

**Analysis of the morphological and physiological parameters during  
the silvering process of the European eel (*Anguilla anguilla* L.  
1758) in the Lake of Grand-Lieu (Loire-Atlantique, France)**

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**ABSTRACT.** – Analysis of morphological and physiological parameters during the silvering process of the European eel (*Anguilla anguilla*) in the Grand-Lieu lake (France).

The aim of the current study was to describe the morphological and physiological changes which occur during the transition from yellow to silver eel (*Anguilla anguilla*). We investigated the different stages present in an eel population prior to downstream migration. We were thus able to observe the sequence of changes during the metamorphosis. Measurements were taken from 305 eels harvested in the Lac de Grand-Lieu (France). To evaluate the degree of metamorphosis, gonads, digestive tract, and liver were weighed and the level of gonadotropic hormone (GtH) was measured. Principal component analysis (PCA) was carried out on a subsample of eels for which we had all four physiological parameters in order to determine homogeneous groups according to their sex and degree of

maturation. Thus, three groups were identified: the first corresponded to silver and intermediate male eels; the second to silver and intermediate females and the third to yellow eels. Discriminant functions based on morphological variables were then calculated and used to reclassify individuals into their initial category. 94% of the eels were correctly reclassified. These functions were then applied to the whole sample. The results of the classification were compared with the initial data, thus enabling us to identify four different stages as well as the sequence of events during the metamorphosis.

Key-words.- *Anguilla anguilla*, silver eel, metamorphosis, physiology, biometry, discriminant analysis.

**RÉSUMÉ.** - L'objectif de cette étude a été de décrire de façon précise les différents stades d'anguilles (*Anguilla anguilla*) avant leur migration d'avalaison de manière à visualiser la succession des changements au cours de la transition anguille jaune – anguille argentée. Des mesures ont été effectuées sur 305 anguilles provenant du Lac de Grand-Lieu (Loire-Atlantique). Afin d'évaluer le degré de métamorphose des anguilles nous avons mesuré les poids des gonades, intestin, foie ainsi que la teneur en GtH (hormone gonadotrope). Une analyse en composantes principales (ACP) a été effectuée sur les anguilles pour lesquelles nous disposions des quatre paramètres physiologiques. Trois groupes ont été identifiés : le premier constitué par des individus mâles argentés et intermédiaires ; le deuxième par des femelles argentées et intermédiaires ; le troisième groupe comprenait des anguilles jaunes et intermédiaires. Dans un deuxième temps, nous avons calculé les fonctions discriminantes permettant de replacer ces individus dans leur groupe respectif uniquement à partir des paramètres morphologiques. Ainsi 94% des anguilles ont pu être correctement reclassées.

Les fonctions discriminantes ont ensuite été appliquées à la totalité de l'échantillon. Ce classement a été comparé aux données initiales, ce qui nous a permis de caractériser quatre stades différents et ainsi d'établir une chronologie des modifications pendant la métamorphose.

## INTRODUCTION

At the end of growth in the continental environment, the eel begins the last phase of its biological cycle. It is during this phase that the second metamorphosis takes place, which will prepare it for marine migration in order to reproduce. It undergoes changes in appearance, behaviour, and physiology. The external changes can be seen as a change in the eel's colour, at first yellow, it then takes on a silvery tint on the belly and black on the back, characteristic of marine species. There is also a thickening of the skin, lengthening of the pectoral fins and a more abundant secretion of mucous. Generally speaking, the sensory organs become more developed: the nostrils dilate, the lateral line becomes more visible and the surface of the eyes increases considerably. Hypoosmoregulatory mechanisms are set in motion before the fish reaches salt water. During this metamorphosis, the eel stops feeding and the digestive tract degenerates. The liver undergoes changes in structure and metabolism with an accumulation of lipid reserves (reexamined in Bertin, 1951; Deelder, 1970; Tesch, 1979; Lecomte-Finiger, 1990; Fontaine, 1994). When it begins its migration downstream, the eel is still immature, although sexually differentiated. The gonads increase in weight during the metamorphosis. Sexual maturity will not be truly completed until the animal reaches the sea, where hydrostatic pressure plays a role in stimulating the gonadotropic function (Dufour and Fontaine, 1985). In the continental environment, however, we observe a slight increase in the gonadotropic hormone content, which is in turn correlated to gonad weight (Marchelidon *et al.*, 1999).

