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Lipid and protein content in *Anguilla anguilla* during growth and starvation

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Abstract

This study is based on elementary chemical analyses made on whole eels.

It is shown that eels during development from elver to silver eel accumulate lipid from about 20 to about 80% calculated as the lipid part of the eel's total energy.

Silver eels can endure long-term starvation. Our record is 1594 days at 14 ± 2 °C. Logarithms of body weights decrease linearly against days of starvation.

Samples of male silver eels taken at intervals from a starving batch were analysed for water, lipid (L) and protein (P). During starvation the lipid reserve (g L/eel) is decomposed at a lower rate than that of the protein reserve (g P/eel). Half-lives are 667 and 416 days respectively. Calculations of energy loss (Cal/kg L or P/day) during starvation showed that the two energy reserves are mobilized in such a way that they (per kg reserve) contribute almost equally to the total metabolism. When the eel's body weight is used as reference (Cal/kg eel/day) an increasing rate of decomposition is typical of L while the rate of P is decreasing. During the entire period of starvation the energy released from L surpasses that of P. The sum of L- and P-energies remains constant.

Determinations of oxygen consumption were made on starving male silver eels kept individually in respirometric bottles over about four years. Their metabolic rate increased by a factor 3. This is in conflict with the above results. The discrepancy is discussed.

Contents

Preface

The present study was made at the 'Physiological Laboratory' run jointly by the Danish Institute for Fisheries and Marine Research and Denmark's Aquarium. This work is a continuation of the laboratory's current studies aiming to reveal the partly unknown phases of the eel's marine life-story.

Experimental

The batches of starving silver eels were kept in concrete tanks (about 2 m^3) connected with the sea water circuit of Denmark's Aquarium. Temperature 14 ± 2°C, salinity 31‰S. The eels were caught during their autumnal migration from the Baltic. The '0-day' of a starving batch refers to the date of the eel's arrival in the laboratory.

For determinations of *oxygen consumption* the experimental eels were installed permanently (up to four years) in 4-litre glass bottles submerged in the tanks with circulating sea water saturated to about 90% with oxygen. The bottles were aerated with air through a filter cone placed near the bottom. The mouths of the bottles were covered with a plastic net allowing a steady exchange of water between bottle and tank. When respirometry was made the net was exchanged with a glass stopper. Determinations of oxygen were made by Winckler titrations. During an experiment the oxygen saturation was not allowed to drop below 70%.

The *chemical analyses* were made on homogenates of whole eels. Eels are not easily homogenized as pieces of their skin are inclined to cling to the knives of the homogenizer. This trouble is avoided by cutting a pattern of squares in the skin by means of a special cutting device with a number of razor blades fixed in parallel (Fig. 1). Next the eel is cut into about 0.5 cm pieces and transferred to the MSE-homogenizer where 50% water is added.

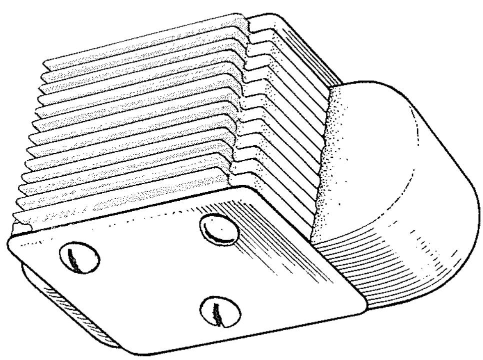

Fig. 1. Device for cutting eel skin in small squares prior to homogenization of whole eels.

Homogenates, each of approximately 2 g, were used for determination of dry matter, lipid, total nitrogen (N) and non-protein nitrogen (NPN).

Samples for dry matter determinations were placed for 24 hrs in an incubator (40-50°C) and then for 24 hrs in a vacuum desiccator. Lipid analyses were made according to the chloroform/methanol extraction method described by Bligh & Dyer (1959). N was determined by the Kjeldahl method as described by Nordisk metodik-komite, 1952. NPN was determined by the Kjeldahl method after precipitation of proteins by a 15% solution of trichloroacetic acid. Samples for ash determinations were treated for 24 hrs in an incubator at 105°C prior to a 4 hrs' stay at 600°C in a muffle furnace.

Analytical data are given in Primary Tables A & B. The figures are means of 6 determinations per eel for water (dry matter) and ash and means of 3 determinations per eel for lipid, total nitrogen and non-protein nitrogen. All the data are given as percentage of body weight. Protein is calculated as (N-NPN) × 6.025, the conversion factor adopted from Love (1970) (footnote p. 238).

Lipid and protein content during development

The material used for the present section is given in Primary Table A, where 'proximate analyses' of freshly caught elvers (E), yellow eels (Y) and silver eels (S) are presented. The data of the 6 female silver eels in Table A originally served as controls in an earlier work by us (Boëtius & Boëtius 1980). To the data of the 3 male silver eels in Table A are added the data of 10 male silver eels (days of starvation = 0) from the present Primary Table B.

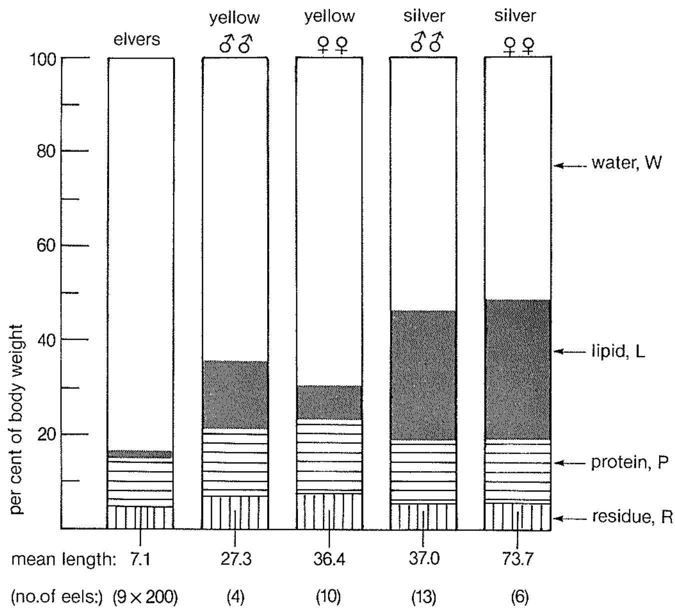

Fig. 2. Histogram demonstrating percentage composition of elementary constituents of eels according to total length, stage and sex.

