Sex differentiation, changes in length, weight and eye size before and after metamorphosis of European eel (Anguilla anguilla L.) maintained in captivity

K. Beullens a, E.H. Eding b, F. Ollevier a, J. Komen b, C.J.J. Richter a,b,*

a Laboratory for Ecology and Aquaculture, Naamsestraat 59, 3000 Leuven, Belgium
b Wageningen Institute of Animal Sciences (WIAS), Department of Fish Culture and Fisheries, Marijkeweg 40, 6709 PG Wageningen, Netherlands

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Abstract

Migrating European eel (Anguilla anguilla L.) glass eels were collected annually in the Garonne Basin (France) during 1987–1989 and subsequently raised under freshwater conditions. In 1990 and 1991 sex differentiation, gonadal development, length/weight and eye size were studied in relation to metamorphosis from yellow to silver eel stage. Differentiation from intersexual gonads to testes took place after 2 years and was synchronized with metamorphosis. Differentiated ovaries, however, were already present in 2+ yellow eels indicating that expression of female gonadal sex was not synchronized with metamorphosis.

Body length and eye size were used to assess the ontogenetic stage of individual fish. The majority of female yellow eel and male and female silver eel of the experimental fish could be identified using these external morphological characteristics. Intersexual yellow eel could not be identified with this method. Intersexual and female yellow eel reached the silver stage at ages of 2–3 and 3–4 years and at body weight ranges of 78–410 and 309–830 g, respectively, implying that metamorphosis in captivity took place at earlier ages and at heavier body weights than in nature. Metamorphosis with respect to enlargement of eyes up to the size of mature silver eels occurred in the hatchery population without hormonal intervention. The testes of silver eels contained spermatogonia in mitotic arrest and the ovaries had oocytes, which were blocked in late prophase of meiosis.

* Corresponding author at: Laboratory for Ecology and Aquaculture, Naamsestraat 59, 3000 Leuven, Belgium.

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Body length and eye size were not suitable characteristics to assess sexual maturity in hatchery raised silver eel. Males and females continued to eat and grow after they became silvery whereas gonadal development gradually stopped. The relationship between age, length/weight, feed intake and metamorphosis (including integumental colour change, enlargement of eyes, degeneration of the alimentary tract, gonadal growth/maturation) as well as the role of gonadotropins are discussed. © 1997 Elsevier Science B.V.

Keywords: European eel (Anguilla anguilla L.); Sex differentiation; Metamorphosis; Garonne Basin (Fr.)

1. Introduction

European eel (Anguilla anguilla L.) has a complex ontogeny passing through different stages from leptocephali larvae to glass eels and further onto pigmented elvers, immature yellow and mature silver eels. The term ‘yellow eel’ is used to describe individuals which have a fully pigmented skin and a yellowish/golden coloured back. With the growth of the body and the gonads, a change in colour takes place. Starting on the lateral side of the body the eel develops a silvery shine which gradually spreads ventrally. On the back and dorsolaterally as well as on the pectoral fins the eel becomes darker until it is almost black. When the silvery shine covers the surface area of the belly the colouring is completed and the silver eel stage has been reached (Tesch, 1991).

Biometric studies of the nucleus of the oculomotor nerve have shown that the yellow eel probably makes little use of its eyes (Kirsche, 1966). With metamorphosis into the silver eel, eye diameter relatively increases in size and, simultaneously, the degree of maturity of the gonads augments, as has been experimentally verified with hormones in male eels (Boëtius and Boëtius, 1967). Pankhurst (1982) presented an index that relates the external surface area of the eye to total body length. In his study which looked at the eye index of hormone treated females of A. anguilla, it was concluded that eels with an eye index > 6.5 were mature. Sexual maturation is also accompanied by sexual dimorphism in growth. The difference between the two sexes is displayed in the size of the migratory stage. After metamorphosis to the silver eel stage, males are 29–40 cm, and females 38–130 cm in length (Tesch, 1991).

The onset of migration is accompanied by fattening of silver eels. The sum of fat and water content is fairly constant; approximately 80% of the total weight during the development from elver to silver eel (Boëtius and Boëtius, 1980). By exchange with water the fat content gradually increases from 20 to 80% of the total energy reserve in silver males and females. Fat content as a factor inducing migratory behaviour in the eel (A. anguilla) to the Sargasso Sea was suggested in a study of a population inhabiting a lake of southern Scandinavia (Larsson et al., 1990). It could trigger the production of hormones responsible for metamorphosis and sexual maturation.