Fontaine (1994) raised the question of the kinetics of the silver eel metamorphosis, stating that "a knowledge of these successive stages is essential if we are to analyse the mechanisms". Indeed, there is no detailed description of the evolution of the different

parameters during the transition from yellow eel to silver eel. According to this author, the beginning of gonad development occurs relatively early in the metamorphosis, to be followed by the increase in eye surface area, changes in pigmentation of the tegument and finally changes in the digestive tract.

The general appearance of the animal (colouring, exophthalmy) gives a very general idea of its state of maturation. Eels are generally classified as yellow-sedentary or silver-migrant, two stages that correspond to two ecophases (Bertin, 1951; Elie and Rigaud, 1984; Dufour, 1994). This classification does not take into account the gradual nature of the metamorphosis. In the natural environment, whether in a sedentary or migrating fraction of the population, we frequently encounter individuals that are neither yellow nor entirely silver, but are probably at an intermediate stage. At the present time, there is no information on these unclassifiable individuals, nor on their state of maturation.

To try and answer these questions, we attempted to make a more detailed classification of the different stages of development of male and female eels present in the environment immediately prior to downstream migration. The physiological parameters we measured were chosen to take into account their state of transformation: weight of gonads, digestive tract, liver and pituitary GtH content. In order to relate the degree of maturity to some morphological criteria, we measured the parameters that could differentiate the various stages in eel development and their sex. After the different groups were defined, based on a subsample in which the pituitary GtH contents had been measured, we attempted to reclassify all the eels into their respective groups based simply on their morphological criteria. The resulting classification was then compared with the stage attributed when the animals

were measured, with the sex of the individuals and also with the data relating to the gonads, the digestive tract and the liver.

## MATERIAL AND METHODS

### Harvesting the eels

The eels were caught (305 individuals) using a hoop net in the Lac de Grand-Lieu (Loire-Atlantique). Ten sampling campaigns were carried out over a period of 4 years between November 1994 and November 1998.

### Parameters studied

#### *External anatomical characteristics*

The following parameters were measured before the animals were sacrificed: body weight (P), total body length (Lt), length of pectoral fin (Ln), horizontal (Dh) and vertical (Dv) diameters of the eye. An eye index (IO) was calculated according to Pankhurst's formula (1982):

$$IO = \left( \frac{Dv + Dh}{4} \right)^2 \times \frac{P}{Lt}$$

Another index (ILn) was calculated, enabling us to compare lengths of pectoral fins:

$$ILn = \frac{Ln}{Lt} \times 100$$

The eels were classified into three categories according to their pigmentation: silver eels (A), yellow eels (J) and intermediate eels (Int). This third group represented individuals that had neither the typical colouring of the silver eel (black back, silver belly, clearly defined lateral line), nor that of the yellow eel.

### *Internal anatomical characteristics*

After the animals were killed and dissected, the following organs were weighed: gonads, liver, digestive tract (emptied). These weights were related to the body weights (P) of each eel to calculate the corresponding indexes: the gonadosomatic index ( $GSI = \% \text{ weight of gonads}/P$ ), the hepato-somatic index ( $HSI = \% \text{ weight of liver}/P$ ) the digestive tract-somatic index ( $DTI = \% \text{ of digestive tract } /P$ ).

### *Sex determination*

This was carried out by macroscopic observation of the gonads and, if necessary, by microscopic observation after histological fixing. Individuals were classified into three categories: females (differentiated ovaries), males (differentiated testicles) and undifferentiated.

### *Hormonal levels*

The type 2 gonadotropic hormone (GtH) plays an essential role in stimulating gonad activity; the rate was measured by radioimmunological assay RIA (Dufour *et al.*, 1983) only in the pituitary extracts, as its presence is undetectable in the serum of the eels at the yellow and silver stages (Dufour, 1994).

### **Data treatment**

Principal Component Analysis was carried out on a subsample of 136 eels (for which we had the GtH values) based on four variables: GSI, HSI, DTI and GtH. We then used discriminant analysis (DA) to calculate linear combinations based on four morphological variables: Lt, P, IO and Iln, enabling us to separate them into groups. The discriminant function thus calculated was applied to all the individuals for which we had no GtH measurements. The classification of each individual into groups was compared with the initial

data. Multivariate analyses were carried out using ADE-4 software (Thioulouse *et al.*, 1997).

## RESULTS

### **Determining groups using principal component analysis (PCA)**

The results of the PCA are presented in figure 1. Axes 1 and 2 account for 62% and 27% respectively of the total inertia. Points were plotted by stage. Correlations of the variables to the axes are presented in figure 1B.

