Dana, vol. 1, pp. 1-28, 1980

Experimental maturation of female silver eels, *Anguilla anguilla*. Estimates of fecundity and energy reserves for migration and spawning

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Abstract

Female silver eels at body weights of 0.5 to 1.5 kg were treated with acetone-dried carp pituitaries and other gonadotrophic substances. Experiments were made in sea water at 23 °C. The most successful treatment proved to be 15 mg carp pituitary + 500 IU HCG twice a week. This dosage resulted in strip-ripe eels in 40-80 days. Maximum gonado-somatic index: 60.7. Attempts at fertilization succeeded in a few cases, but embryonic development ceased at early stages (gastrula). The estimated fecundity of matured eels ranged from 0.7 to 2.6 million eggs. Ovaries and somatic bodies of matured eels were analysed for contents of water, lipid and protein. Based on the calculated energy reserves a rough estimate of an energy budget for migration and spawning was established.

Contents

Introduction

The present study was carried out from October, 1973, to March, 1979, at the Danish Institute for Fisheries and Marine Research, Physiological Laboratory, Denmarks Aquarium.

From 1940 to 1970 experiments on eel maturation were made in this laboratory. The hormones used were human chorionic gonadotrophin (HCG) and mammalian gonadal hormones. The progress with female eels has been described in the papers Bruun *et al.*, 1949, Møller-Christensen *et al.*, 1956, and Boëtius *et al.*, 1962. Full maturity was not arrived at. The maximum gonado-somatic index (GSI = ovaries in % of body weight) obtained was 12.6 only.

A high degree of maturation (max. GSI = 40) was achieved by Fontaine, 1964, who treated female eels with carp pituitary (CP) extracts. Eggs were spawned but no pictures of them were given. Attempts at fertilization were not made. Villani & Lumare, 1975, also applied CP extracts resulting in a maximum GSI of 44.9. Attempts at fertilization failed. Kokhnenko *et al.*, 1977, used 'pituitaries' without mentioning their source. GSI-values were not given.

The above-mentioned results all concern *A. anguilla*. Edel, 1975, obtained maximum GSI = 44.8 in *A. rostrata* treated with CP. It only remains to mention the great Japanese success. Treating *A. japonica* with salmon pituitaries fertilization, hatching and survival of small larvae were achieved. Rearing of larvae is in progress. We refer to the sequence of papers: Yamamoto *et al.*, 1974; Yamamoto & Yamauchi, 1974, Yamamoto *et al.*, 1975a and 1975b, Yamauchi *et al.*, 1976.

The background for resuming our work on female eels in 1973 was the inspiration we took from the work of Ishii on *A. japonica* (see Nose, 1971). This was the first time that a mature female eel in strip-ripe condition had been seen, with photos of the eggs.

The purpose of the present study does differ from that of our earlier work. By inducing sexual maturity we try in our laboratory to through light on the almost completely unknown phases in the eel's life-story: the migration and the breeding biology.

Our experiments are continuing.

Experimental

In October-November in the years 1973 to 1978 batches of about 80 female silver eels were brought to the laboratory. The eels were caught in poundnets in the Sound near Copenhagen during their seaward migration. Body weights of eels at catch averaged about 0.8 kg (range: 0.5 to 1.5 kg).

The eels were acclimatized in 3 concrete tanks (about 2 m^3 each) connected with the 'cold sea water' circuit of Denmarks Aquarium (temperature: 14 ± 2 °C). Duration of stay is given in table 1. Acclimatization mortality was 1 to 10 % during the first three weeks. In the next four months it was almost negligible.

At start of each experimental run the eels were anaesthetized by immersion for about 5 minutes in a 1.5 % solution of ethyl-urethane in sea water. Body weights,

Table 1. Acclimatization periods and experimental temperatures.

Run no.	Arrival of eels	Start of experiment	Acclim. period, days	Temperature, °C, during exp. period, mean (range)
1	73.10.25	73.12.04	40	23.1 (22.1-24.2)
2	–	74.02.19	67	24.1 (22.4-25.8)
3	74.11.11	75.01.21	71	25.0 (24.0-26.0)
4	75.11.17	75.11.21	4	regulation failed
5	–	76.02.06	81	23.4 (21.6-23.8)
6	76.11.17	76.11.29	12	22.3 (21.5-22.8)
7	–	77.01.31	65	22.8 (21.2-24.2)
8	77.10.11	77.10.17	6	23.3 (21.8-24.1)
9	–	77.12.26	76	23.1 (23.0-23.2)
10	–	78.01.16	97	22.5 (21.2-24.0)
11a	–	78.11.27	412	22.6 (21.0-23.2)
11b	78.10.04	–	54	–

total lengths and eye-sizes were measured and the first (intramuscular) injections were given.

Next the eels were tagged. For the eels of run 1 Floy tags were applied while in runs 2 to 11 a system of cuts in the pectorals made it possible to distinguish the eels individually.

After tagging the eels were transferred directly to 3 tanks (1.5 m^3 each) in the 'warm sea water' circuit. Salinity: 31 ± 1 ‰ S, temperature about 23 °C (see table 1).

The hormones and other injected substances are listed in table 2. The ground carp pituitaries (CP) and oestradiol were in suspension, FSH and HCG were in solution in 1 % NaCl. Tocopherol was injected directly.

Table 2. Sources of hormones and other injected material.

Material	Symbol	Source
Carp pituitary	CP	Acetone dried (3 mg = abt. 1 CP) *Run 1-2*: Fish Cult. Res. St., Szarvas, Hungary. *Run 3-11*: Stoller Fisheries, Iowa, U.S.A.
Human chorionic gonadotrophin	HCG	Physex, Bulk 173071, Leo Pharmaceutical Products, Denmark. 1000 IU = .52 mg
Follicle stimulating hormone	FSH	Porcine. Sigma F-8001
Oestradiol	Oe	Follicyclin. Ciba-Geigy (microcryst.)
DL-α-Tocopherol	Toc.	Merck. Art. 8283, .05 ml = 52 IU

Table 3. Chronologically arranged data on hormone injected, female silver eels.

Run no.	Eel no.[1]	Date of first injection	Treatment	Total nb. of treatments	Exp. life span, days[2]	Total length, cm	Body weight, g: Initial	Body weight, g: At death	Change in body weight, %	Change in eye size, %	Ovaries: Weight at death, g	Ovaries: GSI[3]
1	1	73.12.04	3 mg CP + .05 ml Toc./week	3	16	69	679	628	−8	−44	11.1	1.8
–	2	–	– – – –	6	37	71	697	522	−25	+11	16.0	3.1
–	3	–	3 mg CP/week	3	18	78	1078	970	−10	+28	15.5	1.6
–	4	–	– – – –	2	13	78	880	850	−3	+43	21.8	2.6
–	5	–	3 mg CP + 1 U FSH + .05 ml Toc./week	4	22	79	856	770	−10	+11	16.1	2.1
–	6	–	– – – –	6	42	82	955	771	−19	−24	22.0	2.9
–	7	–	3 mg CP + 1 U FSH/week	7	48	75	820	648	−21	−2	24.1	3.7
–	8	–	– – – –	6	36	78	907	785	−14	+2	25.7	3.3
–	9	–	3 mg CP + 1000 IU HCG + .05 ml Toc./week	1	6	81	1186	1150	−3	−15	25.5	2.2
–	10	–	– – – –	6	36	78	800	648	−19	−25	24.1	3.7
–	11	–	3 mg CP + 1000 IU HCG/week	1	1	82	897	897	0	0	16.1	1.8
–	12	–	– – – –	12	80	80	850	672	−21	+57	72.0	10.8
–	13	–	3 mg CP + 1 U FSH + 1000 IU HCG + .05 ml Toc./week	18	125	74	851	587	−31	+47	11.7	2.0
–	14	–	– – – –	18	125	83	928	648	−30	+17	33.5	5.2
–	15	–	3 mg CP + 1 U FSH + 1000 IU HCG/week	3	21	79	1016	890	−12	+39	30.7	3.5
–	16	–	– – – –	1	7	81	1156	1144	−1	−23	17.1	1.5
–	17	–	1 U FSH + .05 ml Toc./week	5	33	75	914	808	−12	−26	13.7	1.7
–	18	–	– – – –	11	71	75	869	770	−11	−10	10.2	1.3
–	19	–	1 U FSH + 1000 IU HCG/week	1	6	71	737	683	−7	−3	14.6	2.1
–	20	–	– – – –	8	50	78	939	741	−21	+28	19.4	2.6
2	25	74.02.19	3 mg CP + 1 U FSH + 1000 IU HCG + .05 ml Toc./week	14	98	67	616	422	−32	+66	8.3	2.0
–	26	–	– – – –	11	73	85	1116	940	−16	+97	181.4	19.3
–	27	–	– – – –	15	99	72	647	460	−29	+139	88.2	19.2
–	28	–	– – – –	14	95	74	684	480	−30	+51	121.3	25.3
–	29	–	3 mg CP + 1 U FSH + 1000 IU HCG/week	8	54	68	572	480	−16	+36	42.7	8.9
–	30	–	– – – –	14	95	76	702	450	−36	+50	11.6	2.6
–	31	–	– – – –	1	5	83	1028	958	−7	−21	18.2	1.9
–	32	–	– – – –	14	94	74	761	575	−24	+97	72.1	12.5
–	34	–	3 mg CP + 1 U FSH + 1000 IU HCG + .05 ml Toc. + ...	2	7	73	712	604	−15	−3	8.4	1.4
–	35	–	– – – .2 mg Oe/week	3	17	73	779	706	−9	−20	20.0	2.8
–	36	–	– – – –	10	69	77	790	620	−22	+73	48.0	7.7
–	37	–	– – – –	18	126	74	862	595	−31	+18	16.6	2.8
–	38	–	3 mg CP + 1 U FSH + 1000 IU HCG + .2 mg Oe/week ...	4	28	80	890	892	0	+4	27.1	3.0
–	39	–	– – – –	12	84	92	1155	742	−36	+78	64.8	8.7
–	40	–	– – – –	11	71	78	862	840	−3	+57	24.8	3.0