We recently found that gonadal differentiation of juvenile European eel (A. anguilla) raised from glass eel to silver eel stage passes through a transitional phase. The majority of gonads develop via an intersexual stage into testes and a minority progress directly into ovaries (Beullens et al., 1997).

In the present work gonadal development, length and weight changes during metamorphosis were studied in glass eel stocks raised under optimal freshwater conditions to
silver eel stage. They were caught annually during 1987–1989 in the Garonne Basin in France. Silver colour with concomitant appearance of scale pattern was used as a primary and eye index as a secondary criterion for metamorphosis.

2. Material and methods

2.1. Raising of glass eels to silver eel stage

The catching data, the maintenance conditions and the observations on gonadal development of the fish sampled in the hatchery in 1990 and 1991 as well as the total number of fish present per year sample have been reported in a previous paper (Beullens et al., 1997; Table 2). About 60 specimens per year sample were randomly collected. They are indicated as (sub)samples in Tables 1 and 2.

2.2. Parameters and statistical analysis

The following parameters for undifferentiated yellow eels, intersexual yellow eels, male and female yellow eels, male and female silver eels were recorded: length, weight, gonado-somatic index (GSI) (Eq. (1)), eye index (Pankhurst, 1982) (Eq. (2)) and the developmental stage of the ovary.

\[
\text{GSI} = \frac{(\text{gonadal weight} - \text{body weight}) \times 100}{\text{body weight}}
\]

\[
\text{Eye index} = \left(\frac{(A + B)}{4}\right)^2 \times \frac{\Pi}{L} \times 100
\]

where \(A\) is the horizontal eye diameter, \(B\) the vertical eye diameter and \(L\) the total body length.

The following statistical procedure was used to study the effect of metamorphosis on the parameters. For length/weight and length/eye index relationships the data were log

<table>
<thead>
<tr>
<th>Year sample</th>
<th>Undiff. yellow</th>
<th>Intersex yellow</th>
<th>Female yellow</th>
</tr>
</thead>
<tbody>
<tr>
<td>89-1⁺</td>
<td>5  -3.06</td>
<td>3.15 1.00</td>
<td></td>
</tr>
<tr>
<td>88-2⁺</td>
<td>1  -3.06</td>
<td>3.17 1.00</td>
<td></td>
</tr>
<tr>
<td>87-3⁺</td>
<td>8  -4.02</td>
<td>3.81 0.99</td>
<td></td>
</tr>
<tr>
<td>89-2⁺</td>
<td>-  -2.79</td>
<td>2.99 0.99</td>
<td></td>
</tr>
<tr>
<td>88-3⁺</td>
<td>-  -1</td>
<td>-  - 0.99</td>
<td></td>
</tr>
<tr>
<td>87-4⁺</td>
<td>-  -1</td>
<td>-  - 0.99</td>
<td></td>
</tr>
</tbody>
</table>

Regression: *, \(P < 0.05\); **, \(P < 0.01\); ***, \(P < 0.001\).

Male yellow eels found are: two specimens in 88-2⁺ and one specimen in 87-3⁺ and 87-4⁺.
Table 2

Number (N) of silver eels in the six year (sub)samples; see also Table 1. Linear regression equations log y = a + b log x refer to body length (x) (cm) and body weight (y) (g).

<table>
<thead>
<tr>
<th>Year sample</th>
<th>Male silver</th>
<th></th>
<th>Female silver</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>89-1⁺</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>88-2⁺</td>
<td>33</td>
<td>-2.23</td>
<td>2.74</td>
</tr>
<tr>
<td>87-3⁺</td>
<td>41</td>
<td>-2.57</td>
<td>2.90</td>
</tr>
<tr>
<td>89-2⁺</td>
<td>44</td>
<td>-2.14</td>
<td>2.66</td>
</tr>
<tr>
<td>88-3⁺</td>
<td>44</td>
<td>-3.37</td>
<td>3.42</td>
</tr>
<tr>
<td>87-4⁺</td>
<td>49</td>
<td>-1.82</td>
<td>2.48</td>
</tr>
</tbody>
</table>

Regression: * , P < 0.05; ** , P < 0.001.

transformed and linear regression equations were calculated for the various ontogenetic stages of each year sample. Comparisons of regression equations were considered to be meaningful if they were based on ten or more observations and if the correlation coefficients were > 0.60 and significant at the 5% level.