Practically all the yellow individuals are grouped into the positive part of axis 1. These present relatively high levels of DTSI and HSI, between 1.43 and 6.49 and between 0.81 and 4.61 respectively.

The silver eels are to be found in the left-hand part of figure 1A, and are subdivided into two groups, corresponding to males and females. The further to the left the points are located, the higher the levels of GtH in the eels and the greater the GSI; the GtH levels go up to 386 ng/pituitary and the GSI to 1.89. The extreme values correspond to the silver females. The silver males have lower values, especially for the GSI, which varies between 0.06 and 0.23. The eels of intermediate colouring do not form a separate scatter plot but are distributed throughout the 3 groups. Some therefore have physiological characteristics that are closer to the yellow eels while others already have a certain degree of maturity.

By taking into account the sex of each eel in the PCA results as well as the stage evaluated when measurements were taken (A, J, Int), we defined 3 groups. The four physiological criteria constituted our reference for defining each group. Groups G1 and G2 corresponded to female and male silver eels respectively. The yellow eels made up group

G3. Two eels assessed as silver were allocated to group G3 since their physiological characteristics put them among the yellow, or immature eels. Table I summarises the composition of each group and their characteristics.

### **Discriminant analysis according to morphological parameters**

Discriminant analysis was carried out on the 3 groups defined in the previous paragraph and for the following 4 variables: total length (Lt), body mass, (P), eye index (IO) and pectoral fin index (ILn). Results are given in figure 2. The discriminant functions calculated for each factorial axis enabled us to reclassify 94% of the 136 individuals into their respective groups, simply from morphological parameters. The classification functions are presented in the box below. Values  $g_1$ ,  $g_2$ ,  $g_3$  were calculated for each individual. The highest value indicates the group to which the individual was allocated.

$$\begin{aligned} g_1 &= -126,54 + 3,17Lt - 0,22P + 26,4ILn + 3,21IO \\ g_2 &= -124,85 + 3,05Lt - 0,24P + 25,99ILn + 4,4IO \\ g_3 &= -105 + 3,35Lt - 0,24P + 24,69ILn + 0,9IO \end{aligned}$$

### **Reclassification of total sample**

The classification functions were applied to the entire sample (305 individuals). The classification was then compared to the stage attributed to each eel when measurements were taken (A, J, Int) and to the sex of the individuals. The results of the classification are presented in figures 3, 4 and 5.

Figure 3 shows the composition of each group after the individuals were classified by discriminant function. Groups G1 and G2 contained 66 and 52 individuals respectively. Classification by sex of individuals was 98% correct; only 5 females were put into the male group (G2). Some classification errors were also made relating to the stages. Group G1 was

made up of 23% yellow eels (J) and group G2, 8%. The discriminant function appears to be more accurate in classifying males than silver females. Group G3 contained the largest number of individuals (187). Only four silver eels were classified in this group. These were individuals with a low eye index, below 9.

Intermediate individuals were distributed into the three groups demonstrating a certain heterogeneity in their degree of maturation. Thus, 62% of these eels were apparently closer to the silver eels (groups G1 and G2) while 38% were associated more with the yellow stage (group G3).

### **Detailed analysis of the organic parameters**

The anatomical characteristics (DTI, HSI and GSI) of the eels that had been “misclassified” and the intermediate eels were analysed in more detail and compared with the entire sample in order to judge the validity of the classification carried out according to their state of maturation. The values of GSI and HSI according to DTI for these eels were compared with those of the eels correctly classified in figures 4 to 7.

#### *Yellow eels classified in G1 and G2*

The yellow eels that were allocated to group G1 presented higher DTI than the silver eels (Fig. 4). Similarly, we noted differences in the GSI; the gonads were much less well developed in these yellow eels. The allocation of these eels into group G1 does not seem justified given their state of maturation. However, compared with the yellow eels classified in group G3, these individuals were among the most mature (Fig. 5); they were in the upper part of the scatter plot of yellow eels in the GSI. The four yellow eels classified in G2 were in fact two females and two individuals that were sexually undifferentiated. This explains the GSI values that were higher than those of the silver males (Fig. 6), as the gonads of the

females were much more developed in terms of volume than those of the males. Only one eel out of the four truly belonged to the silver eels.

#### *Silver eels classified in G3*

Two eels out of the four silver individuals corresponded to the silver eels defined as belonging to group G3 for discriminant analysis. The other two were more mature according to their HSI (1.36 and 1.42), DTI (1.73 and 1.92) and GSI (0.11: individual male and 1.82: individual female) values, but not as mature as the eels that were truly silver.