The histogram Fig. 2 gives the mean values of the elementary composition of the eels according to developmental stage and sex. The columns are arranged as to increasing mean total lengths.

It is evident from the diagram that eels accumulate lipid during development from elver to silver stage. Contents of protein are not altered significantly. Also it is seen that for yellow and silver eels the sum of lipid and water remains rather constant.

The lipid energy expressed as per cent of total energy was calculated as:

$$L \times 9.5 \times 100/(L \times 9.5 + P \times 5.7)$$

where L and P denote lipid and protein in per cent of body weight. The caloric equivalents of L and P (9.5 Cal/g and 5.7 Cal/g respectively) are adopted from Kleiber (1975).

In Fig. 3 the lipid share of the total energy is plotted against total lengths of the eels. It is seen that the relative lipid energy rises from about 20 to about 80% during development from elver to silver eel. The rise seems linear. Males turn silver at lower lengths than females and consequently they also reach maximum lipid contents at lower lengths.

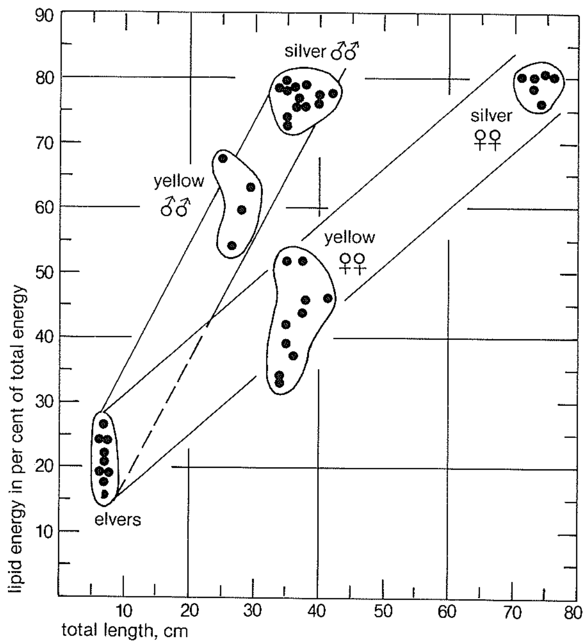

Fig. 3. Lipid energy reserves in percentage of total energy plotted against the eels' total lengths.

Note. Philips, Podoliak *et al.* 1963 (here cited from Love 1970, p. 227) have shown that in *Salvelinus* and *Cristivomer* 'the dry lipid-free residue consisted of 86.5% protein and 13.5% ash, no matter what the water and lipid contents have been.' This is true also for *Anguilla* with reference to the last column in the present Primary Table A. Mean values of P and A (N = 26) as per cent of lipid-free residue are: 86.7% P and 13.3% A.

Silver eels. Loss in body weight during prolonged starvation

Ciaccio (1944), studied long-term starvation in silver eels. His record of 1367 days was held by a female eel (initial body weight (B_0) = 465 g) at temperatures ranging from 7 to 24°C. This record was surpassed by a male silver eel (B_0 = 71 g) which lived for 1515 days in a respirometric flask in our laboratory at 14 ± 2°C (Love (1970), relates this case by personal communication from us). In the present paper still a new record is noted: a female silver eel ($B_0 = 605$ g) survived for 1594 days without food at 14 ± 2°C.

In the present section two batches of silver eel were starved to death: a female batch of five eels (B_0: 605-855 g, day 0 = Nov.11th) and a male batch initially consisting of 148 eels (B_0: about 80 g, day 0 = Aug.24th). These males served in their first year as controls in our earlier work, Boëtius & Boëtius 1967. Details are given there at pp. 343-345.

The two batches were kept in sea water (14 ± 2°C, 31‰S) and at intervals the eels were anaesthetized in order to determine length and weight.

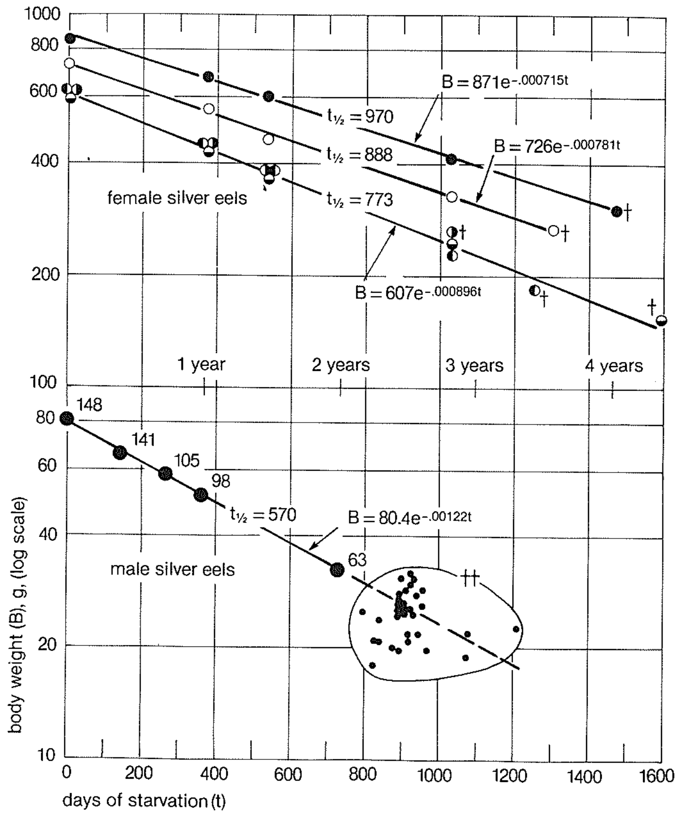

Fig. 4. Starving silver eels. Decreasing body weights (log scale) versus days of starvation. Crosses indicate death from starvation. *Female silver eels.* Signatures refer to individual eels. The 3 eels at initial body weights of about 600 g are kept together in a mutual regression. *Male silver eels.* Big black plots indicate the mean body weights of survivors. Their decreasing number (given for each plot) is caused by mortalities other than starvation. The regression line is calculated for the period 0-730 days only. Encircled small black plots indicate eels which have died from starvation.