For length/weight relationships the following comparisons were made for yellow and silver eels (numbers refer to the year of catch and freshwater age, respectively).
1. Intersex yellow eels 89-1⁺ with male silver eels 89-2⁺
2. Female yellow eels 88-2⁺ with female silver eels 88-3⁺

The weight for a specific length, located in the adjacent area, was computed. Length–weight relationships were considered to be significantly different if the 95% confidence intervals did not overlap (STATISTIX 4.1). For length and GSI relationships the data sets of the 1990 samples were pooled since GSI was not estimated in 1991. Linear regression equations were calculated without log transformation. Intersex yellow eels were compared with male silver eels. The data were also tested for homogeneity of variance and normality (CSS: STATISTICA) but did not meet the requirements for analysis of variance (Sokal and Rohlf, 1969). Therefore differences of means for the GSI were analysed using a non-parametric Kruskall–Wallis ANOVA by ranks (CSS: STATISTICA). Comparisons were made between yellow and silver eels for length/eye index relationships. These external morphological characteristics were also used to predict ontogenetic/gonadal stage of individual fish.

3. Results

3.1. Gonadal differentiation and eye size in relation to ontogenetic stage (Tables 1 and 2)

Undifferentiated gonads were present in the year samples 89-1⁺ and 88-2⁺. Intersexual gonads were mainly present in the youngest year sample 89-1⁺. Both gonadal stages only occurred in yellow eels. Differentiated testes were seldom observed in yellow eels:
two specimens in the year sample 88-2\(^+\), one specimen in the year sample 88-2\(^+\) and one specimen in 87-4\(^+\). Differentiated testes were found in silver eels. The latter ontogenetic stage was only found in the 2\(^+\) and older year samples indicating that metamorphosis from the yellow intersexual eel to the silver male stage took place after about 2 years of captivity. Differentiated ovaries were not found in yellow eels of the youngest year sample (89-1\(^+\)) but they were relatively abundant in the yellow eels of the 89-2\(^+\), 88-2\(^+\) and 87-3\(^+\) year samples showing that ovarian differentiation becomes apparent after 2 years. This ontogenetic stage was almost lacking in the 88-3\(^+\) and 87-4\(^+\) year samples. The decrease in numbers of yellow eels with differentiated ovaries

Fig. 1. Length/eye index relationship of the various ontogenetic stages in the year samples 89-1\(^+\), 88-2\(^+\) and 87-3\(^+\) (yu, yellow undifferentiated eels; yi, yellow intersexes; ym, yellow males; sm, silver males; yf, yellow females; sf, silver females). 38.2 = maximum length of yi and ym; 53.1 = minimum length of sf; 58.2 = maximum length of sm; 7.2 = upper limit of eye index of yellow eels.

Fig. 2. Length/eye index relationship of the various ontogenetic stages in the year samples 89-2\(^+\), 88-3\(^+\) and 87-4\(^+\) (see also Fig. 1).
was accompanied by an increase in numbers of silver eels with differentiated ovaries implying that metamorphosis of females took place after about 3 years.

The relationship between body length and eye index was studied for the various ontogenetic stages. Linear regression equations were statistically significant in yellow intersexes of 89 1+: \( y = 1.09 x - 1.01, \ r^2 = 0.64, \ P < 0.001 \) and yellow females of 88-2+: \( y = 0.63 x - 0.31, \ r^2 = 0.47, \ P < 0.01 \).

In silver eels the correlation coefficients were low and the \( P \)-values high indicating a spurious relationship between length and eye index.

Length in combination with eye index was used to predict the ontogenetic stage of eels (Figs. 1 and 2). Animals with eye indices > 7.2 were silver. A large proportion of the silver eels could be identified with this criterion. Silver eels displayed a sexual dimorphism in length. The upper and lower limits of length ranges of males and females were used for predicting the ontogenetic stage. The maximum length for male silver eels was 58.2 cm and the minimum length for female silver eels was 53.1 cm. The majority of males (86.4%) and females (62.7%) of the total silver eel population could be identified with these two external morphological criteria.