–	41	–	–	–	–	–	10	64	68	737	649	−12	+84	136.5	21.0
–	43	–	3 mg CP + 1 U FSH + .05 ml Toc. + .2 mg Oe/week				14	*98*	71	612	490	−20	+64	25.0	5.1
–	44	–	–	–	–	–	7	48	71	709	670	−6	–	21.7	3.2
–	45	–	–	–	–	–	18	*126*	73	772	572	−26	+57	54.1	9.5
–	46	–	3 mg CP + 1000 IU HCG + .05 ml Toc. + .2 mg Oe/week				12	79	76	719	620	−14	+52	144.5	23.3
–	47	–	–	–	–	–	8	50	76	761	570	−25	+12	36.7	6.4
–	48	–	–	–	–	–	11	73	74	810	750	−7	+50	121.5	16.2
–	49	–	3 mg CP + .05 ml Toc. + .2 mg Oe/week				18	*126*	73	815	620	−24	+73	71.5	11.5
–	50	–	–	–	–	–	14	*98*	76	749	575	−23	+39	14.2	2.5
–	51	–	–	–	–	–	6	41	85	852	754	−12	+17	19.5	2.6
3	52	75.01.21	30 mg CP/week				15	*104*	67	680	515	−24	+45	93.0	18.7
–	53	–	–	–	–	–	19	*140*	77	890	578	−35	+23	72.3	12.5
–	54	–	–	–	–	–	19	*139*	80	880	578	−34	+32	72.6	12.6
–	55	–	–	–	–	–	12	80	68	570	620	+9	+18	255.9	43.9
–	56	–	–	–	–	–	18	*122*	74	775	597	−23	+38	136.1	22.8
–	57	75.02.04	30 mg CP + 1000 IU HCG/week				9	56	72	805	835	+4	+3	264.0	33.9
–	58	–	–	–	–	–	10	64	73	660	570	−14	+13	164.6	32.1
–	59	–	–	–	–	–	8	54	74	770	812	+6	+47	272.1	35.9
–	60	–	–	–	–	–	9	57	83	925	890	−4	+29	260.0	31.1
–	61	–	–	–	–	–	9	57	73	730	655	−10	+35	166.3	26.5
–	62	–	15 mg CP/2 × a week.....				14	48	72	710	620	−13	+15	106.3	17.1
–	63	–	–	–	–	–	13	42	72	740	672	−11	−7	89.7	13.4
–	64	–	–	–	–	–	16	52	72	715	580	−19	+18	104.3	18.0
–	65	–	–	–	–	–	14	46	72	575	700	+22	+14	262.0	40.2
–	66	–	–	–	–	–	14	47	72	625	545	−13	+7	92.2	16.9
5	82	76.02.06	10 mg CP/3 × a week.....				19	46	76	750	685	−9	+99	160.6	23.5
–	83	–	–	–	–	–	8	18	67	583	567	−3	−21	21.1	3.7
–	84	–	–	–	–	–	1	1	72	724	710	−2	−24	9.5	1.3
–	85	–	–	–	–	–	17	39	76	790	758	−4	+17	140.7	18.6
–	86	–	–	–	–	–	16	35	77	932	938	+1	+13	123.4	13.2
–	87	–	10 mg CP + 333 IU HCG/3 × a week				18	47	67	537	>500*4	–	–	>123*4	–
–	88	–	–	–	–	–	7	15	70	714	703	−2	−15	17.9	2.6
–	89	–	–	–	–	–	13	29	68	608	615	+1	+54	51.9	8.4
–	90	–	–	–	–	–	5	11	75	816	717	−12	−6	15.7	2.2
–	91	–	–	–	–	–	17	41	71	638	768	+20	+68	297	38.7
–	92	–	15 mg CP + 500 IU HCG/2 × a week				13	52	81	940	997	+6	+7	467	46.8
–	93	–	–	–	–	–	6	17	72	665	655	−2	0	26.9	4.1
–	94	–	–	–	–	–	13	46	75	780	972	+25	+47	442	45.5
–	95	–	–	–	–	–	7	21	74	793	751	−5	+26	29.0	3.9
–	96	–	–	–	–	–	12	39	71	585	>692*4	>+18	+50	>320*4	>46.2*4

Table 3 continued

Run no.	Eel no.[1]	Date of first injection	Treatment	Total nb. of treatments	Exp. life span, days[2]	Total length, cm	Body weight, g: Initial	Body weight, g: At death	Change in body weight, %	Change in eye size, %	Ovaries: Weight at death, g	Ovaries: GSI[3]
6	97	76.11.29	15 mg CP + 500 IU HCG/2 × a week	12	39	68	720	1012	+41	+75	529.5	52.4
–	98	–	–	14	47	67	642	842	+31	+59	449.5	53.4
–	99	–	–	14	47	74	628	579	−8	+42	214.1	37.0
–	100	–	–	13	45	66	600	787	+31	+64	435.1	55.3
–	101	–	–	13	45	73	662	817	+23	+42	485.9	59.5
–	102	–	–	13	45	68	603	812	+35	+57	458.0	56.4
–	103	–	–	15	50	73	686	773	+13	+27	318.2	41.2
–	104	–	–	13	45	65	545	720	+32	+53	426.2	59.2
7	105	77.01.31	15 mg CP + 500 IU HCG/2 × a week	14	48	71	604	594	−2	+23	114.8	19.3
–	106	–	–	4	11	71	634	678	+7	−24	17.0	2.5
–	107	–	–	20	66	64	519	592	+14	+26	308.4	52.1
–	108	–	–	18	66	70	614	861	+40	+41	480.6	55.8
–	109	–	–	9*[5]	*71*	70	599	530	−12	+15	36.5	6.9
–	110	–	–	8	25	63	442	436	−1	+15	13.2	3.0
–	111	–	–	10*[5]	*71*	65	573	507	−12	+54	67.4	13.3
–	112	–	–	6	18	74	626	606	−3	−26	26.5	4.4
8*[6]	113	77.10.17	15 mg CP + 500 IU HCG/2 × a week	18	61	74	696	860	+24	+42	415	48.3
–	114	–	–	14	48	76	1000	1123	+12	+28	456	40.6
–	115	–	–	19	66	83	1339	1487	+11	−4	611	41.1
–	116	–	–	20	45	71	737	1022	+39	+16	576	56.4
–	117	–	–	23	48	82	1317	1956	+33	+71	1147	58.6
–	118	–	–	26	52	75	942	>1022*[4]	>+9	+37	>462*[4]	>45.2*[4]
–	119	–	–	11	74	86	1095	1037	−6	+21	439	42.3
–	120	–	–	11	42	81	791	984	+24	+3	430.7	43.8
–	121	–	–	6	20	81	1203	1095	−9	+5	50.2	4.6
–	122	–	–	11	*91*	90	1368	1179	−14	+38	233.8	19.9
9*[7]	123	77.12.26	15 mg CP + 500 IU HCG/2 × a week	12	39	81	1144	1111	−3	+78	157.5	14.2
–	124	–	–	5	*16*	71	769	709	−8	+32	27.0	3.8
–	125	–	–	3	10	78	1029	968	−6	−13	25.3	2.2
–	126	–	–	3	*10*	78	826	793	−4	−9	25.9	3.3

–	127	–	–	–	–	–	3	*10*	80	813	849	+4	+9	33.2	3.9
–	128	–	–	–	–	–	5	*16*	73	841	926	+10	+51	46.4	5.0
–	129	–	–	–	–	–	3	*10*	71	716	735	+3	−8	19.5	2.7
–	130	–	–	–	–	–	5	*16*	71	910	904	−1	+33	38.9	4.3
–	131	–	–	–	–	–	5	*16*	68	578	546	−6	+46	21.3	3.9
–	132	–	–	–	–	–	3	*10*	78	838	882	+5	−9	27.1	3.1
10	133	78.01.16	15 mg CP + 500 IU HCG/2 × a week				14	46	74	752	950	+26	+67	446	46.9
–	134	–	–	–	–	–	17	58	72	836	1106	+32	+101	550	49.7
–	135	–	–	–	–	–	14	49	75	800	1133	+42	+99	612	54.0
–	136	–	–	–	–	–	15	50	65	619	713	+15	+57	332	46.6
–	137	–	–	–	–	–	16	*63*	82	1152	1614	+40	+83	892	55.3
–	138	–	–	–	–	–	16	63	72	791	920	+16	+83	402	43.7
–	139	–	–	–	–	–	13	44	83	1107	1276	+13	+76	520	40.8
–	140	–	–	–	–	–	11	38	80	1001	985	−2	+36	147	14.9
–	141	–	–	–	–	–	15	50	79	995	1308	+31	+117	666	50.9
–	142	–	–	–	–	–	15	52	79	1052	1457	+39	+35	884	60.7
11*8	143	78.11.27	15 mg CP + 500 IU HCG/2 × a week				13	44	67	428	489	+14	+39	207	42.3
–	144	–	–	–	–	–	24	*84*	81	615	602	−2	+40	250	41.5
–	145	–	–	–	–	–	18	61	74	592	846	+43	+98	428	50.6
–	146	–	–	–	–	–	17	57	74	604	754	+25	+52	383	50.8
–	147	–	–	–	–	–	18	60	81	820	1171	+43	+73	671	57.3
–	148	–	–	–	–	–	18	63	68	412	>400*4	>−3	+44	>145*4	>36.3*4
–	149	–	–	–	–	–	3	7	72	635	584	−8	–	16.7	2.9
–	150	–	–	–	–	–	16	53	68	676	834	+23	+37	368	44.1
–	151	–	–	–	–	–	13	45	72	696	802	+15	+37	297	37.0
–	152	–	–	–	–	–	8	25	77	850	841	−1	+7	50.6	6.0
–	153	–	–	–	–	–	16	55	72	646	723	+12	+49	301	41.8
–	154	–	–	–	–	–	3	7	69	569	560	−2	–	13.0	2.3

1. Missing nos (21-24, 33, 42 and 67-81) were occupied by part of the non-injected controls and by the eels of the unsuccessful run 4.
2. Figures in italics and underlined indicate *sacrified* eels.
3. Eels at GSI-values > 40 with few exceptions (nos 55 and 65) proved strip-ripe just prior to death.