#### *Intermediate eels*

The intermediate eels classified in G1 formed two distinct scatter plots in figures 4 and 5, corresponding to two groups with different degrees of maturation. In the males, that is group G2 (Fig. 6), the intermediates formed only a single group, which presented the characteristics of a silver eel. The two individuals with high GSI in figure 6 corresponded to females.

### **Kinetics of the appearance of changes**

From all the observations carried out, we were able to characterise different degrees of metamorphosis from the different groups of individuals. This information gave us an idea of the succession of internal and external changes that occurred throughout the metamorphosis. The characteristics of each of these stages are summarised in Table II, also the successive phases for each sex.

The increase in eye surface associated with an increase in gonad weight were among the first changes to occur. At this stage (A1), some eels began to change colour; some individuals had even been classified as intermediary according to their pigmentation. It also emerged that some eels were not yet sexually differentiated. The decreases in HSI and DTI occurred at stage A2, in the females; the eels seemed to have stopped accumulating any

reserves. It was also in this phase that total lengths ceased to increase. The change in pigmentation had not yet necessarily taken place as some eels were still yellow in colour. In the males, the increase in GSI coincided with the degeneration of the digestive tract and the decrease in liver weight. However, the limited numbers at stage A2 (two individuals) meant that we could not obtain any significant results. Whether in males or females, we observed that stages A3 and A4 differed only in the change in pigmentation, which then became truly silver.

## DISCUSSION

Until now we had only empirical descriptions of the way in which the transformation occurred in eels. The observations that we have made show that the metamorphosis occurs gradually. The stages we have described correspond to the succession of changes associated with average values for each physiological parameter. These are the first elements of information on the kinetics of the metamorphosis of the migrating eel which enable us to situate an individual in the sequence of events.

Experiments in artificial maturation have shown that the eye index can reach 27 (Boëtius and Boëtius, 1967) and that the weight of the gonads can represent as much as 31.8% of the animal's body weight (Fontaine *et al.*, 1964). It is therefore highly probable that the phases that we describe make up only a small part of the animal's preparation for reproduction. A description of the later stages would enable us to reconstitute the complete kinetics and this will be done at a later date.

The sample analysed in this study came from the Lac de Grand-Lieu (catchment area of the river Loire). We must now generalise these results into other catchment areas. It is probable that, depending on the upstream-downstream location of the population studied,

there are differences in the ranges of values measured for each parameter. Indeed, the “distance to the sea” factor could be linked with the stage at which the eel begins its downstream migration.

The modifications occur gradually and do not necessarily manifest as changes in pigmentation. Thus, some of the yellow eels analysed in the course of this study already presented high GSR levels (stage A3). Pankhurst and Lythgoe (1982) compared the structure and pigmentation of the eel tegument at sexual maturity. Their results showed that the pigmentary composition did not change radically with maturation. So colour can be used to distinguish a yellow eel from a silver eel, but it cannot be used as a basis for assessing the maturity index. It is also a very subjective criterion which can be affected by the degree of experience of each observer. The eye index, on the other hand, would appear to be a criterion that could potentially be used to evaluate the degree of the eel’s transformation. Indeed, each stage (A1 to A4) corresponds to a very specific value and there is practically no overlap. A further advantage of this index is that it does not require any eels to be sacrificed. Measuring equipment does, however, need to be standardised in order to avoid errors from one experimenter to another.

In studies relating to the phenomenon of downstream migration, authors sometimes describe the presence of non-silver eels in the migrating fraction. Bouillon and Haedrich (1985) have studied lengths and ages of *Anguilla rostrata* during downstream migration. They state that as well as catching migrating eels, they also caught young yellow eels (smaller) and some that were bronze in colour. In their analyses, the authors did not take into account these “intermediate” specimens which they were unable to define as either silver or yellow. Smith and Saunders (1955) also observed that only some of the eels going downstream were

silver. They added that the relationship between the total number of individuals moving downstream and the degree of maturity of the eels “remains obscure”. Langon and Dartiguelongue (1997) identified as yellow or unclassifiable more than half the eels in their sample of downstream eels. The results obtained in the present study could explain these apparent contradictions between the migration behaviour of the eel and the absence of silver colouring. However, what we must do next is to characterise in the same way the different types of individuals that make up the fraction moving downstream, in order to situate them in the metamorphosis dynamic. Thus, estimating the flux of eels moving downstream, and thus numbers of potential spawners, could not be done without using external criteria with which to characterise in an entire eel population the fraction that could potentially migrate in a given year.