Yellow eels also displayed a sexual dimorphism in length with a maximum length for intersex and male yellow eels of 38.2 cm and a maximum length for female yellow eels of 51.8 cm. All yellow eels located in the length range of 38.2–51.8 cm could be identified as being female (59.4% of the total number of female yellow eels). Intersexual yellow eels could not be identified on the basis of their length ranges and eye indices.

### Table 3
Ranges and mean values for length, weight, eye index and GSI for the various ontogenetic stages (samples of 1990 and 1991 are pooled)

<table>
<thead>
<tr>
<th>Ontogenic stage</th>
<th>Length range (mean ± SE) (cm)</th>
<th>Weight range (mean ± SE) (g)</th>
<th>GSI range (mean ± SE)</th>
<th>Eye index range (mean ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Undiff. yellow</td>
<td>14.90–24.70 (20.32 ± 1.40)</td>
<td>4.43–21.62 (12.56 ± 2.50)</td>
<td>0.01–0.01 (0.01 ± 0.00)</td>
<td>2.10–4.15 (2.96 ± 0.33)</td>
</tr>
<tr>
<td>Intersex yellow</td>
<td>16.00–36.50 (26.70 ± 0.65)</td>
<td>5.22–87.65 (32.10 ± 2.43)</td>
<td>0.01–0.04 (0.02 ± 0.00)</td>
<td>2.19–5.66 (3.58 ± 0.12)</td>
</tr>
<tr>
<td>Male yellow</td>
<td>31.90–38.20 (35.25 ± 1.31)</td>
<td>54.85–94.80 (80.06 ± 8.70)</td>
<td>0.027–0.03 (0.03 ± 0.00)</td>
<td>3.99–6.16 (5.09 ± 0.45)</td>
</tr>
<tr>
<td>Female yellow</td>
<td>25.20–51.80 (40.97 ± 1.11)</td>
<td>23.49–253.48 (123.68 ± 10.80)</td>
<td>0.08–1.06 (0.50 ± 0.05)</td>
<td>3.56–7.22 (5.20 ± 0.15)</td>
</tr>
<tr>
<td>Male silver</td>
<td>35.10–58.20 (42.03 ± 0.29)</td>
<td>77.50–409.60 (168.28 ± 3.93)</td>
<td>0.031–0.285 (0.06 ± 0.00)</td>
<td>4.72–16.51 (9.98 ± 0.15)</td>
</tr>
<tr>
<td>Female silver</td>
<td>53.10–79.50 (63.10 ± 1.22)</td>
<td>309.2–830.30 (580.23 ± 30.59)</td>
<td>1.349 (9.08 ± 0.39)</td>
<td>5.71–14.53 (9.08 ± 0.39)</td>
</tr>
</tbody>
</table>

The \( N \) values between brackets are the number of fish used for the determination of GSI (only measured in 1990).

Mean values in the GSI column that are not significantly different (\( P > 0.05 \)) according to the Kruskal–Wallis test are indicated by a similar superscript.

\( N \), number of fish; SE, standard error; GSI, gonado-somatic index.
3.2. GSI, gonadal development and eye size before and after metamorphosis (Table 3)

3.2.1. Intersexes and males

Intersex yellow eels and male silver eels had relatively low GSIs in the ranges of 0.01–0.04 and 0.03–0.29, respectively. The mean value of GSI of male silver eels, 0.06 ± 0.00, was significantly higher than that of intersex yellow eels 0.02 ± 0.00 (P < 0.05). Linear regression equations for length and GSI were calculated (Fig. 3). Correlation coefficients of intersexes and male silver eels were 0.12 and 0.00 indicating a spurious relationship between length and GSI.

Fig. 3. Length/GSI relationship of the various ontogenetic stages in the year samples 89-1+, 88-2+ and 87-3+ (regression equations are given below; see also Fig. 1). Yellow intersex, \( y = 1.15 x - 3.35 \) (\( r^2 = 0.12, P < 0.01 \)); silver male, \( y = 0.33 x - 1.79 \) (\( r^2 = 0.00, P < 0.50 \)); yellow female, \( y = 2.79 x - 4.83 \) (\( r^2 = 0.68, P < 0.01 \)).