Results are shown in Fig. 4. In the semi-logarithmic presentation the body weights of the starving eels decrease linearly against time. Thus the decomposition of the eels' bodies is conveniently described by the equation:

$$B = B_0 e^{-at}$$

where B is the eel's body weight at time t, B_0 the body weight at $t = 0$ and $-a$ is a constant (= the slope of the semilog line). This equation is well known from descriptions of radioactive decay. In the present starving eels their 'half-lives' ($t_{1/2} = \ln 2/a$) are used to characterize their rate of decomposition.

It is seen from Fig. 4 that the half-lives of the eels decrease by decreasing initial body weights. This feature most likely reflects the general rule that small animals have a higher metabolic rate than big ones. When silver eels die from starvation they have lost 60-70 % of their initial body weight. This loss does not seem to be influenced by size or sex. Also total lengths are somewhat reduced. Table 1 gives reductions in body weights, total lengths and condition indices of the male batch described in Fig. 4. The condition indices of eels died from starvation (about 0.6) are not far from those of ascending elvers (about 0.3).

Table 1. Male silver eels. Changes in condition during starvation.

	Days of starvation	No. of eels	Body weight, g mean ± 2 × SE	Total length, cm mean ± 2 × SE	Condition* mean
Live eels	0	148	81.86 ± 2.14	37.09 ± 0.30	1.60
	144	141	66.49 ± 1.89	36.59 ± 0.30	1.36
	271	105	60.50 ± 2.07	36.66 ± 0.33	1.23
	365	98	52.66 ± 1.93	36.34 ± 0.34	1.10
	730	63	33.06 ± 1.46	35.92 ± 0.40	0.71
Dead eels	924.5 ± 27.8** (800-1208)	32	24.75 ± 1.34	34.78 ± 0.60	0.59
		Reduction:	69.8 %	6.23 %	

*$W \times 10^3/L^3$ (W = body weight, g. L = total length, cm)
**Survival times (mean ± 2 × SE (range)) of 32 eels died from starvation.

Male silver eels. Decomposition of lipid and protein during starvation

A batch of about 100 male silver eels was kept starving in sea water (14 ± 2°C, 31 ‰S) during a period of about 800 days (day 0 = Sept.10th). Our efforts to obtain eels of equal size resulted in a range of 34-42 cm in total lengths. Mean initial body weight (91 g) was determined by weighing the total batch. Our best estimate of the range was 65-105 g. At intervals samples of about 10 eels were selected at random. The eels were sacrificed and the homogenized whole eels were analysed for contents of water (W), lipid (L) and protein (P). Primary data of this experimental run are given in Primary Table B.

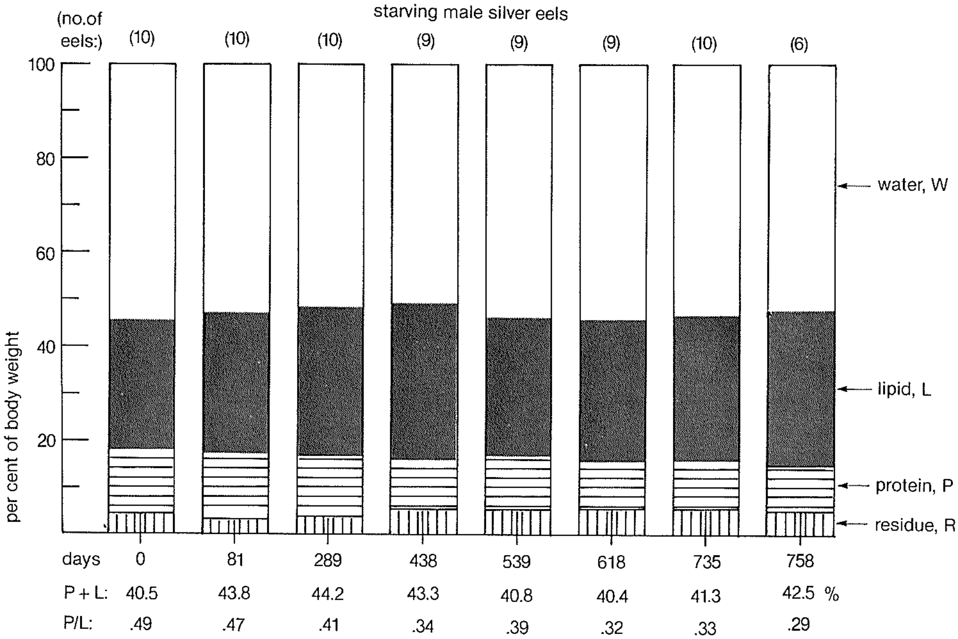

Fig. 5. Histogram demonstrating percentage composition of elementary constituents of male silver eels during long-term starvation.

From Fig. 5 is seen that the relative representation of the constituents remains remarkably constant throughout the period of starvation. The sum of water and lipid hardly changes and also the sum of lipid and protein fluctuates only little and in no way systematically. The ratio P/L, however, decreases from 0.49 to 0.29. That is to say: lipid contents relative to protein rise during starvation.

In Fig. 6 the logarithmic values (g/eel) of body weight, contents of water, lipid and protein are plotted against days of starvation.

Body weight and water content. The B/t-regression in Fig. 6 resembles very much the regression of male silver eels given in Fig. 4 where the data were based on repeated weight determinations of anaesthetized eels of corresponding initial size. In Fig. 6 the decline in absolute water content follows the decline in body weight very closely.

Lipid and protein contents. In Fig. 6 it is clearly demonstrated that the decomposition of the lipid reserve (gL/eel/day) takes place at a lower rate than that of protein (gP/eel/day). Half-lives of lipid and protein reserves are calculated to 667 days and 416 days respectively.