*4. Eels nos 87, 96, 118 and 148 spawned part of their eggs during the last 1-6 days before dying.

*5. Injections discontinued after 10 % increase in body weight.

*6. After injection no. 11, eels nos 116-118 recieved daily injections, while injections of eels nos 119, 120 and 122 were discontinued.

*7. Eels nos 123-132 were diseased.

*8. Eels nos 143-148 were starved one year before start of experiment.

Maturation of females

Details of the maturation experiments (runs 1-11) are listed chronologically in table 3. A few general remarks on the individual runs are given here.

Runs 1 and 2. The rather complex treatment of the eels was an attempt to simulate the procedure of Ishii's successful experiment with *A. japonica* mentioned above. Maximum achieved GSI was 25.3 and it was concluded that only CP or CP + HCG treatment was essential for the gonadal response.

Runs 3 and 5 (run 4 failed) include variations in CP and CP + HCG dosage. Maximum GSI was 46.8 and it was concluded that treatment by CP + HCG was more successful than treatment by CP alone. Only by combined treatment were strip-ripe eels obtained. As the most favourable 'standard treatment' we agreed upon: 15 mg CP + 500 IU HCG/2 × a week.

In runs 6, 7, 8 and 10 (in run 9 the eels were diseased) the 'standard treatment' was maintained except for a few variations in runs 7 and 8. The season (or duration of acclimatization period) was the experimental variable. Maximum GSI achieved was 60.7.

In run 11 eels acclimatized for one year were run simultaneously with freshly caught eels.

Controls. 3 to 6 non-injected eels shared conditions with experimental eels in runs 1 to 5. No gonadal changes could be observed.

Development of ovaries

Growth of ovaries is demonstrated in fig. 1 where GSI's are plotted against time for CP-treated eels. Eels at GSI > 40 are nearly all fully ripe. This condition is arrived at after 40-80 days of experiment. GSI-values rise steeply shortly before maturity is reached (water uptake). In fig. 2 changes in body weights are plotted against ovary weights. Both variables are given in absolute figures. At ovary weights from control size (about 10 to 20 g) to about 100 g the changes in body weights are scattered and predominantly negative. During this period the loss in body weight due to respiration exceeds the possible gain caused by water uptake of ovaries. At ovary weights of about 200 g water uptake has brought the body weight up to the level of initial weight. From now on a gain in body weight follows.

Fig. 3 demonstrates more directly the water uptake of individual eels, which have been weighed at intervals during experiment. Two batches of eels are shown. The first (above in fig.) comprises six 'standard treated' eels from run 6. A very steep rise in body weight is indicated between the 8th and the 12th injection (25 to 40 days of experiment). The successful result was GSI-values between 52.4 and 59.5. The second batch (below in fig.) comprises five eels from run 3 receiving the same weekly amount of hormones as the first batch, but injected only once a week. Here the water uptake follows after nearly the same number of injections and is consequently correspondingly delayed. GSI-values obtained ranged from 26.5 to 35.9 only. In addition to demonstrating water uptake we consider the result given in fig. 3 as an argument for our choice of 'standard treatment'.

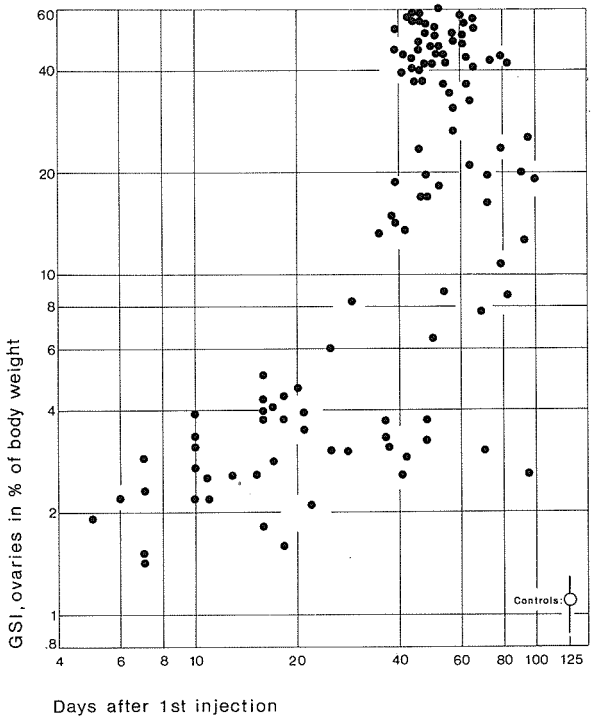

Fig. 1. Growth of ovaries. GSI-values (log scale) versus time elapsed from first injection (log scale). All 112 eels have been treated with CP alone or in combination. They have survived 4 days of experiment. Sacrified eels are not included except for the eels of run 9. GSI-values (mean $\pm 2 \times$ S.E.) are given for 5 non-injected controls sacrified after 125 days.

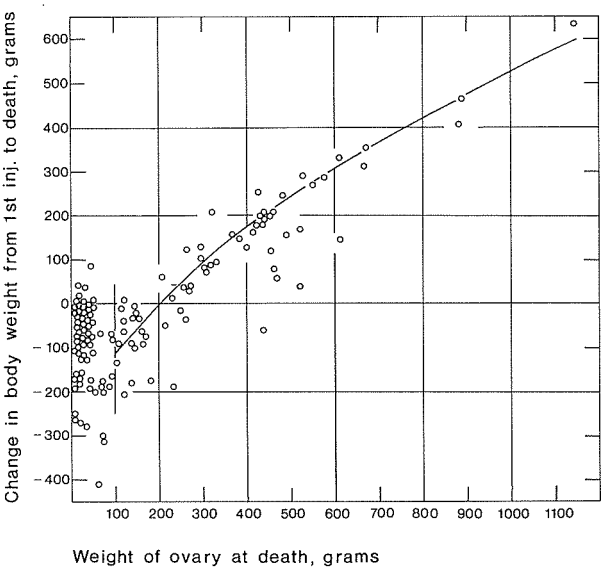

Fig. 2. Change in body weight from start of experiment to death plotted against weight of ovaries at death. The figure includes all eels from table 3 treated with CP (N = 129). The graph for ovaries above 100 g is fitted by eye.

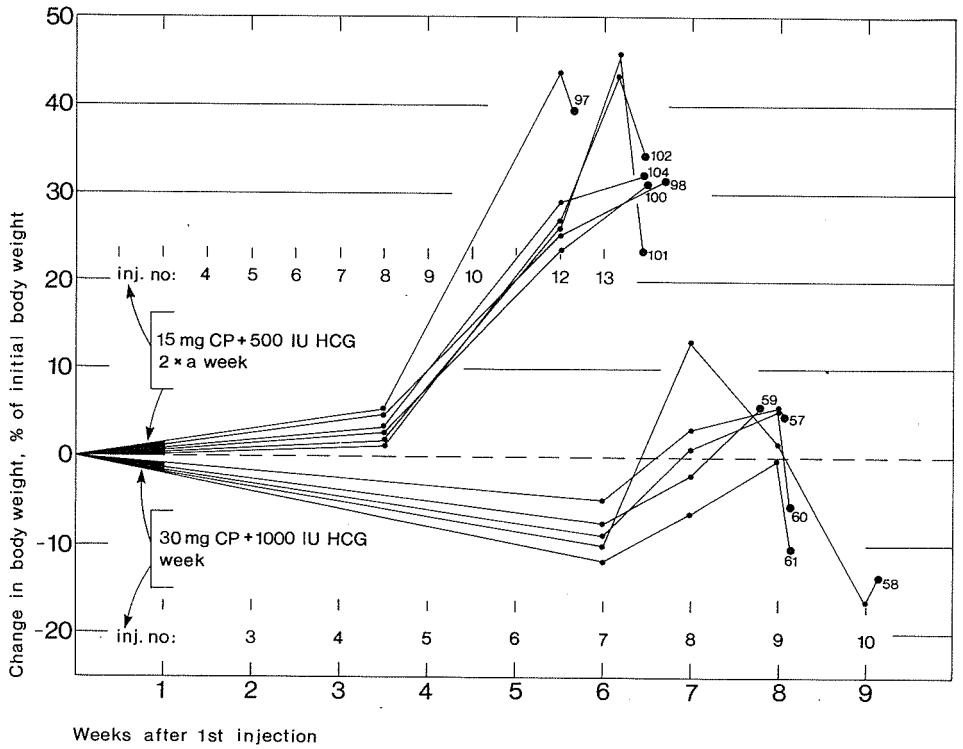

Fig. 3. Change in body weight during experiment. Two different principles of hormone treatment have been applied. Small black spots indicate live eels, large black spots indicate eels at death. Figures following the large spots indicate individual eel nos as listed in table 3.

Strip-ripeness. Our first strip-ripe eel (no. 96) was obtained in run 5. Any eel from runs 5-11 at GSI > 40 proved strip-ripe. As demonstrated in the photo sequence in fig. 4 eggs were easily stripped. When opening a strip-ripe eel it is evident that the gonadal structure is widely disintegrated. It often looks as if the body cavity were full of loose eggs. Strip-ripeness occurs as early as a week before dying thus allowing us to obtain egg samples for attempted fertilization. Strip-ripeness has not been described by other authors working on experimental maturation of the European eel.