Fig. 4. Length eye index in relation to the degree of ovarian maturity in the year samples 88-2+ and 87-3+ (St A and St B—see text). 25–40: refer to eels with eye-indices < 7.2 and having stage A ovaries; 40–80: refer to eels with eye-indices > 7.2 and having predominating stage B ovaries.
3.2.2. Females

Female yellow eels had relatively high GSIs ranging from 0.07 to 1.06 with a mean value of 0.50 ± 0.04. The linear regression equation was statistically significant: $y = 2.79x - 4.83$, $r^2 = 0.68$, $P = 0.00$. GSIs of female silver eels could not be estimated due to their absence in the year samples of 1990.

Body length and eye index was related to the developmental stage of the ovary in yellow and silver eels. Stage A (equivalent to one to third stage ovaries, see Beullens et al., 1997) refers to transparent pink ovaries (ovarian width 1.9–9.7 mm) with transverse folds reaching the middle of the ovaries. The oocytes (0.02–0.04 mm) were located in nests and their nuclei had reached the early and late prophase stage of meiosis. Stage B (equivalent to fourth stage ovaries, see Beullens et al., 1997) refers to white ovaries.
(ovarian width 10.9–15.1 mm) with transverse folds dividing the gonad in elongated compartments. The ovaries had long chains of growing oocytes (0.03–0.13 mm) with cytoplasm containing lipid vesicles. The nuclei had reached the late perinuclear stage of meiosis. Females with eye indices < 7.2 could be divided into animals with a length range of 25–40 cm having ovaries in stage A (100%) and animals with a length range of 40–53 cm having ovaries in stage A (53%) or B (47%) (Figs. 4 and 5).

The majority of females with an eye index > 7.2 (84%) and length range of 40–80 cm had ovaries at an advanced stage of development (stage B).

3.3. Body length/weight before and after metamorphosis (Tables 1 and 2)

1. Yellow intersexes 89-1+ and silver males 89-2+ (Fig. 6): At a length of 35 cm (estimated weights (e.w.): 65.67 g and 92.73 g, respectively) there was a statistically significant difference (P < 0.05) between the regression lines indicating that at this length silver males are relatively heavier than yellow intersexes.

2. Yellow females 88-2+ and silver females 88-3+ (Fig. 7): At a length of 53 cm (e.w.: 263.32 g and 340.54 g) there was no statistically significant difference (P > 0.05) between yellow and silver eels.

4. Discussion

4.1. Synchronization of gonadal differentiation and metamorphosis

The formation of testis tubules in our previous study (Beullens et al., 1997) was used as criterion to discriminate between intersexual and male gonads. Testes tubules
formation was seldom observed in yellow eels and it was always present in male silver eels indicating that gonadal differentiation into testis is synchronized with metamorphosis.

Differentiated ovaries were already present in yellow eels with relatively high GSIs ranging from 0.07 to 1.06. This implies that expression of female gonadal sex was not synchronized with metamorphosis.

4.2. Eye index and body length to assess ontogenetic stage

Body length increased linearly with eye index in yellow eels. In silver eels such a relationship was not present. Animals with eye indices $> 7.2$ were silver. Yellow and silver eels displayed a sexual dimorphism in body length. The majority of female yellow eel and male and female silver eels could be identified with the use of these two external morphological characteristics. This method of predicting ontogenetic stage in European eel has not been applied before. Relationships between eye size and body length have only previously been used to predict ovarian development (Pankhurst, 1982) and testis maturation stage (Dollerup and Graver, 1985).

4.3. Eye index and body length to assess developmental stage of gonads

4.3.1. Females

In subadult $A. \textit{anguilla}$ collected from the River Parrett (UK) eye size was correlated with body length and gonad development in 112 untreated and 33 hormone injected female fish (Pankhurst, 1982). Untreated eels in non-migratory stage of ontogenetic development and of eye index of $\leq 6.5$ and body length range 0–49.99 cm had oocyte diameters of $< 0.01$ mm. Their gonadal development was comparable to stage A and B ovaries in our experiments. Yellow eels of eye index of $< 7.2$ and a body length range of 25.2–51.8 cm in the present hatchery raised population had oocyte diameters of 0.02–0.13 mm. These yellow eels had apparently reached a more advanced stage of ovarian development than their conspecifics grown under natural conditions. Eels after treatment with human chorionic gonadotropin (hCG) and chum salmon pituitary extract had eye indices in the range of 3–13 (with a majority of animals having an index $> 6.5$) and oocyte diameters with values up to 0.8 mm. Their ovaries showed oocytes with development of yolk granules in addition to cytoplasmic lipid droplets. These animals were classed as ‘sexually maturing adult’ and having reached the migratory stage of ontogenetic development (Pankhurst, 1982). Female silver eels of the hatchery population had an eye index range of 5.71–14.53 (Table 3) with a majority of animals having an index $> 7.2$. Body length and oocyte diameter ranges were 53.10–79.50 cm and 0.03–0.13 cm, respectively. Oocytes with yolk granules were not observed.

