures. The model predicted food consumption reasonably well, and although there was no sign of bias associated with temperature (ε = 16·0, 12·9 and 18·0% at 10, 12 and 15° C, respectively), the validity of the model should be assessed at fluctuating temperatures as well. In ecological studies, the present model may suffice for quantifying the effect of young fish on their prey populations, but modelling energy allocation at the individual level clearly needs further research of egestion, excretion and specific dynamic action as functions of temperature, ration and fish size.

E. Kamler and two anonymous referees provided valuable comments to improve the manuscript. This work was supported financially by the Academy of Finland, the Maj and Tor Nessling Foundation, the Olvi Foundation and the National Graduate Programme in Fish Biology and Fisheries with a grant to HH.

References

Bartell, S. M., Breck, J. E., Gardner, R. H. & Brenkert, A. L. (1986). Individual parameter perturbation and error analysis of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 160–168.

Beamish, F. W. H. & Trippel, E. A. (1990). Heat increment: a static or dynamic dimension in bioenergetic models. *Transactions of the American Fisheries Society* **119,** 649–661.

Boisclair, D & Leggett, W. C. (1988). An in situ experimental evaluation of the Elliott and Persson and Eggers models for estimating fish daily ration. *Canadian Journal of Fisheries and Aquatic Sciences* **45,** 138–145.

Boisclair, D. & Leggett, W. C. (1989). The importance of activity in bioenergetics models applied to actively foraging fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **46,** 1859–1867.

Cui, Y. & Wootton, R. J. (1988). Bioenergetics of growth of a cyprinid, *Phoxinus phoxinus*: the effect of ration, temperature and body size on food consumption, faecal production and nitrogenous excretion. *Journal of Fish Biology* **33,** 431–443.

Dabrowski, K., Takashima, F. & Law, Y. K. (1988). Bioenergetic model of planktivorous fish feeding, growth and metabolism: theoretical optimum swimming speed of fish larvae. *Journal of Fish Biology* **32,** 443–458.

Eggers, D. M. (1977). Factors in interpreting data obtained by diel sampling of fish stomachs. *Journal of the Fisheries Research Board of Canada* **34,** 1018–1019.

Elliott, J. M. (1976). Energy losses in the waste products of brown trout (*Salmo trutta* L.). *Journal of Animal Ecology* **45,** 561–580.

Elliott, J. M. & Persson, L. (1978). The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology* **47,** 977–991.

Hanel, R., Karjalainen, J. & Wieser, W. (1996). Growth of swimming muscles and its metabolic cost in larvae of whitefish at different temperatures. *Journal of Fish Biology* **48,** 937–951.

Héroux, D. & Magnan, P. (1996). In situ determination of food daily ration in fish: review and field evaluation. *Environmental Biology of Fishes* **46,** 61–74.

Hewett, S. W. & Johnson, B. L. (1992). A generalized bioenergetics model of fish growth for microcomputers. *University of Wisconsin Sea Grant Technical Reports* No. WIS-SG-91-250. Second edn. 79 pp.

Huuskonen, H. & Karjalainen, J. (1997). Predator-induced respiratory responses in juveniles of vendace *Coregonus albula*, whitefish *C. lavaretus*, perch *Perca fluviatilis* and roach *Rutilus rutilus*. *Environmental Biology of Fishes* **49,** 265–269.

Jobling, M. (1994). *Fish Bioenergetics*. London: Chapman & Hall.

Karjalainen, J., Huuskonen, H. & Medgyesy, N. (1995). Differences in metabolic rates during the early life history of vendace (*Coregonus albula* (L.)) and whitefish (*C. lavaretus* L.). *Polskie Archiwum Hydrobiologii* **42,** 247–256.

Karjalainen, J., Huuskonen, H. & Kinnunen, H. (1996). Changes in the metabolic rate of coregonids during early development. *Marine and Freshwater Behaviour and Physiology* **28,** 137–143.

Karjalainen, J., Miserque, D. & Huuskonen, H. (1997*a*). The estimation of food consumption in larval and juvenile fish: experimental evaluation of bioenergetics models. *Journal of Fish Biology* **51** (Suppl. A)**,** 39–51.

Karjalainen, J., Turunen, T., Helminen, H., Sarvala, J. & Huuskonen, H. (1997*b*). Food selection and consumption of 0+ smelt (*Osmerus eperlanus* (L.)) and vendace (*Coregonus albula* (L.)) in pelagial zone of Finnish lakes. *Archiv für Hydrobiologie Special Issues Advances in Limnology* **49,** 37–49.

Keckeis, H. & Schiemer, F. (1990). Consumption, growth and respiration of bleak, *Alburnus alburnus* (L.), and roach, *Rutilus rutilus* (L.), during early ontogeny. *Journal of Fish Biology* **36,** 841–851.

Kitchell, J. F., Stewart, D. J. & Weiniger, D. (1977). Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* **34,** 1922–1935.

Mayer, D. G. & Butler, D. G. (1993). Statistical validation. *Ecological Modelling* **68,** 21–32.

Ney, J. J. (1993). Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* **122,** 736–748.

Olson, R. J. & Mullen, A. J. (1986). Recent developments for making gastric evacuation and daily ration determinations. *Environmental Biology of Fishes* **16,** 183–191.

Post, J. R. (1990). Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* **47,** 554–560.

Wieser, W. (1994). Cost of growth in cells and organisms: general rules and comparative aspects. *Biological Reviews* **68,** 1–33.

Wieser, W. & Medgyesy, N. (1990*a*). Aerobic maximum for growth in the larvae and juveniles of cyprinid fish, *Rutilus rutilus* (L.): implications for energy budgeting in small poikilotherms. *Functional Ecology* **4,** 233–242.

Wieser, W. & Medgyesy, N. (1990*b*). Cost and efficiency of growth in the larvae of two species of fish with widely differing metabolic rates. *Proceedings of the Royal Society of London B* **242,** 51–56.