Spawning. Both Fontaine *et al.*, 1964, and Villani & Lumare, 1975, describe spontaneous emission of the sexual products. After such activities Fontaine's eel still had a GSI of 31.8.

Only a few of our eels were directly observed to spawn a significant amount of eggs (nos 87, 96, 118 and 148). But no doubt several other eels at intervals (especially by night?) have released small amounts of eggs. During maturation periods free eggs were often noted in the experimental tanks.

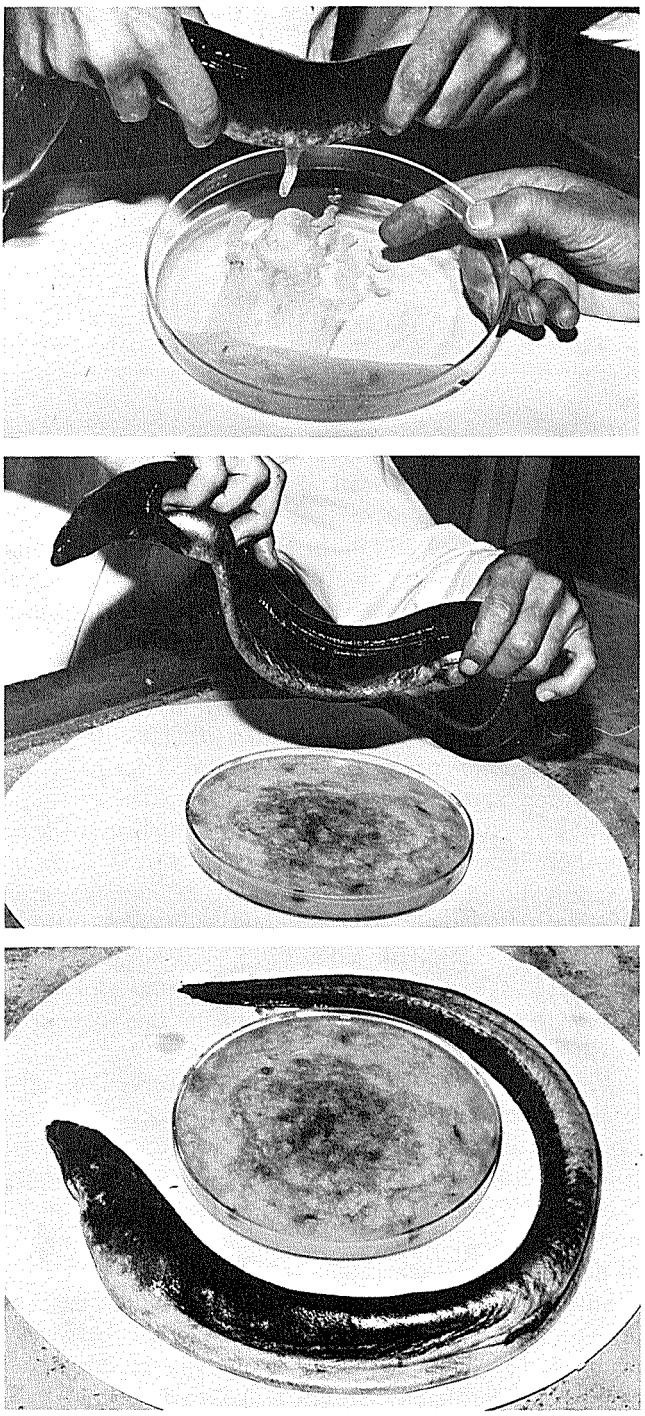

Fig. 4. Stripping procedure. Eel no. 96. 1976.03.16. In the bottom picture the total egg mass (about 320 g) has been stripped into the dish. Weight of the spent eel is about 370 g.

Table 4. GSI and maturation periods of 'standard treated' strip-ripe eels listed according to rising length of acclimatization period.

Acclim. period, days	Run no.	Initial no. of eels	Nos of strip-ripe eels	GSI of strip-ripe eels, mean (range)	Maturation period of strip-ripe eels, mean (range)
6	8	3	3	43.3 (40.6-48.1)	58 (48-66)
12	6	8	7	49.6 (41.2-59.5)	45 (39-50)
54	11b	6	2	43.0 (41.8-44.1)	54 (53-55)
65	7	6	2	54.0 (52.1-55.8)	66 (66-66)
81	5	5	3	46.2 (45.5-46.8)	46 (39-52)
97	10	10	9	49.8 (40.8-60.7)	53 (44-63)
412	11a	6	5	48.5 (41.5-57.3)	61 (44-84)

'Season'. Is it possible to indicate a special favourable season for experimental maturation? In table 4 all 'standard treated' strip-ripe eels of individual runs are listed according to increasing length of the acclimatization period. Variations in the GSI's obtained and in the maturation times are small and in no way systematic. This differs from the results obtained with male silver eels. Here a decline in the rate of maturation from autumn to spring was indicated (Boëtius & Boëtius, 1967).

The eggs

Hundreds of egg-samples from strip-ripe eels (live or dead) have been studied under the microscope in sea water of 31 ‰. In this salinity all eggs sink.

Egg diameters are relatively uniform: 1.05 ± 0.15 mm. When observed immediately after sampling the perivitelline spaces of the eggs are very small. During about half an hour the size of the perivitelline space increaces and stabilizes at the egg diameters mentioned. The sphere of yolk occupies about 0.6 mm.

Great variation occurs, however, as to transparency. Clear eggs are present together with opaque specimens. Also variable is the number of oil globules in the yolk. This is demonstrated in fig. 5 where eggs of three types from the same eel are selected for presentation: eggs with several globules, eggs with few globules and eggs with one globule only. We consider this sequence as developmental stages, for three reasons:

1. Under the microscope we have observed directly the fusion of two globules.
2. Russel, 1976, (writing about fish eggs in general): 'In a number of species, classed as having a single oil globule, there may at first be several globules which coalesce during the development of the embryo to form the single oil globule'.
3. In the fertilized *A. japonica* eggs pictured by Yamamoto *et al.*, 1975 a, the number of oil globules changed from a few to a single one during the earliest stages of development.

Some discrepancy exists between different authors as to the size of the European eel egg. Fontaine *et al.*, 1964, give diameters between 0.93 and 1.4 mm, Villani & Lumare, 1975: 1.0-1.1 mm (as the eggs in this work), while Kokhnenko *et al.*, 1978, give diameters as high as 1.2 to 1.6 mm. Yevseyenko, 1974, pictures eggs

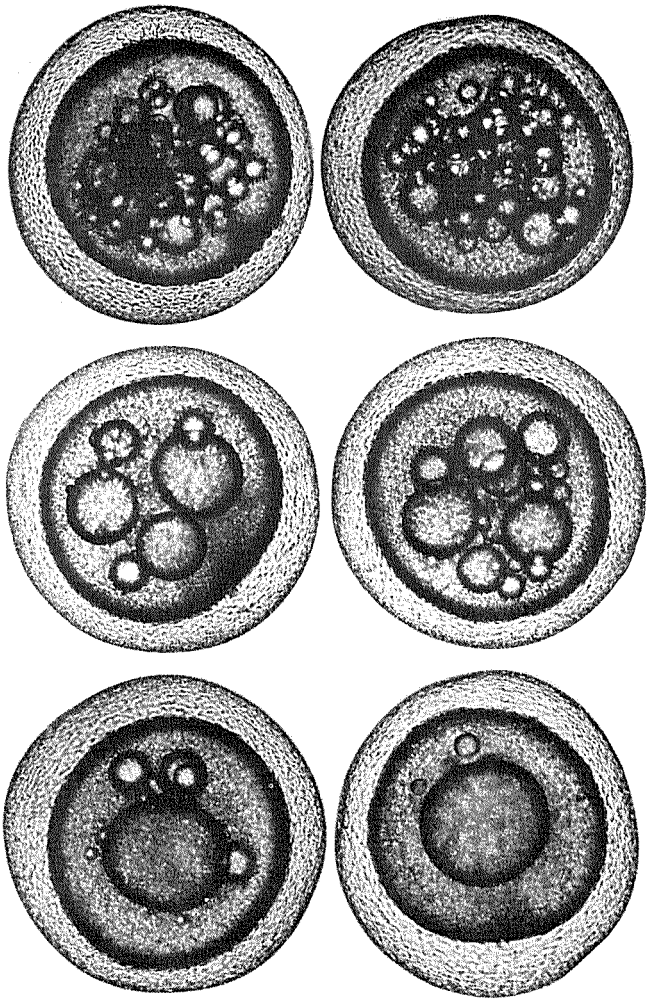

Fig. 5. Eggs stripped from eel no. 103. 1977.01.18. Selected to demonstrate variation in number and size of oil droplets.

received from Fontaine. Diameters: 0.9-1.3 mm. Yevseyenko is of the opinion, that eel eggs during further development will swell to diameters of 2.3 to 2.9 mm thus fitting well to an egg material from George's Bank which he claims to be *Anguilla anguilla*. The eggs caught off Bermuda and claimed by Fish, 1927, to belong to *A. rostrata* were 3.3 mm in diameter, while a maximum diameter of 1.25 mm for the same species was achieved from experimental studies by Edel, 1975.

Identification of Atlantic eel eggs caught at sea must, however, remain guesswork until we possess complete developmental series. (It may be noted that eggs of *A. japonica* successfully hatched by Yamamoto *et al.*, 1975 a, had diameters of about 1.0 mm).

Maturation of males, attempts at fertilization

Male silver eels (about 38 cm, 80 g) were brought to the laboratory at the same time as the females. They shared acclimatization and experimental conditions with the females but were kept in separate tanks. At the start of each run 30 males received a single injection of 1000 IU HCG which, according to Boëtius & Boëtius, 1967, would induce full sexual maturity.