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BERTIN L., 1951. - Les anguilles. Variation, croissance, euryhalinité, toxicité, hermaphrodisme juvénile et sexualité, migrations, métamorphoses. 188 p. Paris: Payot.

BOËTIUS I. & J. BOËTIUS, 1967. - Studies in the European Eel, *Anguilla anguilla* (L.). Experimental induction of the male sexual cycle, its relation to temperature and other factors. *Meddr Danm. Fisk.- og Havunders.* 4: 339-405.

- BOUILLON D.R. & R.L. HAEDRICH, 1985. - Growth of silver eels (*Anguilla rostrata*) in two areas of Newfoundland. *J. Northwest Atl. Fish. Sci.* 6: 95-100.
- DEELDER C.L., 1970. - Synopsis of biological data on the eel *Anguilla anguilla* (Linnaeus) 1758. *FAO Fisheries Synopsis* 80.
- DUFOUR S., 1994. - Neuroendocrinologie de la reproduction de l'anguille: de la recherche fondamentale aux problèmes appliqués. *Bull. Fr. Pêche Pisc.*, 335: 187-211.
- DUFOUR S., DELERUE-LE BELLE N. & Y.A. FONTAINE, 1983. - Development of a heterologous radioimmunoassay for eel (*Anguilla anguilla*) gonadotropin." *Gen. Comp. Endocrinol.*, 49: 403-413.
- DUFOUR S. & Y.A. FONTAINE, 1985. - La migration de reproduction de l'anguille européenne (*Anguilla anguilla* L.): un rôle probable de la pression hydrostatique dans la stimulation de fonction gonadotrope. *Bull. Soc. Zool. Fr.*, 110: 291-299.
- ELIE, P. & C. RIGAUD, 1984. - Etude de la population d'anguilles de l'estuaire et du bassin versant de la Vilaine : examen particulier de l'impact du barrage d'Arzal sur la migration anadrome (civelles), proposition d'amélioration du franchissement de cet obstacle. Rapport Cemagref/Université de Rennes. 162 p et 174 p.
- FONTAINE M., BERTRAND E., LOPEZ E. & O. CALLAMAND, 1964. - Sur la maturation des organes génitaux de l'anguille femelle (*Anguilla anguilla* L.) et l'émission spontanée des oeufs en aquarium. *C. R. S. Acad. Sci. Paris*, 259: 2907-2910.
- FONTAINE, Y.A., 1994. - L'argenture de l'anguille: métamorphose, anticipation, adaptation. *Bull. Fr. Pêche Pisc.*, 335: 171-186.
- LANGON, M. & J. DARTIGUELONGUE, 1997. - La dévalaison des anguilles (*Anguilla anguilla* L.) argentées - Test de deux exutoires de dévalaison à la centrale hydroélectrique

E.D.F. d'Halsou (Nive, Pyrénées-Atlantiques), 1996, Revue bibliographique, 110 p., rapport I.N.R.A./S.C.E.A.

LECOMTE-FINIGER R., 1990. - Métamorphose de l'anguille jaune en anguille argentée *Anguilla anguilla* L. et sa migration catadrome. *Année Biol.* 29: 183-194.

MARCHELIDON J., LE BELLE N., HARDY A., VIDAL B., SBAIHI M., BURZAWA-GERARD E., SCHMITZ M. & S. DUFOUR, 1999. - Etude des variations de paramètres anatomiques et endocriniens chez l'anguille européenne (*Anguilla anguilla*) femelle, sédentaire et d'avalaison: application à la caractérisation du stade argenté. *Bull. Fr. Pêche Pisc.* 355: 349-368.

