

## SILVERING OF FEMALE EELS (*ANGUILLA ANGUILLA*) IN TWO SUB-POPULATIONS OF THE RHÔNE DELTA.

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### SUMMARY

The eel population of the Camargue lagoon system can be divided into two sub-units living in two distinct biotopes (freshwater and brackish water) and characterised by different population structures and especially growth patterns. The sub-population living in the Fumemorte canal (average salinity: 0.9 g/l) is a freshwater population type (81.6% females, maximum ages observed = 9 - 11 years, slow growth (annual gain 46 mm)) whereas that of the Vaccarès lagoon (average salinity: 9.7 g/l over the same period) is typical of a lagoon (45.6% females, maximum ages 5 – 6 years, fast growth (annual gain 90 mm)).

In each sub-population, Gonadosomatic Index (GSI) and OI (Ocular Index) were measured on female eels over a sampling period that started in January 1997 and ended in December 2000.

In both types of habitat, and in agreement with previous studies, we observed a threshold value of  $GSI \geq 1.4$  % characterising the silver stage (MARCHELIDON *et al.*, 1999). The increase in eye area was a progressive phenomenon, initiated in the yellow stage and was significantly correlated ( $p < 0.001$ ) with the GSI. As with the GSI, OI increased in silver eels, the threshold value of  $\geq 8.0$  discriminating silver eels.

We will show that silvering follows different patterns between the two habitats. Age at metamorphosis in female eels take place very early in the Vaccarès lagoon (83.3% of females metamorphose between 4 and 5 years) compared to those in the Fumemorte drainage canal (94% of females metamorphose between 7 and 9 years). We suggest that the growth potential provided by Vaccarès lagoon accounts for this difference in age at metamorphosis. Although, such a turnover cannot explain alone the different proportions of female silver eels observed in the Fumemorte drainage canal (23%) and Vaccarès lagoon (2.4%). Influence of population's parameters like sex-ratio, population structure and abundance on silvering process, is discussed.

**Key-words:** European eel, *Anguilla anguilla*, silvering, ocular index, gonadosomatic index, growth pattern, age at metamorphosis, freshwater, brackish water.

## L'ARGENTURE CHEZ DES ANGUILLES FEMELLES (*ANGUILLA ANGUILLA*) DE DEUX SOUS-POPULATIONS DU DELTA DU RHÔNE.

### RÉSUMÉ

Le peuplement anguillicole du système lagunaire camarguais peut être scindé en deux sous unités caractérisées par des structures de population et notamment des patrons de croissance différents en rapport avec deux biotopes distincts (eau douce et eau saumâtre). La sous population du Fumemorte (salinité : 0,9 g/l en moyenne) s'apparente à une population de type « eau douce » (81,6 % de femelles, âges maximum observés = 9 - 11 ans, croissance faible (gain annuel de 46 mm)) tandis que celle de l'étang du Vaccarès (salinité : 9,7 g/l en moyenne sur la même période) est caractéristique d'une lagune (45,6 % de femelles, âges maximum 5 - 6 ans, forte croissance (gain annuel de 90 mm)).

Pour chaque sous-population, nous avons mesuré le Rapport Gonadosomatique (RGS) et l'Index Oculaire (IO) des anguilles femelles sur une période d'échantillonnage qui débute en janvier 1997 et se termine en décembre 2000.

Dans les deux types de milieu, et en accord avec les études précédentes, nous observons une valeur seuil de RGS  $\geq 1,4$  % caractérisant le stade argenté (MARCHELIDON *et al.*, 1999). L'augmentation de la surface oculaire est également un phénomène progressif, initié dès le stade jaune et corrélé significativement au RGS ( $p < 0.001$ ). Comme le RGS, l'accroissement de l'IO s'accroît chez les anguilles argentées, la valeur seuil  $\geq 8,0$  discriminant les anguilles argentées.

Nous montrons que l'acquisition de l'argenture répond à des modalités différentes entre les deux milieux. Les âges à la métamorphose des anguilles femelles de l'étang du Vaccarès sont très précoces (83,3 % des femelles s'argentent entre 4 et 5 ans) par rapport à ceux du canal de drainage du Fumemorte (94 % des femelles s'argentent entre 7 et 9 ans). Nous pensons que les potentialités de croissance qu'offre la lagune du Vaccarès induisent un tel résultat. Cependant, ce turnover seul ne peut expliquer les différentes proportions d'anguilles femelles argentées observées dans le canal de drainage du Fumemorte (23 %) et de l'étang du Vaccarès (2,4 %). L'influence des paramètres de population (sex ratio, structure de population et abondance) sur l'acquisition de l'argenture dans les deux biotopes est discutée.