At the experimental temperature (about 23 °C) full development of the male gonads (stage 5) was attained in about 60 days. However, as great variations occurred in the development of individual eels we always had ripe males at hand for the strip-ripe females. The motility of sperm cells varied very much.

Fertilization attempts were made with freshly stripped eggs from 21 out of the 37 strip-ripe eels at GSI > 40. 1 to 3 samples (a few g each) from each eel were studied, all samples being taken within the last week before death. 1 to 5 minutes after sampling the eggs were brought together with sperm from 1 to 3 males. Immediately before, a few ml seawater was added. About 5 minutes later excess sperm was washed away through nylon gauze. The egg samples were transferred to tanks with aerated seawater (5 litres, 31 ‰ S, 21-23 °C) to which was added penicillin and streptomycin.

Eggs from 16 out of the 21 strip-ripe eels did not show any sign of fertilization. In the remaining 5 eels (nos 98, 116, 117, 118 and 148) a few early developmental stages were observed. In a 1 gram sample from eel no. 148 (79.01.24, 5 days before death) 20-30 developmental stages were observed about 20 hrs after the fertilization attempt. They were similar to the gastrula pictured by Yamamoto *et al.*, 1975 a (plate I, 6). The eggs, however, did not develop further.

Other responses to hormones

Sexual behavior

In order to study possible courtship ripened female and male eels were brought together in a separate tank. This was made on the dates 1977.1.4, 4.4, 12.3, 1978. 2.28 and 3.7 with female eels nos 97, 108, 117, 139 and 141 respectively. The number of participating males was 1-3 per female. Courtship was observed in four out of the five experiments. In the fifth case (eel no. 139) no courtship at all was observed during a 2 hours period. This female, however, died a few hours later. Below is given a description of sequences representative of the observations in the four positive cases.

During the first about 15 minutes or so the male will swim around as if he were searching for something while the female will remain almost quiet. When finally the male has detected the female he starts rubbing her belly with his head. He is especially attracted by her abdominal apertures. The female is thereby pushed slowly forwards through the water and starts a slow swimming.

Still while the couple is moving, the stimulated male will try to obtain maximum contact between the bodies and is often seen to cling to the female with his back against her belly as seen in the photo fig. 6.

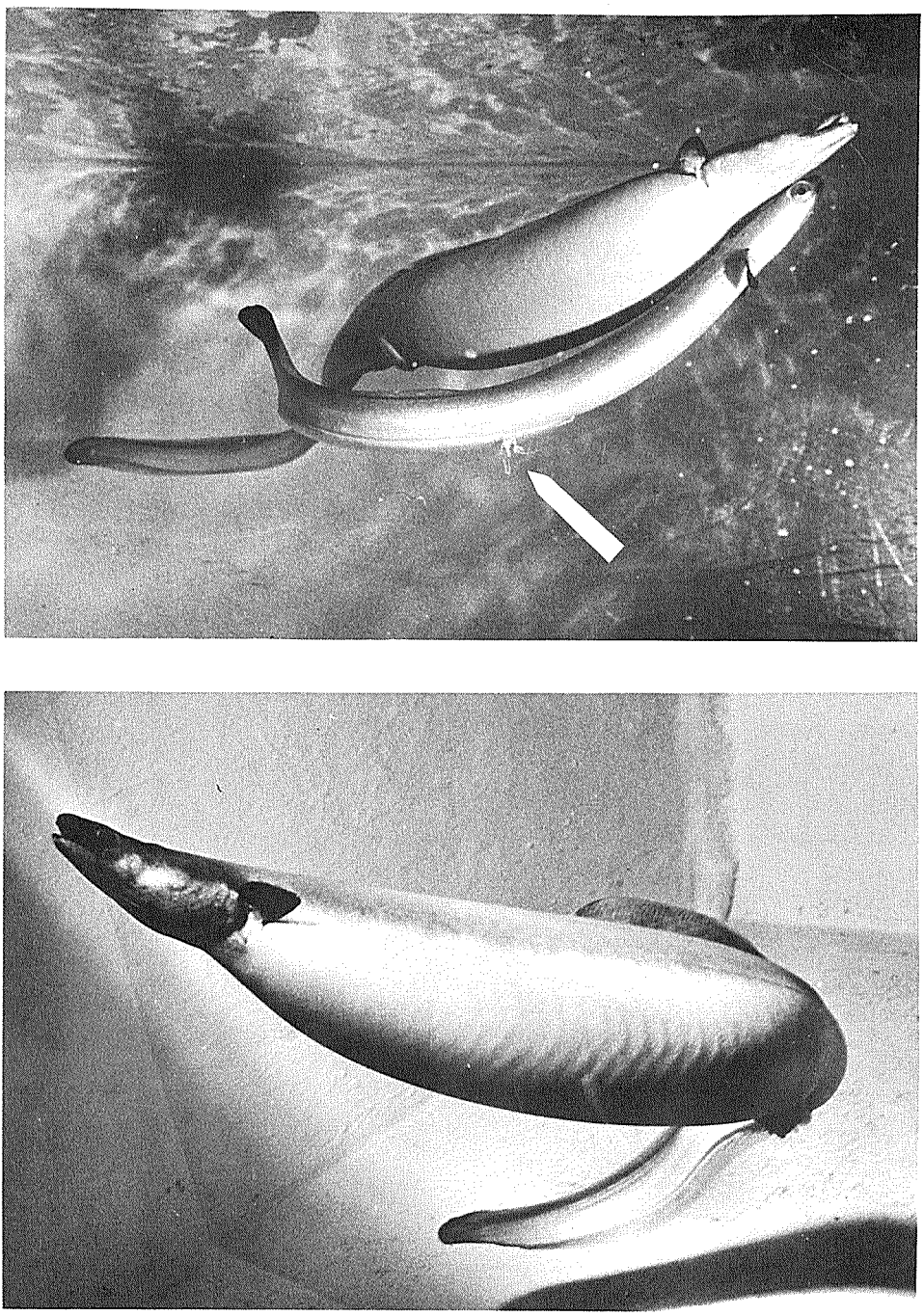

Fig. 6. Two photos of stripe-ripe eel no. 108. 1977.04.04. Top: Courtship. Sperm emission from the male is indicated by arrow.

After a few minutes of contact the male will release his first cloud of sperm. In the succeeding 20 minutes or so 7 to 10 ejections of sperm will follow. Fig. 6 also shows the emission of sperm as indicated by the arrow. Exposure time of the flash-light used is less than 1/2000 seconds. Shortly afterwards the couple will be surrounded by a milky cloud of sperm.

When two or three males were placed together with one female they all took part in the initial courtship. In every case, however, only one of the participating males released sperm during the experiment.

From the above description it can hardly be told whether the female has at all responded to the male's activities. As no spawning was observed, the description must be considered valid for the male behaviour only.

Eye-size

Horizontal (h) and vertical (v) axes of the eel's eye were measured to nearest 0.1 mm at start of experiment and at death. The change in eye-size was expressed as percentage change of the area $h \times v$.

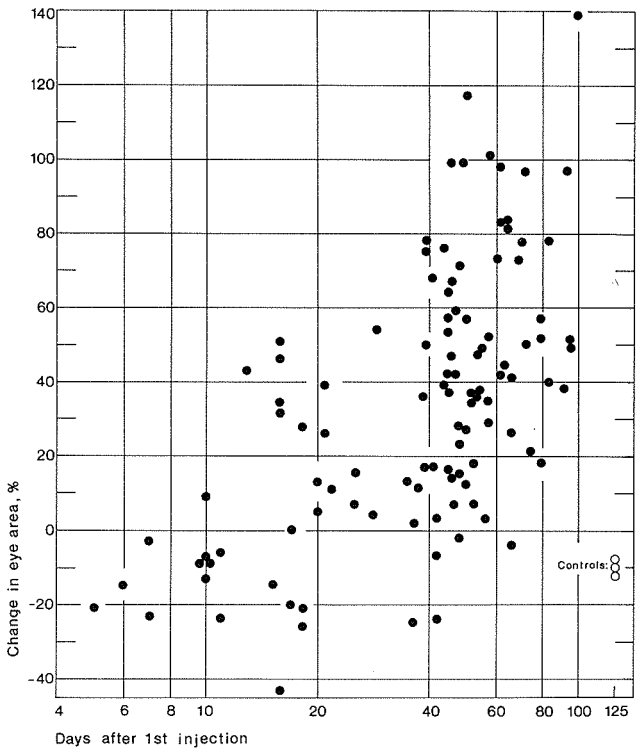

Fig. 7. Change in eye area versus time elapsed from first injection (log scale). N = 109. Same eels as used for fig. 1 except for 3 eels where eyes were not measured. Eye areas are given of 3 non-injected controls sacrified after 125 days.

In fig. 7 this change is plotted against time. It is seen, that eye-size in the greater part of the eels increases as time goes by. Between 40-80 days where GSI's according to fig. 1 were at a maximum the increase in eye-size ranged from about 0 to about 100 %. According to Boëtius & Boëtius, 1967, male silver eels treated with HCG alone have increased by about 50 % in eye-size when fully ripe (stage 4-5). Female silver eels treated with HCG only did not increase in eye-size, nor did the ovaries develop properly. (Boëtius *et al.*, 1962).

Thus in both sexes eye-size increases considerably parallel to gonadal development. The biological significance of this increase is not clear, but it may be related to sexual rather than migratory activities.

Table 5. Fecundity. Egg counts of 29 hormone-treated eels.