At any time t there is a constant proportion between the rate of decomposition (L′) and the energy reserve present (L). As

$$L'/L = -aL_0e^{-at}/L_0e^{-at} = -a$$

it is seen that this ratio is denoted by the slope of the regression line lnL/t.

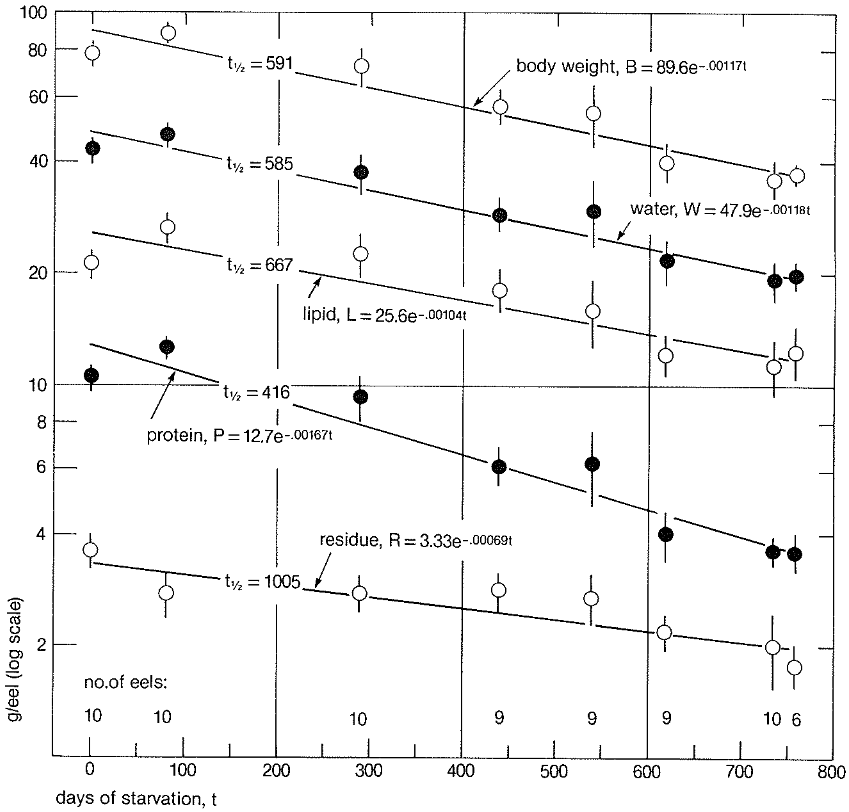

Fig. 6. Body weights and elementary constituents (g/eel, log scale) plotted against days in a batch of starving male silver eels. The signatures give mean $\pm 2 \times$ SE-values. The regression lines are calculated for all eels in the batch ($N = 73$).

Thus directly from the slope values we get the relative rates of decomposition:

Lipid. 1.04 g L ~ 9.88 Cal/kg L/day
Protein. 1.67 g P ~ 9.53 Cal/kg P/day

The caloric equivalents indicate that the L- and P-reserves are mobilized in such a way that they contribute almost equally to the production of energy per kg energy reserve and day.

From Table 2 is seen that the rate of lipid decomposition when calculated as mg L/kg eel/day increases slightly during long-term starvation while protein decomposition (mg P/kg eel/day) decreases remarkably. From the conversions into energy is seen that the sum of energy released from the two sources remains constant during the entire period of starvation. In other words: the eels in the present starving batch seem to have maintained a constant metabolic rate to which we return in the section on oxygen consumption.

Table 2. Starving male silver eels. Rates of decomposition of lipid and protein. The figures are calculated from the regression equations in Fig. 6.

Days of starvation	Body weight, B, g	mg/kg eel/day L′/B	mg/kg eel/day P′/B	Cal/kg eel/day L′/B	Cal/kg eel/day P′/B	Cal/kg eel/day (L′ + P′)/B
0	89.6	297	237	2.82	1.35	4.17
100	79.7	301	225	2.86	1.28	4.14
200	70.9	305	213	2.89	1.21	4.10
300	63.1	309	204	2.93	1.17	4.10
400	56.1	314	194	2.98	1.11	4.09
500	49.9	317	184	3.01	1.04	4.05
600	44.4	322	176	3.06	0.99	4.05
700	39.5	327	167	3.11	0.96	4.07
(800)	35.1	331	160	3.13	0.91	4.04

Lipid and water contents of individual eels of the starving batch are combined in Fig. 7. As is seen a so-called 'fat-water line' can be established. According to Love (1970), this pattern is typical of 'fatty' fish storing the predominant part of their lipid reserve in the muscle tissue.

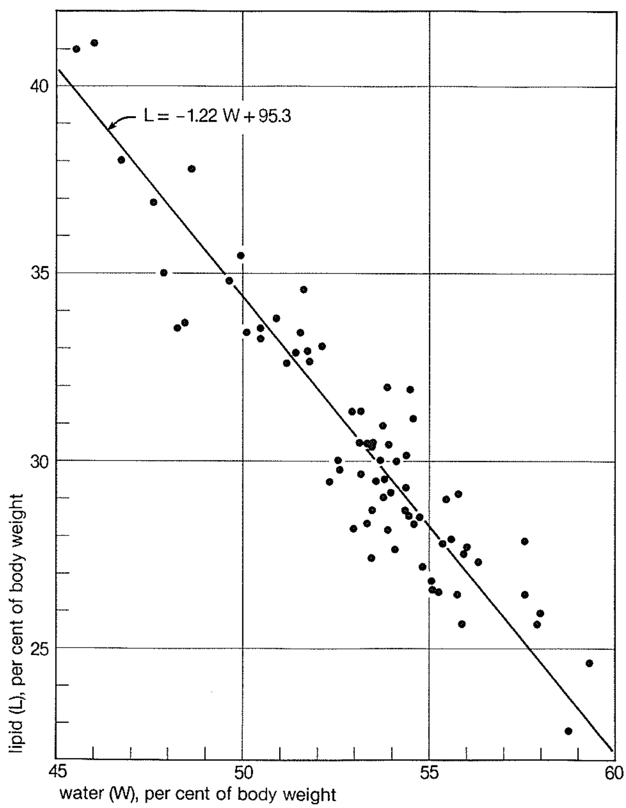

Fig. 7. Combined values of lipid and water contents in the 73 starving male silver eels listed in Primary Table B.