**Mots-clés :** Anguille européenne, *Anguilla anguilla*, argenture, index oculaire, rapport gonadosomatique, croissance, âge à l'argenture, eau douce, lagune.

### INTRODUCTION

The change from yellow eel to silver eel is a metamorphosis. It precedes the gamodromous migration in the life cycle of the eel. This metamorphosis involves a whole series of morphological and physiological transformations that mark the limit between two stages characterised by different life styles and environments. This "smoltification" is a transitional period between a growth stage (yellow eels) and a seaward migration stage (silver eels).

In a context of a major decline in eel stocks throughout its distribution range, it seems to be fundamental to characterise the yellow and silver ecophases with the long-term aim of "defining how many future spawning silver eels should be allowed to escape, both in terms of quantity and quality" (LAMBERT and FEUNTEUN, 1998).

Silver eels are characterised by a very contrasting colour pattern with a blackish brown back and a silvery white belly (FONTAINE, 1994). But this criterion, on its own, is insufficient to discriminate between the two stages (PANKHURST and LYTHGOE, 1982). The length of the fins also increases (LEE, 1979) and there is a general increase in the size of sensory organs, including the lateral line (ZACCHEI and TAVOLARO, 1988), the olfactory epithelium (SORENSEN and PANKHURST, 1988 in *Anguilla rostrata*) and especially the eye (PANKHURST, 1982; FONTAINE, 1994).

Metamorphosis is a gradual phenomenon that starts in the yellow stage, and that in neuro-endocrine terms consists of several stages that succeed one another from spring to autumn (FONTAINE, 1994). As a result, the discrimination of individuals during metamorphosis is subjective and varies between observers. It therefore seems to be important to find macroscopic criteria that can be measured in the field to give an objective status to eels being examined.

The ocular index (OI), that reflects changes in eye diameter (PANKHURST, 1982), has proved to be a useful criterion for assessing the degree of transformation of the eel (DURIF *et al.*, 2000). Several authors have compared the OI of groups of female eels that were in principle either already silver and in their migration phase (reference group) or sedentary and in principle still yellow, with the aim of finding threshold values for metamorphosis that could be used to discriminate the two ecophases.

The threshold values of OI that characterise silver eels vary between 6.5 (PANKHURST, 1982) and 8.0 (MARCHELIDON *et al.*, 1999), the division in individual values of the ocular indices between the two stages explaining these differences in threshold values.

Metamorphosis matches with an increase in ovary weight in female fish, as measured by the gonadosomatic index (GSI), which increases from 0.3 to 1.5% (FONTAINE *et al.*, 1976). Furthermore in sedentary female eels there is a correlation between OI and the GSI, reflecting the state of ovarian development. MARCHELIDON *et al.* (1999) showed that a threshold value of GSI of 1.4% of body weight characterised the silver stage.

Since four years, we have monitored the eel population in the Camargue lagoon system. This system can be divided into two sub-units characterised by different population structures and especially different growth patterns in two distinct biotopes (freshwater and brackish water lagoons), and identified by means of structures within their otoliths (PANFILI *et al.*, 1990).

The aim of this study is to characterise these two sub-populations by analysing internal and external criteria of metamorphosis (respectively GSI and OI) in females eels belonging to “freshwater” and “brackish water” ecotypes, according to the terminology used by MOUNAIX (1992) and PANFILI and XIMENES (1994). Then, we will compare the proportion of silver eels between the two sub-populations. Results are discussed in regard to the characteristics of the distinct populations (growth, age, length frequencies, abundance).

## MATERIALS AND METHODS

The Ile de Camargue (southern France) has been completely embanked since 1869. It is bounded to east and west by the two existing distributaries of the Rhône (Grand and Petit Rhône) and to the south by a seawall. The aim of these works was to prevent, in one hand, flooding from the Rhône, and in the other hand, incursions of salt water from the sea. The hydraulic connections between the Ile de Camargue and the exterior are therefore restricted. Connections with the sea are restricted to sluices in the seawall at the Grau de la Fourcade, and the main connection with the Rhône is via the irrigation pumps used to flood ricefields (POIZAT *et al.*, 1999).

The first sampling site chosen was the Fumemorte drainage basin (68 km<sup>2</sup>), which collects drainage water from a complex network of ditches and canals nearly 400 km long (CHAUVELON, 1998). Its hydrology therefore depends upstream on pumping from the Grand Rhône for irrigation, and downstream on the Vaccarès lagoon, the lower lagoons nearer the sea and exchanges with the sea. The Fumemorte flows by gravity into the Vaccarès and the "Lower Lagoons".