Eel no.	Init. body weight, g	Body weight at death, g	GSI	Nos of counts	Fecundity, nos of eggs $\times 10^{-6}$	95 % conf. limits
27	647	460	19.2	3	0.73	
28	684	480	25.3	3	0.91	
29	572	480	8.9	1	0.74	
39	1155	742	8.7	2	0.77	
46	719	620	23.3	2	0.93	
48	810	750	16.2	2	0.79	
52	680	515	18.7	2	0.85	
53	890	578	12.5	2	0.88	
54	880	578	16.6	2	0.96	
55	570	620	43.9	2	0.96	
56	775	597	22.8	2	1.14	
57	805	835	33.9	3	1.43	
58	660	570	32.1	2	1.02	
59	770	812	35.9	4	1.41	
60	925	890	31.1	2	1.35	
61	730	655	26.5	3	1.81	
62	710	620	17.1	2	0.75	
63	740	672	13.4	2	1.05	
64	715	580	18.0	2	1.06	
65	575	700	40.2	3	1.80	
66	625	545	16.9	2	1.11	
107	519	592	52.1	10	0.79	0.76-0.83
108	614	861	55.8	10	0.93	0.90-0.95
114	1000	1123	40.6	3	1.89	
115	1339	1487	41.1	10	2.33	2.24-2.43
116	737	1022	56.4	10	1.63	1.58-1.68
117	1317	1956	58.6	10	2.63	2.49-2.77
135	800	1133	54.0	10	2.10	2.00-2.20
137	1152	1614	55.3	10	2.17	2.05-2.29

Fecundity

Eels chosen for egg counting are listed in table 5. Prior to counting two different procedures ((1) and (2) overleaf) were applied.

(1) Eels nos 27-66. From frozen stored ovaries 1-4 samples of 4-8 g were transferred to Gilson's fluid (as modified by Simpson, 1951). Samples were kept in Gilson for 2-3 months after which time the eggs were free of ovarian tissue. Next the samples were washed over a nylon gauze (Monodur 224, Krefeld) of a mesh size of 0.224 mm.

(2) Eels nos 107-137. Fresh entire ovaries were transferred to Gilson immediately after death of the eel. The ovaries of these almost fully ripe eels had only little and weak tissue. Storage in Gilson for about one month was sufficient. Then the total egg mass was washed as in (1) and afterwards samples of equal sizes (ranging from 5 to 8 grams for individual ovaries) were collected for counting.

Egg counts were made with the apparatus designed by Kott, 1953. Firstly the sample was divided into ten sections. Secondly the content of a randomly chosen section was divided once more into ten fractions. Only one of these fractions (1 % of the eggs) was counted.

Results are presented in table 5 and fig. 8.

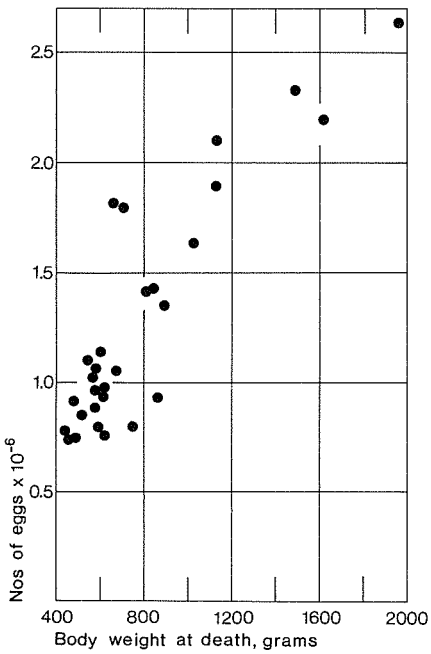

Fig. 8. Fecundity (mill. eggs/eel) plotted against body weight at death.

The relation between body weight at death and egg number as noticed from fig. 8 is biased because the experimental eels represented different physiological conditions at the time of dying. During maturation body weights have decreased in some eels (metabolic loss, small GSI's) and increased in others (water uptake, large GSI's). Consequently the body weights at death as given in fig. 8 are not representative of fully ripe eels.

Correlations between egg number and initial weight, initial length and initial condition ($W_{init.}/L^3_{init.}$) have been tested. Only between fecundity and initial weight could an approximate proportionality be stated which was vitiated by a mean error of about 35 % in individual observations. This indicates that other factors as well influence the fecundity.

Data from the literature on fecundity of Atlantic *Anguilla* are few and to some extent conflicting.

For *immature* eels the U.S. authors Bigelow & Schroeder, 1953, give records of European specimens having 5-10 million eggs on average with 15-20 million for the largest specimens. No details of source and counting method are given. Vladykov, 1955, notes a fecundity of 10-20 million eggs for American eels, still without comments. The preceding records contrast with the well established data of Wenner & Musick, 1974, who counted only 0.5-2.6 million eggs in immature (but catadromous) American eels from Chesapeake Bay.

A single *matured* American eel was counted by Edel, 1975, to have 1.3-1.5 million eggs. This figure matches the data of Wenner & Musick quite well. Kokhnenko *et al.,* 1977, is our only reference to matured European eels. Their finding is 3 million eggs/kg. No further comments are given. The data in the present paper can be converted to average 1.6 million eggs/kg, which is only about half of the Russian figure. Our relatively low counts could possibly have been influenced by the procedure described. When eggs are washed over 0.224 mm gauze immature eggs (diam. < 0.20 mm) will pass through so that only ripened eggs are counted.

Wenner & Musick have established an equation relating egg numbers to body weights in immature American eels. Initial body weights of the ripened European eels in the present paper were inserted in this equation. As a result we arrived at egg numbers approximately twice as high as our actual counts. At least two reasons are possible: the washing procedure (see preceeding paragraph) or a difference due to species.

Water, lipid and protein in ovaries and somatic bodies during maturation

The 27 experimental eels listed in table 6 were selected for the present study from runs 2, 3 and 5. Immediately after death the gonads were dissected. Gonads and somatic bodies were stored frozen. Analyses of contents of water (W), lipid (L) and protein (P) were made on gonads and somatic bodies of all the 27 eels.

Also analysed were 10 non-injected controls (whole eels). Six of the controls were sacrified at the start of an experimental run, 4 of them at the end of an experiment. The 6 first mentioned were used for determinations of total initial energy (see next section) while all 10 controls were used for the 'fat-water line' described below.

Analytical

Somatic bodies of the matured eels (and also the 10 controls) were totally homogenized in three steps: *1.* eels were cut in slices about 0.5 cm thick, 2. 15 mins treatment with Hobart Food Cutter-84141 and finally *3.* a sample of about 50 g

Table 6. Contents of water (W), lipid (L), total nitrogen (N), non-protein nitrogen (NPN), protein (P) and unspecified remainder (R) in ovaries and somatic bodies of hormone-treated eels.

		Ovaries							Somatic body						
Eel no.	GSI	weight, g	W, %	L, %	N, %	NPN, %	P, %	R, %	weight, g	W, %	L, %	N, %	NPN, %	P, %	R, %
26	19.3	181	70.0	17.7	1.68	0.27	8.5	3.8	759	50.6	31.6	2.48	0.36	12.8	5.1
27	19.2	88	67.5	15.9	2.16	0.31	11.1	5.5	372	51.2	30.7	2.38	0.33	12.4	5.7
28	25.3	121	69.0	15.1	2.12	0.27	11.1	4.8	359	43.1	39.4	2.31	0.34	11.9	5.7
41	21.0	137	68.9	14.3	2.14	0.31	11.0	5.8	512	49.2	31.0	2.50	0.34	13.0	6.8
46	23.3	145	69.9	17.1	1.66	0.26	8.4	4.6	475	57.0	24.6	2.38	0.31	12.4	6.0
48	16.2	122	69.7	18.1	1.63	0.19	8.7	3.5	628	57.6	24.9	2.42	0.40	12.2	5.3
52	18.7	93	58.6	27.0	1.85	0.29	9.4	5.0	404	54.8	26.1	2.51	0.31	13.2	6.0
53	12.5	72	51.7	33.4	1.83	0.19	9.9	5.0	506	51.2	30.2	2.41	0.35	12.4	6.2
54	12.6	73	58.4	28.6	1.81	0.13	10.1	2.9	505	50.6	31.8	2.32	0.15	13.1	4.5
55	43.9	256	81.1	10.6	1.26	0.23	6.3	2.0	327	54.2	28.2	2.20	0.21	12.0	5.6
56	22.8	136	72.8	15.6	1.15	0.27	5.3	6.4	461	56.5	26.7	2.02	0.38	9.9	6.9
57	33.9	264	79.1	10.4	1.55	0.26	7.8	2.7	515	53.1	30.2	2.14	0.79	8.1	8.5
58	32.1	165	74.4	13.2	1.74	0.25	9.0	3.4	349	55.2	28.2	2.16	0.16	12.1	4.5
59	35.9	272	78.4	10.7	1.66	0.25	8.5	2.4	486	53.9	29.4	1.99	0.28	10.3	6.4
60	31.1	260	75.0	11.8	1.79	0.29	9.1	4.2	576	56.7	23.5	2.43	0.23	13.2	6.6
61	26.5	166	76.2	11.7	1.73	0.29	8.7	3.4	461	54.9	26.1	2.21	0.33	11.4	7.6
62	17.1	106	65.5	18.4	2.02	0.37	9.9	6.2	514	48.7	34.3	2.24	0.33	11.5	5.5
63	13.4	90	61.7	19.8	2.36	0.19	13.1	5.4	582	51.8	27.3	2.38	0.46	11.6	9.2
64	18.0	104	62.8	19.3	2.38	0.40	11.9	6.0	476	49.4	33.9	2.13	0.17	11.8	4.9
65	40.2	262	79.0	11.5	1.52	0.29	7.4	2.1	390	57.4	26.8	2.07	0.22	11.2	4.6
66	16.9	92	65.3	15.8	2.46	0.45	12.1	6.7	453	54.3	28.5	2.22	0.46	10.6	6.6
82	23.5	161	63.6	18.3	2.35	0.27	12.5	5.6	524	52.0	28.5	2.35	0.28	12.5	7.0
85	18.6	141	69.2	14.1	2.25	0.28	11.9	4.8	617	49.3	36.0	1.93	0.34	9.6	5.1
86	13.2	123	60.3	23.5	2.10	0.21	11.4	4.8	815	52.5	29.6	2.24	0.35	11.4	6.5
91	38.7	297	80.9	7.4	1.48	0.33	6.9	4.7	471	58.2	26.5	1.92	0.31	9.7	5.6
92	46.8	467	79.9	9.3	1.66	0.35	7.9	3.0	530	54.0	31.3	2.02	0.25	10.6	4.1
94	45.5	442	83.0	5.3	1.35	0.26	6.6	5.2	530	57.3	27.1	2.04	0.26	10.7	4.9

(from 2.) with about 30 g water added was homogenized for 45 mins in an MSE-homogenizer. Gonads were treated as described for 3. – lipid determinations, however, were made without previous homogenization.