Table 3. Starving male silver eels. Ash contents.

Days of starvation	No. of eels	No. of analyses	Ash in % of body weight, mean $\pm 2 \times$ SE
0	8	23	2.34 ± 0.16
360	9	27	1.69 ± 0.08
686	20	59	1.69 ± 0.08

Ash. The present starvation experiment has not included determinations of ash. As a supplement, however, a special batch of male silver eels (body weight about 80 g) was set up. Results are given in Table 3. Ash contents are reduced markedly during the first year of starvation, during the second year no change is observed.

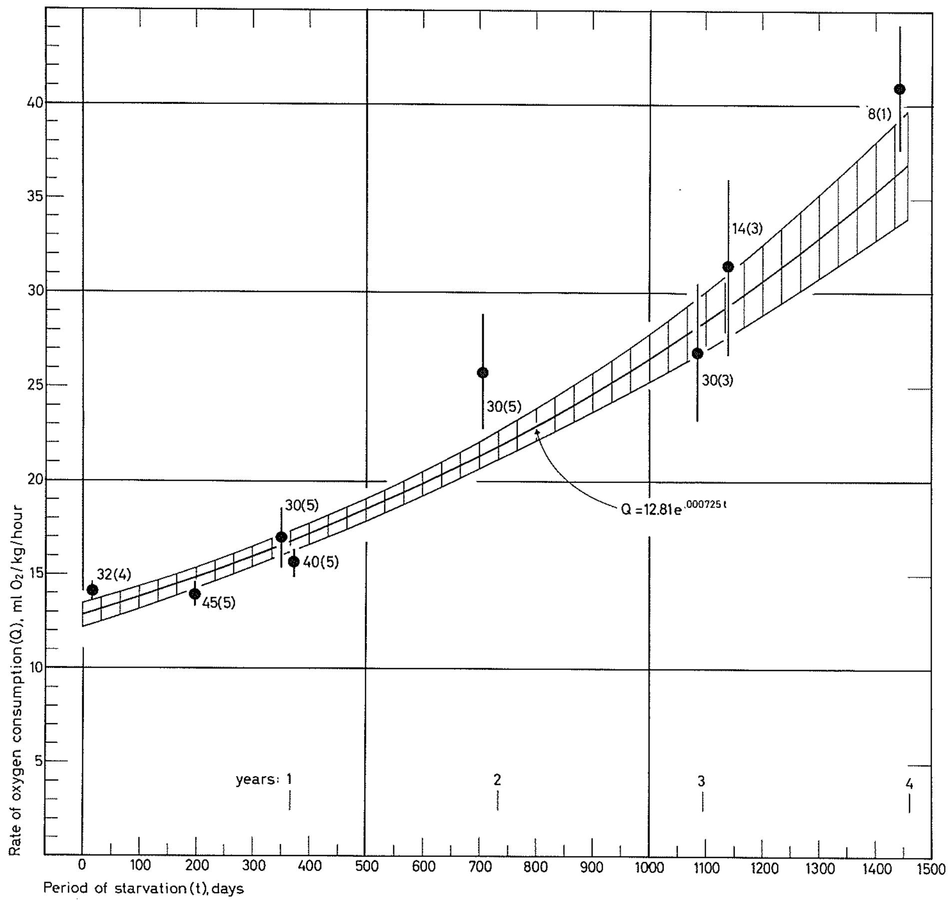

Fig. 8. Male silver eels. Rate of oxygen consumption during a period of about 4 years of starvation. Plots indicate mean $\pm 2 \times$ SE-values. Figures indicate number of determinations and (in brackets) number of eels. The hatched area indicates interval of 95 % confidence.

Male silver eels. Respiratory rate during starvation

The metabolic rate as calculated in Table 2 (4.1 Cal/kg eel/day) is unaltered during the period of starvation and must be considered surprisingly high. Converting into ml O_2/kg eel/hour (1 Cal ~ 220 ml O_2) gives a rate of 37.6 which is about three times as high as earlier stated by us for non-starving resting silver eels of the same body size and at the same temperature.

For the present purpose we determined the oxygen consumption of 12 male silver eels during long-term starvation. The range of the eels' initial body weights was 75-95 g. The eels were installed in individual respiration bottles and kept there during the full starvation period (up to four years). The experimental temperature was 14 ± 2°C, salinity 31‰S. (Day 0 = Sept.6th.) Results are given in Fig. 8, the data in Primary Table C.

From Fig. 8 it is clearly seen that the respiratory rate of the eels increases during starvation. Up to the day of death from starvation (about 4 years) the rate has reached the same level as was calculated for the Table 2-eels during the entire period.

This discrepancy is most likely due to the fact that the Table 2-eels, unlike the eels in the respirometric experiments, have been kept together in one and the same