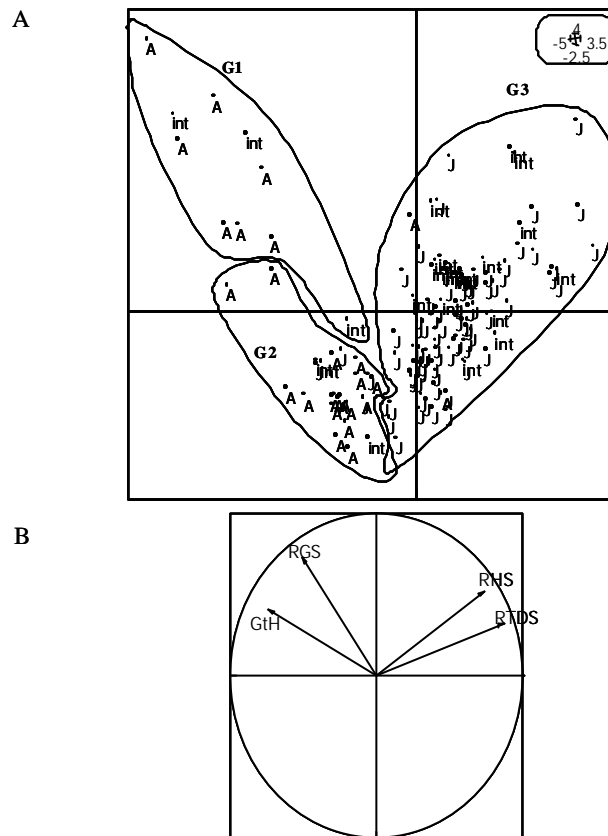
PANKHURST, N.W., 1982. - Relation of visual changes to the onset of sexual maturation in the European eel *Anguilla anguilla* (L.). *J. Fish. Biol.* 21: 127-140.

PANKHURST N. W. & J. N. LYTHGOE, 1982. - Structure and color of the integument of the European eel *Anguilla anguilla* (L.). *J. Fish Biol.* 21: 279-296.

SMITH M.W. & J.W. SAUNDERS, 1955. - The American eel in certain fresh waters of the maritime provinces of Canada. *J. Fish. Res. Bd. Canada*, 12: 238-269.

TESCH, F.W., 1979. - The Eel: Biology and management of anguillid eels. 434 p. London: Chapman and Hall.

THIOULOUSE J., CHESSEL D., DOLEDEC S. & J.M. Olivier, 1997. - ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7: 75-83.



**Figure 1:** Graphical displays of the PCA realized on 136 eels and 4 variables. **A:** Individuals are represented on axes 1 and 2 (each axis represents 62% and 27% of total inertia). Labels correspond to the A: silver colored eels, J: yellow colored eels and Int: intermediate eels. Group G1 represents female silver eels, G2: male silver eels and G3: yellow eels. **B.** Correlations of variables to axes. GtH: Gonadotropin hormone; RGS: gonado-somatic index; RHS: hepato-somatic index; RTDS: digestive tract index.

**Table I.** –Main characteristics of the three groups of eels defined according to their sex and degree of metamorphosis. Groups G1 and G2 each represent females and males that display typical characteristics of silver eels as well as in-between specimens (relative to color). Group G3 represents yellow eels of both sexes.

Groups	G1	G2	G3
Number	10	21	101
Females (%)	100	0	86
Males (%)	0	100	7
Sexually undifferentiated (%)	0	0	7
Silver stage	70	86	2
Yellow stage	0	0	78
Intermediate stage	30	14	20
RGS	0,84-1,89	0,06-0,23	0,01-1,02
RHS	0,96-1,65	0,96-1,80	0,81-4,61
RTDS	0,21-2,18	0,95-2,29	1,43-6,49
GtH (ng/hypophyse)	11,84-386,47	30,38-364,56	0,03-127

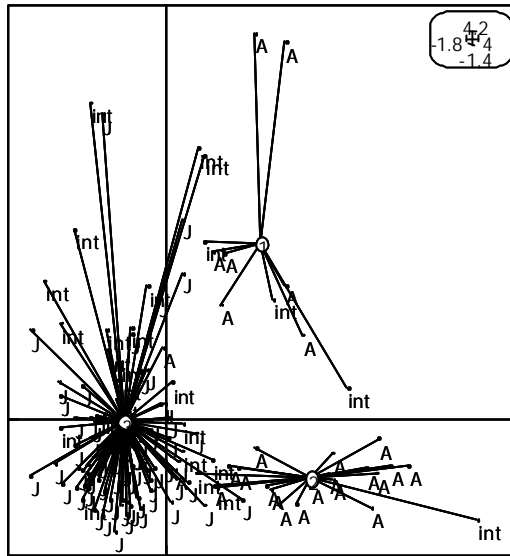


Figure 2: Graphical display of the discriminant analysis realized on 136 individuals and four biometrical variables: total length, weight, ocular index and fin index.