Homogenates, each of 2 g, were used for each 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 Kjeldahl's method as described by Nordisk metodik komite, 1952.

NPN was determined as follows: to 2 g of homogenate was added 15 % trichloro-acetic acid to make up 100 ml, with filtering after precipitation of proteins. 40 ml of filtrate was determined for N by Kjeldahl's method.

Protein was calculated as $(N - NPN) \times 6.025$, the conversion factor adopted from Love, 1970 (footnote p. 238).

Results

Results are presented in table 6. The figures in the table are means of 6 water determinations per eel and means of 3 determinations per eel for L, N and NPN.

The undetermined remainder ($R = 100 - (W + L + P)$) for gonads amounts to (mean $\pm 2 \times$ S.E.): 4.4 ± 0.6 % and in the somatic bodies to 6.1 ± 0.5 %. By far the greater part of this remainder is represented by matters which are not metabolized. Ash contents of totally homogenized silver eels have been shown (by us) to average 2.5 %. Part of the NPN no doubt represents a small amount of energy. Glycogen contents were not analysed by us, but from data given by Lewander *et al.*, 1974, it can be estimated that glycogen contents of silver eels do not exceed 0.2 % of the body weight.

In fig. 9 relative contents of water, lipid and protein in gonads are plotted against GSI. The water uptake by gonads during sexual development is clearly

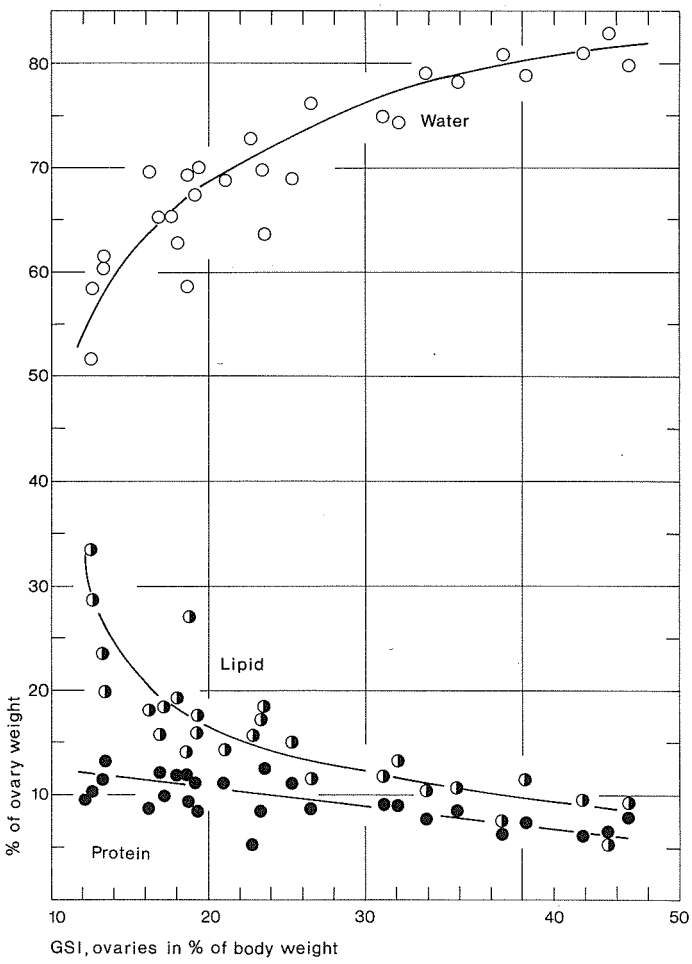

Fig. 9. Contents of water, lipid and protein in ovaries during maturation (expressed as GSI). Graphs are fitted by eye.

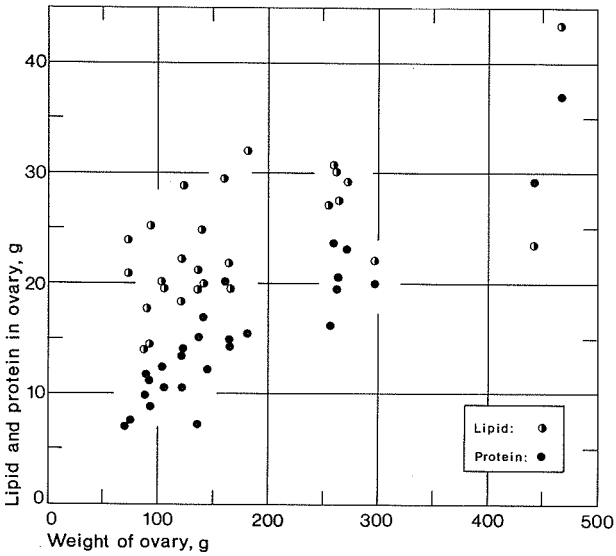

Fig. 10. Accumulation of lipid and protein in ovaries during growth (expressed as increasing weight of ovaries).

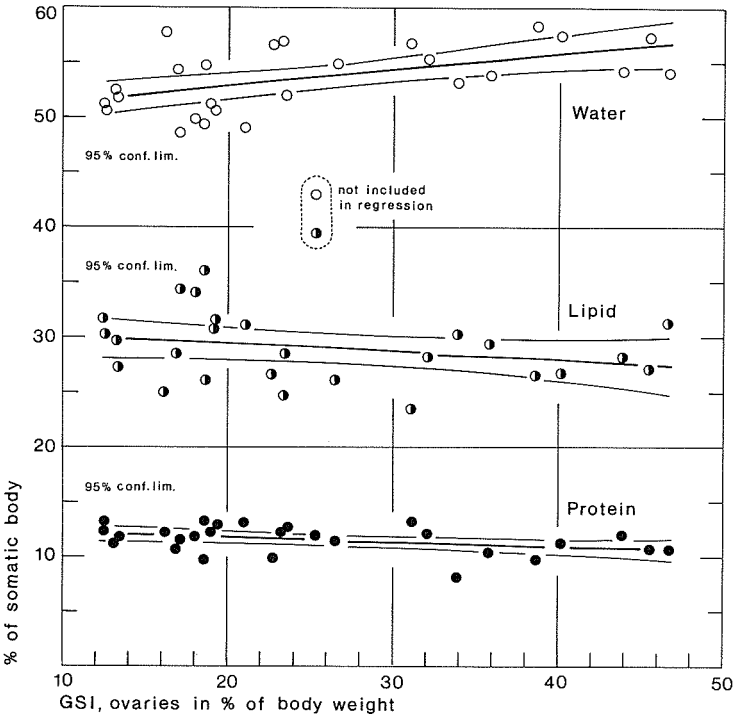

Fig. 11. Contents of water, lipid and protein in somatic bodies during maturation (expressed as GSI). Regression lines are calculated.

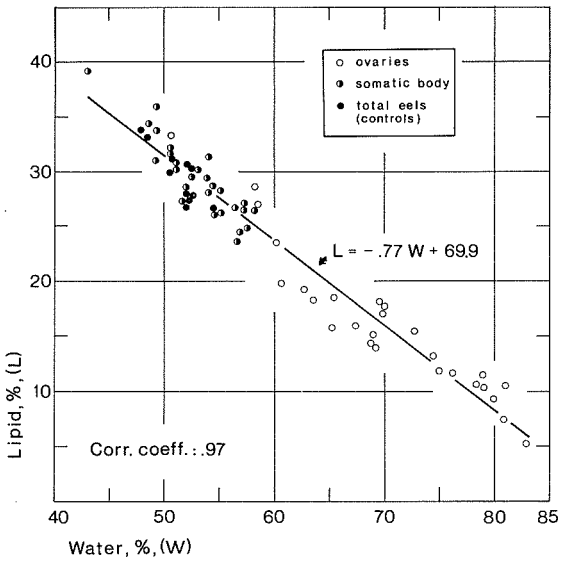

Fig. 12. Calculated 'fat-water line' determined by data from ovaries, somatic bodies and whole eels (controls).

demonstrated. Correspondingly relative values of lipid and protein decrease. The accumulation of lipid and protein in the growing ovary, however, is demonstrated in fig. 10.

Fig. 11 gives relative contents of water, lipid and protein of the somatic part of the bodies during maturation (GSI). Only a small rise in water contents (about 6 %) takes place – the corresponding value for ovaries was about 30 % (see fig. 9). Lipid and protein contents decrease almost insignificantly.

In fig. 12 the table 6-data on lipid contents are plotted against water contents. Also corresponding data from the above mentioned 10 controls (whole eels) are included. It is seen that plots from ovaries, somatic bodies and whole eels in common determine a good 'fat-water line'. This type of lipid/water-relation predominantly occur in 'fatty' fish storing most of the lipid reserve in the muscle (see review of Love, 1970, pp 225-226). Thus such a relation would be expected in the somatic bodies and whole eels. More surprising is the fact that the gonads also fit onto the line.