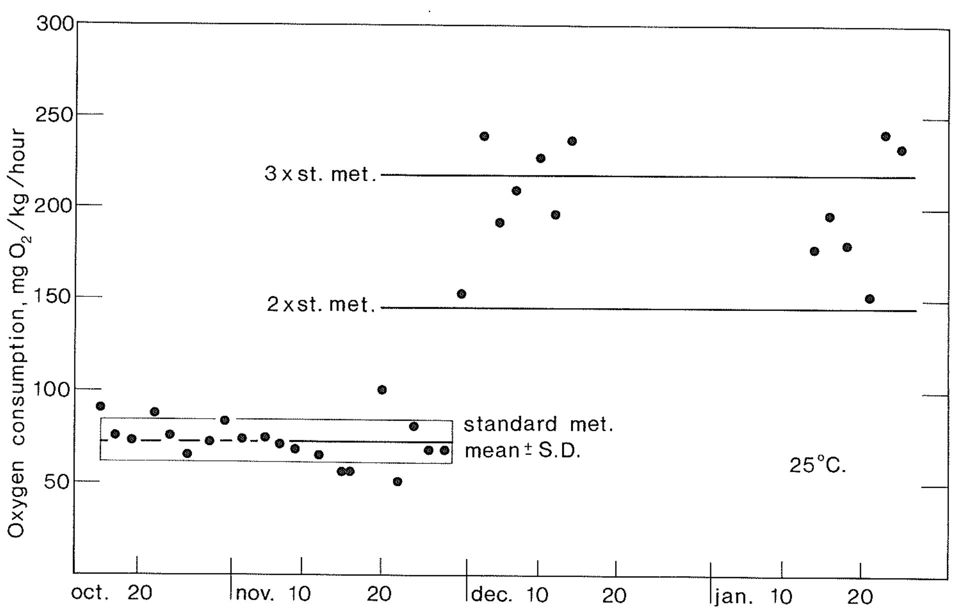

Fig. 9. Respiratory data of a non-starved male silver eel (body weight about 80 g) which was permanently installed in a respirometric bottle at 25 °C. As is seen the eel maintained a rather well defined metabolic rate (standard metabolism) during October-November. About Dec.1st, however, the eel turned very active causing an elevation of its respiratory rate up to about 3 times the standard (note that the rate of oxygen consumption is given here as mg O_2/kg/hour).

tank. Such conditions no doubt keep the total batch in a permanent state of agitation corresponding to an elevated metabolic rate.

Silver eels kept solitarily in tanks or respirometric bottles have several times been observed by us to increase their swimming activity during long-term starvation.

We take this opportunity to relate a rather untypical case of a non-starved male silver eel. The eel served as one out of five controls in an experiment which is not related to the present work. The eel's oxygen consumption was determined at intervals at 25°C. At a certain day (about Dec.1st) the eel for reasons not stated turned very active and remained so for months. The routine determinations of oxygen consumption were continued and the results are given in Fig. 9. It is seen that the active eel maintains a metabolic rate during the active period which is about three times the standard metabolism.

Discussion

Long-range migrating animals (birds, insects) normally cover their activities by an almost exclusive combustion of nitrogen-free energy reserves. Thus it would seem reasonable to suggest that the lipid reserve in the silver eel (about 77% of its total energy) was accumulated especially to serve as fuel for its trans-oceanic migration activities during which it does not eat. A preferential mobilization of lipid energy in the starving silver eel was actually expected by us.

From the metabolic data in Table 2 can be calculated that the lipid part of the total energy release is raised from 68 to 77% during the period of starvation. That is to say: at no moment does the lipid part of the metabolism exceed the lipid part of the total energy stored in the eel. Still in other words: the starving silver eel shows no signs of a preferential mobilization of lipid energy.

The lipid reserves in the silver eel are not exclusively accumulated in preparation for migration activities. Also they are spared for later formation of sexual products. From our 1980-paper (table 6, p.20) can be calculated that in ripening ovaries and eggs the lipid part of the total energy ranges from 57 to 85%.

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Primary Tables A-C

Primary Table A.

Locality, Season	Stage	Sex	Total length, cm	Body weight, g	% water (W)	% lipid (L)	% total nitrogen (N)	% non-prot. nitrog. (NPN)	% protein (P)*	% residue (R)	% ash (A)	P in % of (100−W−L) (P_1)	A in % of (100−W−L) (A_1)	P_1 in % of (P_1+A_1)
Højer Sluse, North Sea, May	E		mean: 7.1	means of 200 specimens 0.25	84.3	2.1	1.96	0.19	10.7	3.0	1.7	78.1	12.6	86.1
	E			0.24	83.0	1.6	1.93	0.23	10.2	5.1	1.6	66.6	10.6	86.3
–	E			0.23	83.6	1.8	2.03	0.23	10.8	3.8	2.1	74.3	14.7	83.5
–	E			0.22	84.0	2.1	1.93	0.33	9.7	4.3	1.8	69.4	13.2	84.0
–	E			0.23	82.8	1.4	2.05	0.27	10.7	5.0	2.1	68.2	13.3	83.7
–	E			0.24	83.9	2.0	1.98	0.25	10.4	4.7	2.2	69.2	14.3	82.9
–	E			0.23	83.3	1.2	2.06	0.28	10.7	4.8	1.8	69.0	11.8	85.4
–	E			0.24	83.6	1.5	2.02	0.31	10.4	4.5	1.9	69.7	12.9	84.4
–	E			0.24	84.5	1.5	2.04	0.23	10.9	3.1	2.0	78.1	14.0	84.8
Ringkøbing Fj. October	Y	♂	25	23	62.2	17.6	2.65	0.35	13.9	6.4	1.8	68.5	8.7	88.7
	Y	♂	26.5	26	68.3	10.4	2.90	0.46	14.7	6.1	1.9	70.8	9.3	88.4
–	Y	♂	28	33	65.9	12.8	2.93	0.54	14.4	7.0	1.8	67.3	8.3	89.0
–	Y	♂	29.5	32	64.3	14.9	2.84	0.44	14.5	6.3	2.5	69.6	12.0	85.3
The Sound, June	Y	♀	34	65.7	71.6	5.2	3.20	0.43	16.7	6.9	2.6	72.1	11.2	86.6
	Y	♀	34	56.1	72.2	4.9	3.11	0.41	16.3	6.7	2.1	72.1	9.2	88.7
–	Y	♀	35	70.7	70.2	6.4	3.25	0.47	16.7	6.8	2.2	71.5	9.3	88.1
–	Y	♀	35	68.3	70.4	7.0	3.08	0.42	16.1	6.5	2.3	71.1	10.3	87.4
–	Y	♀	35	69.5	67.2	10.2	3.03	0.41	15.8	6.9	2.3	69.6	10.0	87.5
–	Y	♀	36	57.6	70.1	6.0	3.22	0.42	16.8	7.1	2.6	70.5	10.8	86.7
–	Y	♀	37.5	74.8	69.2	7.7	3.17	0.43	16.5	6.5	2.4	71.5	10.3	87.4
–	Y	♀	37.5	77.3	69.3	9.7	2.91	0.40	15.1	5.9	1.9	72.0	9.2	88.6
–	Y	♀	38	80.3	61.4	8.0	3.11	0.48	15.9	8.8	1.4	64.4	5.7	91.8
–	Y	♀	41.5	88.6	70.7	8.2	3.02	0.34	16.1	5.0	2.3	76.3	10.9	87.5
The Sound, October	S	♂	35	60.6	46.2	34.3	2.45	0.32	14.8	4.7	2.0	75.9	10.3	88.1
	S	♂	35	65.5	58.3	22.8	2.31	0.34	13.9	5.0	2.3	73.7	12.2	85.8
–	S	♂	42	92.5	44.3	28.0	2.57	0.35	13.4	4.3	1.7	80.4	10.4	88.5
–	S	♀	71	722	47.8	33.8	2.53	0.25	13.8	4.6	–	–	–	–
–	S	♀	73	768	48.4	33.2	2.51	0.20	13.9	4.4	–	–	–	–
–	S	♀	73	630	52.1	27.9	2.54	0.40	12.9	7.1	–	–	–	–
–	S	♀	74	768	54.6	26.5	2.52	0.19	14.0	4.9	–	–	–	–
–	S	♀	75	630	52.1	30.6	2.41	0.38	12.2	5.1	–	–	–	–
–	S	♀	76	850	50.6	29.9	2.39	0.35	12.3	7.2	–	–	–	–