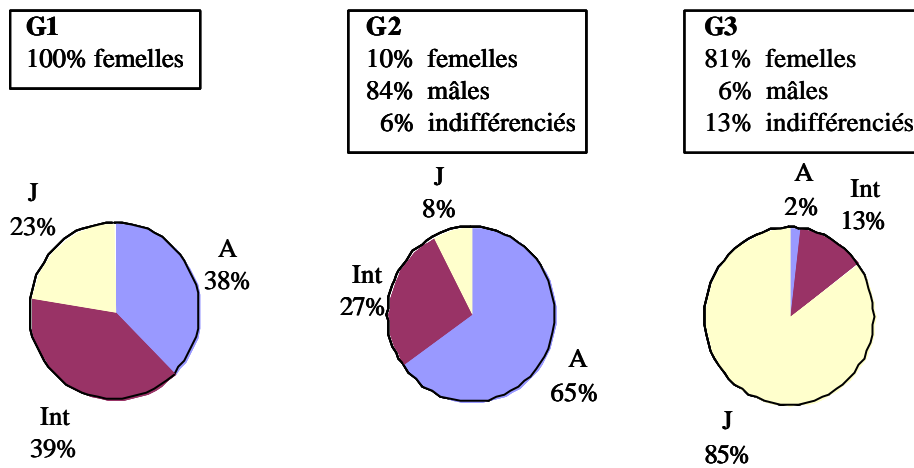


Figure 3: Composition in sex, and color of eels for each group after classification of the total sample of eels by the discriminant functions. A: silver; J: yellow; Int: intermediate.

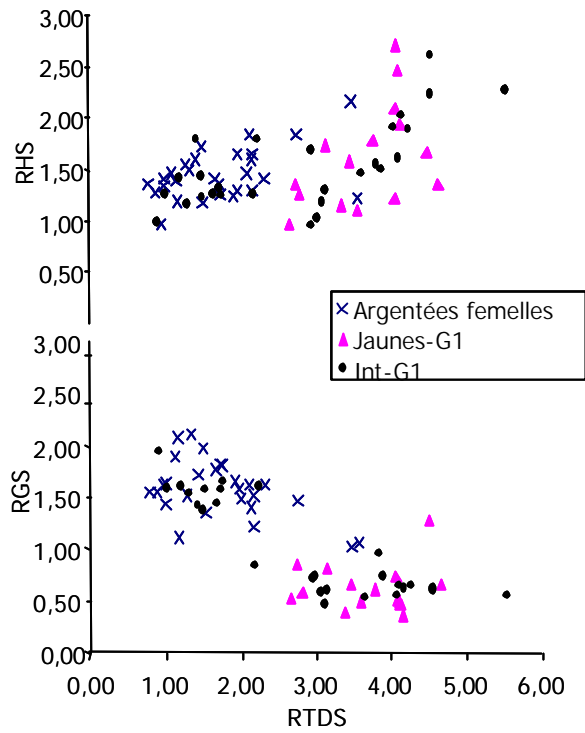
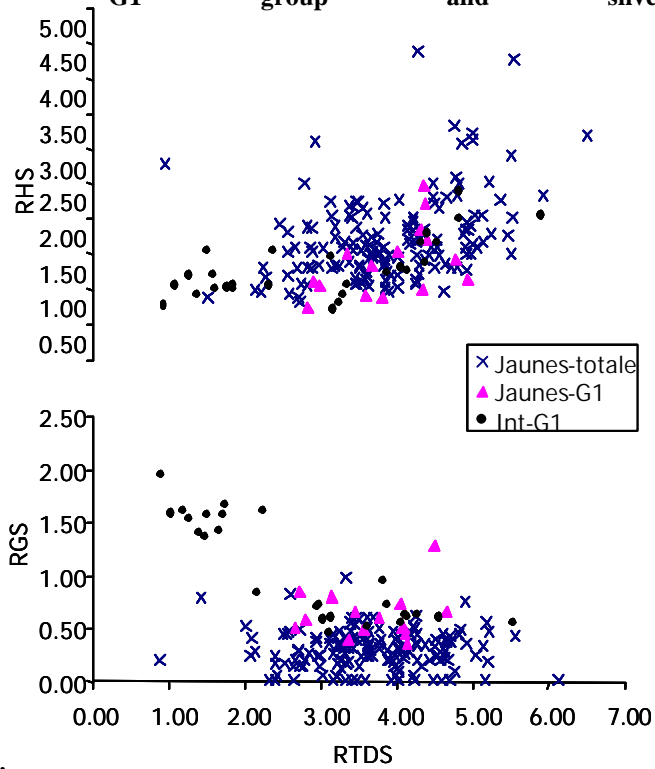
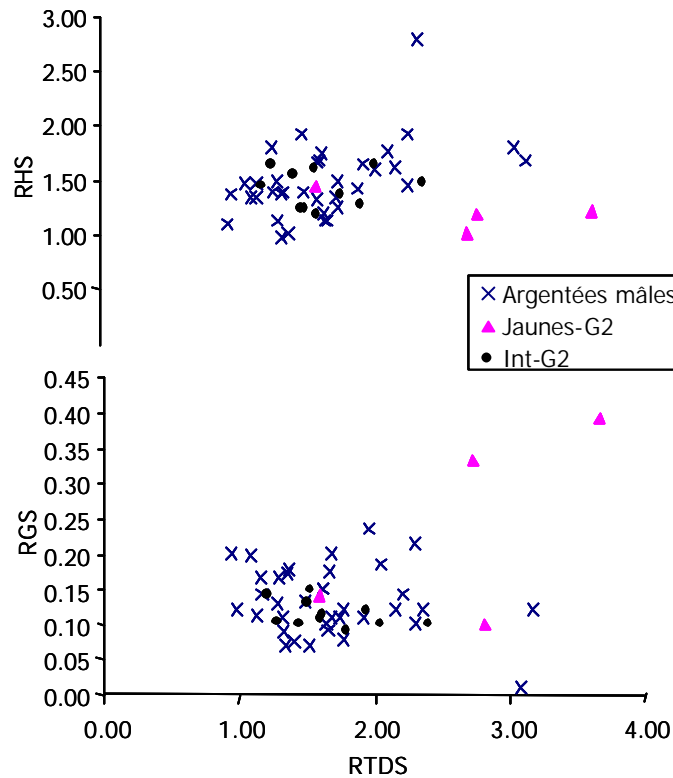