Estimate of an energy budget for migration and spawning

The total initial amount of energy of the experimental eels was estimated as follows. Six non-injected silver eels were sacrified after an acclimatization period corresponding to that of the experimental eels' in run 5. The eels were totally homogenized and analysed for lipid and protein. Factors used for converting L and P into Joules (J) were: 38.9×10^3 J/g and 17.2×10^3 J/g respectively. The total initial energy (E_T) is here defined as the sum of the L- and P-energies. The small amount of energy represented by the undetermined remainder is not considered.

Table 7. Total energy (E_T) of 6 sacrified non-injected eels.

Body weight, g	Lipid, g	Protein, g	E_T, J × 10^{-6} of eel	E_T, J × 10^{-6} per kg
630	176	81	8.2	13.1
630	193	77	8.8	14.0
722	244	100	11.2	15.5
768	204	108	9.8	12.7
768	255	107	11.8	15.3
850	254	105	11.7	13.7
			mean:	14.1

Results are given in table 7. The initial total energies per kg eel are given in the last column. E_T (mean ± 2 × S.E.) of the six eels was calculated to (14.1 ± 0.9) × 10^6 J/kg eel. Thus to estimate E_T for an experimental eel we use the expression: E_T = initial body weight (kg) × 14.1 × 10^6 J.

We have no reason to believe, that silver eels in nature take food during their period of migration and breeding. Thus the energy required for these two activities would need to be covered by the reserves already present in the eel at the start of its migration. Consequently a rather simple model of an energy budget can be proposed:

$E_T = E_G + E_{loss} + E_S + E_{M1}$, where

E_T is the eel's total amount of energy at the start of the experiment.
E_G is the energy stored in the gonads (ovaries) during the experiment.
E_{loss} is the energy lost during the experiment.
E_S is the supposed energy residue in the eel's spent body after having spawned in the breeding area.
E_{M1} is the energy left available for migration activities at the end of the experiment.

In the following we attempt roughly to estimate the relative sizes of the individual energy pools mentioned.

E_T. *Total initial energy reserve* equals the sum of the pools and is thus fixed at 100 %.

E_G. *Energy stored in gonads.* Table 8 gives energy data of two strip-ripe eels (run 5, nos 92 and 94, GSI-values 46.8 and 45.5 respectively) present in the material analysed for L and P (see table 6). E_T-values are estimated as described above. E_G-values are calculated as the sum of the L- and P-energies and expressed in % of E_T. The two strip-ripe eels have E_G-values of 18 % and 13 %. For our budget estimate we choose the highest value: *18 % of E_T.*

E_{loss}. *Energy lost during experiment.* The energy lost during the experiment covers routine metabolism at the experimental temperature and metabolic activities related to maturation processes. E_{loss} is estimated in table 8 from the expression $E_{loss} = E_T - (E_G + E_{som})$. E_{som} is the sum of L- and P-energies of the somatic part of

Table 8. Strip-ripe eels nos 92 and 94. Estimates of total initial energy reserve (E_T), determinations of energy present in ovaries (E_G) and somatic body (E_{som}), estimates of loss of energy during experiment.

Eel no.	Initial body weight, g	E_T $J \times 10^{-6}$*	E_G		E_{som}		E_{loss} % of E_T**
			$J \times 10^{-6}$	% of E_T	$J \times 10^{-6}$	% of E_T	
92	940	13.2	2.32	18	7.42	56	26
94	780	11.0	1.41	13	6.56	60	27

* calculated as: init. body weight (kg) × 14.1
** calculated as: $E_T - (E_G + E_{som})$ in % of E_T

the eels' bodies (see table 6). E_{loss} of eels nos 92 and 94 is estimated as 26 % and 27 % respectively. Again we choose the highest value: *27 % of E_T*.

E_S. *Energy residue after natural spawning.* The amount of energy left in the eel's spent body after migration and spawning in the Sargasso Sea is an unknown pool in our budget. A spent eel was never caught in the breeding area. The figure proposed here, however, is based on the study of longterm starved silver eels of nearly the same size as the present experimental eels (by J. Boëtius, unpublished).

Residual energies of eels starved to death during a 4-5 years' period (16 °C, seawater) ranged between 11 % and 32 % of the initial energy. On this basis we propose $E_S = 25\%$ *of E_T* as a reasonable (over-estimated?) guess for the energy left in the spent eel.

E_{M1}. *Energy available for migration at the end of experiment.* E_{M1} is calculated from: $E_{M1} = E_T - (E_G + E_{loss} + E_S)$ or $E_{M1} = 100 - (18 + 27\ 25) = 30\%$ *of E_T*. This figure is considered a minimum estimate.

Estimate of the total energy available for migration

In this section we try to estimate the total amount of energy for migration. It should be remembered that the above estimated E_{M1} represents the migration energy left at the end of the experiment. To E_{M1} we must add that amount of energy (E_{M2}) which represents the eel's routine metabolism during acclimatization. If the eel had not been captured E_{M2} would also have been available for migration activities. E_{M2} is estimated from determinations of oxygen consumption.

Rates of oxygen consumption (routine metabolism) were determined for 9 silver eels at body weights ranging from 540 to 750 g. Experiments were made in sea water at 15 °C with well acclimatized eels in February-March. Method: 'sealed vessel'-setup, Winckler titrations. Oxygen saturation was not allowed to drop below 70 % during experiments.

Routine metabolism (23 determinations) was determined to (mean $\pm 2 \times$ S.E.): $30.6 \pm 3.0 mg\ O_2/kg/h$ or, converted to energy (1 mg $O_2 \sim 13.3$ J): 407 ± 40 J/kg/h.

Calculation of E_{M1}: E_{M1} = 30 % of $E_T = 0.3 \times 14.1 \times 10^6$ J/kg eel = 4.23×10^6 J/kg eel.

Calculation of E_{M2}: E_{M2} is the routine metabolism over the acclimatization period (run 5: 81 days): $81 \times 24 \times 407$ J/kg eel $= 0.79 \times 10^6$ J/kg eel.

Estimate of total energy available for migration: $E_{M1} + E_{M2} = (4.23 + 0.79) \times 10^6$ J/kg eel $= 5.02 \times 10^6$ *J/kg eel.*

The problem is now whether the energy estimated is sufficient to cover the energy cost of the eel's transatlantic swim which by us is assumed to be a distance of about 4000 km lasting about 120 days. The corresponding swimming speed is 1.4 km/h or 38 cm/sec. It is not known, however, if the eel during migration maintains a steady state of active swimming or if it is more or less dependent on being borne by some convenient current.

Schmidt-Nielsen, 1972, has calculated the energy expenditure of swimming eels from unpublished data of B. Holmberg & R. L. Saunders. Determinations of metabolic rates at swimming speeds of 35 to 65 cm/sec (15 °C) were made on yellow and silver eels at body weights about 250 g. The energy calculated ranges from 0.329 to 0.417 cal/g body weight/km. Silver and yellow eels gave similar results within the range of speed noted. It was concluded that the eels's energy expenditure for swimming is similar to that of other fishes.

Applying the above range of energy expenditure for a 1000 g eel migrating a distance of 4000 km we get (converting cal to J): (0.329 to 0.417) $\times$ 4.185 $\times$ 1000 $\times$ 4000 = (5.51 to 6.98) $\times 10^6$ J.

We are well aware that this direct conversion from 250 g eels to a 1 kg eel leads to a small over-estimate as large eels have relatively lower energy costs per km than small eels. We have not attempted to make corrections.

Our (minimum) estimate of the energy reserves for migration (5×10^6 J) is in good agreement with our somewhat over-estimated calculation from the data in Schmidt-Nielsen's paper.

Concluding this section we may state, that the total energy reserves of a silver eel are sufficient to cover the costs of a 4000 km active migration and full sexual development as well.

In his 'new solution to the Atlantic eel problem' Tucker, 1959, suggests, that the European eel will never reach the *Anguilla* breeding area in the western Atlantic. If so, the reason is not the lack of sufficient energy reserves.

Estimate of energy costs of development of the ovaries

The energy pool, E_{loss}, is the sum of the energies covering activities related to ovarial development (E_{dev}) and routine metabolism during experiment (R). As we have no determinations of the routine metabolism at the experimental temperature (about 23 °C) R is estimated as 2 $\times$ the routine metabolism at 15 °C (Q_{10} = about 2.3) or 814×10^6 J/kg/hour.

In table 9 E_{dev} is estimated for the strip-ripe eels nos 92 and 94. It is seen that the energy expenditure on gonadal development (E_{dev}) constitutes not less than about 20 % of the total initial energy.

The energy cost of storing one unit of energy in the gonads (E_{dev}/E_G) is estimated in the last column of the table. We consider the figure obtained from eel no. 92 as the best. Eel no. 94, although strip-ripe, has an atypically low E_G especially due

Table 9. Strip-ripe eels nos 92 and 94. Estimates of energy costs of ovarial development (E_{dev}).

Eel no.	Days of matur-ation	E_{loss} $J \times 10^{-6}$/kg	E_{dev} $J \times 10^{-6}$/kg*	E_{dev} % of E_T	E_G $J \times 10^{-6}$/kg	E_{dev}/E_G
92	52	3.73	2.71	19.2	2.47	1.1
94	46	3.88	2.98	21.1	1.81	1.6

*calculated as: E_{loss} ($J \times 10^6$/kg) – (metabolic rate at 23 °C ($J \times 10^6$/kg/hour) × days of maturation × 24)

to a low lipid content (see fig. 10, where P- and L-contents are plotted against ovary weights. No. 94 has ovary weight 442 g).

Keeping to the E_{dev}-value of eel no. 92 we conclude, that energy expenditure for storing energy in ovaries is of the same magnitude as the energy stored.

Acknowledgements

In the initial phase of the present study we received CP-material from the now late director, Dr M. Szalay. We render our best thanks to his institute, the 'Fish Culture Research Station', Szarvas, Hungary. Also we wish to express our gratitude to Løvens Kemiske Fabrik, Ballerup, Denmark, for continued supplies of HCG ('Physex', Leo).

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