*Protein is calculated as (N-NPN) 6.025

Primary Table B. Male silver eels.

Starvation, days (t)	Total length, cm	Body weight, g	% water (W)	% lipid (L)	% total nitrogen (N)	% non-prot. nitrogen (NPN)	% protein (P)	% residue (R)
0	38.0	78.1	53.9	28.2	2.57	0.48	12.6	5.3
–	36.9	81.6	55.3	26.5	2.68	0.39	13.8	4.4
–	33.9	66.0	54.1	27.7	2.64	0.41	13.5	4.8
–	36.3	71.1	54.6	28.3	2.48	0.36	12.8	4.3
–	40.0	97.8	55.1	26.6	2.57	0.36	13.3	5.0
–	35.4	68.4	52.6	29.5	2.55	0.34	13.3	4.6
–	40.0	88.1	53.5	28.7	2.50	0.34	13.0	4.8
–	35.0	69.4	58.8	22.8	2.66	0.36	13.9	4.5
–	36.6	75.6	55.1	26.8	2.67	0.34	14.0	4.1
–	37.3	80.1	55.9	25.7	2.63	0.31	14.0	4.5
81	39.3	91.1	53.0	28.2	2.66	0.26	14.5	4.4
–	41.4	90.6	54.4	28.5	2.63	0.26	14.3	2.8
–	39.0	87.8	53.2	29.6	2.59	0.28	13.9	3.3
–	38.5	83.1	54.8	27.2	2.76	0.28	14.9	3.0
–	42.1	103.9	54.1	30.0	2.56	0.31	13.6	2.3
–	40.1	84.6	48.4	33.6	2.60	0.28	14.0	4.0
–	39.7	94.1	53.2	30.5	2.58	0.25	14.1	2.3
–	38.0	78.7	53.4	28.3	2.65	0.25	14.4	3.9
–	40.5	99.7	51.4	32.9	2.55	0.28	13.6	2.1
–	37.3	70.8	54.3	28.6	2.53	0.26	13.7	3.4
289	38.6	87.1	51.2	32.6	2.48	0.26	13.4	2.8
–	39.7	75.4	48.6	33.6	2.60	0.24	14.2	3.6
–	34.5	49.5	53.8	29.5	2.46	0.25	13.3	3.4
–	40.6	91.9	55.4	27.8	2.54	0.31	13.4	3.4
–	36.7	68.3	52.6	29.8	2.55	0.27	13.8	3.8
–	40.7	88.3	50.1	33.4	2.37	0.30	12.5	4.0
–	38.2	70.2	50.5	33.5	2.31	0.31	12.1	4.0
–	36.9	67.7	54.0	29.1	2.51	0.33	13.1	3.8
–	36.9	55.9	52.6	30.0	2.36	0.35	12.2	5.3
–	37.7	63.6	50.5	33.2	2.23	0.33	11.4	4.9
438	35.7	47.8	53.1	31.3	2.17	0.34	11.0	4.6
–	36.1	42.2	54.8	28.5	2.30	0.35	11.8	4.9
–	38.3	56.8	54.4	30.2	2.09	0.32	10.7	4.8
–	40.0	70.2	49.6	34.8	2.17	0.30	11.2	4.4
–	37.6	49.6	47.9	35.0	2.08	0.31	10.7	6.5
–	40.6	67.9	53.3	30.5	2.12	0.19	11.6	4.6
–	36.7	55.9	53.5	30.5	2.11	0.22	11.4	4.6
–	39.6	57.2	47.6	36.9	1.74	0.25	9.0	6.6
–	38.5	58.1	50.9	33.8	2.20	0.44	10.6	4.7
539	39.9	63.8	56.0	27.7	2.23	0.27	11.8	4.4
–	35.1	45.4	55.9	27.5	2.17	0.27	11.5	5.1
–	40.8	52.3	56.5	27.3	2.01	0.33	10.2	6.0
–	36.3	44.3	54.4	29.3	2.13	0.27	11.2	5.2
–	37.1	37.1	53.8	30.9	2.03	0.35	10.2	5.2
–	41.2	71.8	50.0	35.4	1.88	0.25	9.8	4.8
–	36.6	49.2	51.7	32.9	2.12	0.30	11.0	4.4
–	39.5	82.7	55.7	26.5	2.54	0.34	13.3	4.5
–	36.3	41.3	53.5	27.4	2.66	0.47	13.2	5.9