Metamorphosis of female yellow to silver eel under hatchery conditions is obviously different from hormonally induced metamorphosis of eels collected from natural waters. Integumental colour change and enlargement of eyes occurred in captivity without hormonal intervention whereas ovarian growth with concomitant yolk vesicle formation in oocytes did not take place. A length related measure of eye size and index of sexual maturity based on seven stages of ovarian development (Pankhurst, 1982) could not be used for hatchery raised female European eel.
4.3.2. Males

Eels collected from natural waters and injected with hCG follow a similar pattern of increasing eye size and progressing maturation (Boëtius and Boëtius, 1967). These authors assigned seven stages to testicular development in artificially matured males and reported an increase in eye size with increasing development. Eye indices ranges calculated from their data using the method of Pankhurst (1982) give approximate values for males classed as ‘yellow’ (3.4–3.5), ‘silver’ (6.5–8.4) and ‘hormonally induced maturing silver’ (13.0–16.8). Intersex/male yellow eels of the hatchery population had an eye index range of 2.2–6.2, which increased up to 5.7–14.5 in male silver eels (Table 3). Metamorphosis with respect to enlargement of eyes up to the size of male silver and the so called ‘maturing male silver stage’ (Pankhurst, 1982) obviously occurred in the hatchery population without hormonal intervention.

Eye indices could not be used in males to distinguish quantitative estimates of gonadal development (GSI) (data not presented).

4.4. Age, body length/weight and feed intake in relation to metamorphosis

The factors (age, length/weight, fat content of the body) inducing metamorphosis, (integumental colour change, enlargement of eyes, degeneration of the alimentary tract, gonadal growth/maturation and related migratory behaviour) have been the subject of speculation (Larsson et al., 1990). Metamorphosis in nature occurred at differing age, length and weight. Ranges of age and weight of migrating eels of European inland and coastal waters were for males 2.5–9.1 years and 32.5–46.6 cm and for females 3.4–12.3 years and 42.6–65.4 cm (Vøllestad and Jonsson, 1986). In the present experiments intersexual yellow and female yellow eels reached silver stage at ages of 2–3 and 3–4 years and at length ranges of 35.1–58.2 and 53.1–79.5 cm, respectively, indicating that metamorphosis under hatchery conditions occurs at an earlier age and at a greater body length than in nature. The relationship between body weight and metamorphosis was studied in an eel population of the Imsa River in Norway (Vøllestad and Jonsson, 1986). Male and female eel in this study had weight ranges of 28–162 and 129–2105 g at the time of migration. These numbers were 78–410 and 309–830 g for male and female silver eel in the present experiments, showing that metamorphosis under hatchery conditions took place at a heavier body weight.

Age, length and weight at metamorphosis in natural and hatchery raised populations vary greatly according to the environmental conditions the eels have been exposed at. It is therefore not likely that these factors trigger the production of metamorphosis regulating hormones (Larsson et al., 1990).

The question whether feed intake continues or stops after metamorphosis was experimentally investigated in male silver eel (A. anguilla) caught in the Baltic during its seaward migration (Dollerup and Graver, 1985). Repeated induction of testicular maturation with hCG alternating was carried out. After spermiation the eels were given food. Food intake gradually increased and the eels grew both in length and weight. Their condition increased and their strongly atrophied alimentary tract regenerated. When the second maturation was induced, food intake decreased, growth stopped and the alimentary tract underwent atrophy. Male eels in the hatchery population also continued to eat
and grow after metamorphosis and silver males appeared to be relatively heavier than yellow intersexes (Fig. 6).

It can be concluded that gonadotropins induce maturation of testes and degeneration of the alimentary tract (Dollerup and Graver, 1985). External changes related to metamorphosis like integument colour and enlargement of eye, however, occurred in the hatchery raised males without hormonal intervention. These changes are apparently triggered by other pituitary hormones.

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