Figure 4: Comparison between the yellow (jaunes-G1) and intermediate (Int-G1) eels classified in the G1 group and silver mature female eels.



eels.

Figure 5: Comparison between the yellow (jaunes-G1) and intermediate (Int-G1) eels classified in the G1 group and yellow eels.



**Figure 6: Comparison between the yellow (jaunes-G2) and intermediate (Int-G2) eels classified in the G2 group and male silver eels.**

**Table II. - Sequence of events during the transition between the yellow and silver phases for males and females. Arrows indicate a significant increase or decrease ( $p=0.05$ ) relative to the previous stage. The A2 stage for males only representing two individuals, values are given for information. ns: not significant.**

Stades	J	A1	A2	A3	A4
<b>MALES</b>	Yellow : males and sexually undifferentiated	Int-G3 : males and sexually undifferentiated	Yellow-G2: Males	Int-G2 : Males	Silver : Males
Length (cm)	34±5	39±3 ↗	38-39	40±1 ns	40±3 ns
Eye index	4,7±1,2	6,3±1,3 ↗	8,2-10,4 ↗	10,3±1,5 ↗	10,1±1,4 ns
GtH (ng/hypophyse)	0,7-12,68	0,7-30,38		158,62-175,12	32,5-364,56
RGS	0,05±0,06	0,06±0,05 ns	0,10-0,14 ↗	0,11±0,02 ↗	0,14±0,34 ↗
RHS	1,95±0,68	2,01±0,81 ns	1,19-1,44 ↘	1,42±0,17 ↘	1,47±0,34 ns
RTDS	3,47±0,97	3,31±1,29 ns	1,60-2,81 ↘	1,67±0,35 ↘	1,63±0,47 ns
<b>FEMALES</b>	Yellow	Int-G3	Int-G1 Jaune-G1	Int-G1	Silver
Length (cm)	43±3	54±6 ↗	67±7 ↗	70±7 ns	71±1 ns
Eye index	5,5±1,1	6±0,9 ↗	8,3±0,7 ↗	11,4±1,8 ↗	11±1,7 ns
GtH (ng/hypophyse)	0,03-127	4,92-110	7,78-70,01	341,4	35,73-386,47
RGS	0,34±1,16	0,61±0,16 ↗	0,64±0,18 ns	1,57±0,16 ↗	1,63±0,33 ns

RHS	1,86±0,6	2,18±0,46 ↗	1,63±0,48 ↘	1,34±0,25 ↘	1,42±0,21 <b>ns</b>
RTDS	3,69±0,84	4,39±0,92 ↗	3,72±0,73 ↘	1,48±0,38 ↘	1,70±0,65 <b>ns</b>