Primary Table B, continued

Starvation, days (t)	Total length, cm	Body weight, g	% water (W)	% lipid (L)	% total nitrogen (N)	% non-prot. nitrogen (NPN)	% protein (P)	% residue (R)
618	35.8	32.1	57.6	27.9	1.73	0.25	8.9	5.6
–	38.0	45.7	53.5	30.4	2.08	0.28	10.9	5.3
–	38.8	52.5	54.5	31.9	1.96	0.32	9.9	3.7
–	37.4	41.8	53.7	30.0	1.95	0.34	9.8	6.5
–	38.2	46.4	55.5	29.0	2.09	0.30	10.8	4.8
–	37.1	37.3	51.8	32.6	1.82	0.26	9.4	6.1
–	35.2	29.8	46.7	38.0	1.97	0.28	10.2	5.1
–	38.6	35.6	53.9	30.4	1.79	0.37	8.6	7.1
–	38.4	39.4	59.3	24.6	1.97	0.26	10.3	5.8
735	32.4	26.1	55.6	27.9	2.14	0.21	11.6	4.9
–	33.2	26.4	53.6	29.5	2.04	0.19	11.2	5.8
–	34.6	31.5	58.0	25.9	2.19	0.54	9.9	6.2
–	36.0	34.6	51.6	34.5	1.81	0.24	9.5	4.4
–	36.5	40.1	53.8	29.1	1.86	0.25	9.7	7.4
–	36.7	35.4	45.5	40.9	1.84	0.17	10.1	3.5
–	35.9	37.6	51.6	33.4	2.09	0.26	11.0	4.0
–	37.4	47.5	52.1	33.0	1.94	0.62	8.0	6.9
–	38.0	35.4	57.9	25.7	2.07	0.28	10.8	5.7
–	39.8	45.7	52.9	31.3	1.97	0.31	10.0	5.7
758	36.0	33.7	55.8	29.2	2.04	0.27	10.6	4.5
–	36.0	41.2	48.6	37.7	1.77	0.21	9.4	4.3
–	37.2	35.7	53.9	32.0	1.97	0.27	10.2	3.9
–	37.9	38.2	57.6	26.4	2.14	0.30	11.1	4.9
–	38.7	39.8	54.6	31.1	1.84	0.36	9.0	5.4
–	39.1	36.1	46.0	41.1	1.54	0.31	7.4	5.5

Primary Table C-1. Properties of eels nos 1-12 used for determination of oxygen consumption.

Eel no:	1	2	3	4	5	6	7	8	9	10	11	12
Init. tot. length, cm:	37.4	37.4	35.5	35.1	38.9	35.0	38.2	37.0	36.1	37.1	35.3	37.4
Starvation, days	Body weights, g											
22	75.2	95.3		79.8		79.8						
203								76.7	71.8	68.3	53.0	65.2
358	53.6		62.5	54.1	78.5		64.1					
378								69.7	63.3	60.5	48.4	59.3
714								57.6	49.7	47.6	37.4	47.6
1098			40.9		48.8		45.6					
1147									34.7	37.3	26.2	
1454											18.0	
Survival time, days:	1062	149	1129	770	1129	154	1146	852	1303	1314	1515	917
Body weight at death:	31.0	–	–	–	–	–	34.0	43.0	–	25.5	17.0	40.9
Total length at death:	35.1	–	–	–	–	–	36.4	35.9	–	35.0	33.2	36.5

Primary Table C-2.

Eel no:	1	2	3	4	5	6	7	8	9	10	11	12
Starvation, days	Rate of oxygen consumption, ml O_2/kg/hour											
12	13.8	14.7		17.0		16.5						
13	11.4	12.1		15.2		14.3						
15	12.9	13.5		15.5		15.4						
18	12.9	13.4		14.0		16.2						
19	12.8	12.5		14.4		14.9						
20	12.8	12.8		15.7		14.4						
21	14.0	13.4		14.7		15.8						
22	13.0	14.1		13.6		15.0						
192								14.8	17.6	16.3	18.7	16.0
193								11.3	15.7	13.0	13.7	12.9
194								12.3	16.6	14.0	16.2	17.0
195								11.6	12.5	13.3	12.0	15.6
196								11.3	13.1	13.3	15.7	13.4
199								14.6	14.9	13.4	16.6	15.2
200								12.1	14.5	10.5	9.7	18.1
202								11.0	16.1	12.0	13.6	14.8
203								11.8	15.2	10.3	12.9	12.9
341	20.8		16.7	18.6	16.2		17.8					
345	22.4		16.3	17.2	11.5		17.4					
348	21.9		16.3	21.1	15.2		18.4					
350	20.1		13.9	18.3	15.5		17.9					
356	24.4		15.8	18.8	12.3		14.9					
358	24.3		20.1	18.5	14.7		14.8					
368								15.2	18.9	19.5	21.1	14.3
369								15.3	15.7	13.6	17.1	13.7
371								9.8	14.3	13.5	16.7	14.3
374								17.5	19.2	17.8	14.1	15.1
375								14.3	17.5	13.1	15.9	16.0
376								13.9	19.0	15.6	14.7	15.3
377								13.9	19.0	12.8	16.2	16.4
378								14.9	13.4	11.8	17.1	14.8
697								21.4	24.8	24.8	27.6	23.7
701								19.2	26.1	22.2	31.3	19.6
704								20.4	30.9	26.3	41.0	16.2
706								16.2	23.6	29.7	37.1	19.6
712								17.6	32.5	31.9	35.5	19.2
714								9.7	27.8	17.8	51.7	27.9

Primary Table C-2, continued

Eel no:	1	2	3	4	5	6	7	8	9	10	11	12
Starvation, days	Rate of oxygen consumption, ml O_2/kg/hour											
1072			30.9		12.2		18.1					
1075			26.9		24.5		24.7					
1076			27.8		26.9		29.2					
1077			24.9		24.3		27.1					
1089			59.7		22.8		22.4					
1090			43.8		19.2		20.7					
1091			31.4		18.3		20.4					
1092			52.7		20.5		22.3					
1096			38.3		18.6		27.4					
1098			29.1		20.5		19.9					
1132									40.2	20.0	33.7	
1133									29.1	28.1	33.9	
1137									34.2	24.4	49.4	
1145									27.8	22.2	36.8	
1147									42.4	17.2	–	
1431											41.9	
1432											31.3	
1433											36.4	
1446											43.7	
1447											42.6	
1448											40.7	
1452											42.7	
1454											48.2	