The Vaccarès lagoon, which was the second sampling site, is a permanently flooded lagoon with a mean depth of 1.5 m and an area of 64 km<sup>2</sup>. The average salinity of the Vaccarès recorded between 1997 and 2000 was 9.7 g.l<sup>-1</sup>. In the Rhône and the Fumemorte canal, the average salinities are less than 1 g.l<sup>-1</sup> (CHAUVELON, 1996). The average seasonal changes in temperature of the water in the Fumemorte and Vaccarès are similar. For example, in 1996, the mean water temperatures of Fumemorte and Vaccarès were 7.4 and 7.6°C in winter (November to February), and 21.1 and 22.0°C in summer (June to September).

Regular monthly sampling was conducted at these two sampling sites over a period of 4 years (January 1997 to December 2000). Each site was sampled using passive fishing in the form of fyke nets (known locally as ganguis) of 6 mm mesh. The nets were set for 4 days per month and were controlled every 24 hours. All the eels captured were measured and weighed (to the nearest mm and g).

For fish  $\geq 300$  mm, the sex was determined by macroscopic observation of gonads, using the criteria described by COLOMBO *et al.* (1984). The horizontal and vertical diameters of the right and left eyes were measured to the nearest tenth of a millimetre using a slide calliper. The ocular index (OI), based on a relation between the total length of the eel and the mean size of the two eyes, was calculated using the following formula (PANKHURST, 1982) :

$$OI = 25\pi/8TL\{(A+B)^2_R+(A+B)^2_L\}$$

Where A and B are respectively the horizontal and vertical eye diameters, TL the total length and R and L are right and left eyes. In this study, the silver eel stage is considered as corresponding to the onset of sexual maturation, since the metamorphosis of the yellow eel into the silver eel stage is the first step in the irreversible process leading to complete maturity (DEELDER, 1984).

The state of sexual development was estimated by the gonadosomatic index (GSI), calculated using the following formula :

$$GSI = \text{weight of gonads} * 100 / \text{carcass weight}$$

The individual age of the eels was determined by measurements on otoliths on a sample of 401 eels from the Fumemorte (140 - 820 mm) in 1989 and 243 eels from the Vaccarès (66 - 668 mm) in 1997-1998. A right otolith (sagitta) was extracted from each eel and examined in reflected light against a dark background.

The age at capture was estimated by counting the number of opaque lines corresponding to periods of active growth (PANFILI and XIMENES, 1994). The last opaque line was not counted if the eel was captured before the month of May. The age is given in months with a date of birth that is fixed for the 1 June, the date by which all elvers have colonised the Vaccarès (CRIVELLI, unpublished data). The corresponding formula is: Age = 12 \* N + (M - 5), where N is the number of opaque lines, M the rank of the month of capture (M = 1 in January, etc.).

Different models (linear, exponential, logarithmic and Verhulst) were tested to determine the best relation between Age and the Length. The Length-Age relations

obtained from the two samples from the Fumemorte and Vaccarès were then used to estimate the age of all the eels captured throughout the sampling period.

## RESULTS

### Structures of the populations sampled

For the entire sampling period (from January 1997 to December 2000), the two sub-populations consisted of eels whose length varied between 100 and 825 mm for the Fumemorte (N = 1350) and 60 and 717 mm for the Vaccarès (N = 8423) (Figure 1). The size structures of the eels from the two sites differed significantly (Kolmogorov-Smirnov test, df = 9758, p < 0.001).

In the Vaccarès lagoon there was a distinct peak corresponding to recently recruited young eels (160 – 200 mm). In the Fumemorte drainage canal, this peak was shifted toward larger sizes (200 – 240 mm).

Eels of  $\geq 300$  mm accounted for 58.0% (N = 782) of fish in the drainage canal and 15.4 % (N = 1295) in the Vaccarès lagoon. If the selectivity of the fishing gear (6 mm mesh) played a major role on the length distribution of the eels that were captured, this bias would have been the same in both sites and could not therefore have explained these different proportions.

The gonads were examined in eels  $\geq 300$  mm. The sex ratios of eels captured in the Fumemorte canal and Vaccarès lagoon differed significantly ( $\chi^2 = 5.26$ , df = 1, p < 0.05). In the Fumemorte, the sex ratio was dominated by females (81.6%, 532 females and 120 males) but was slightly dominated by males in the Vaccarès (54.4%, 617 males and 517 females).

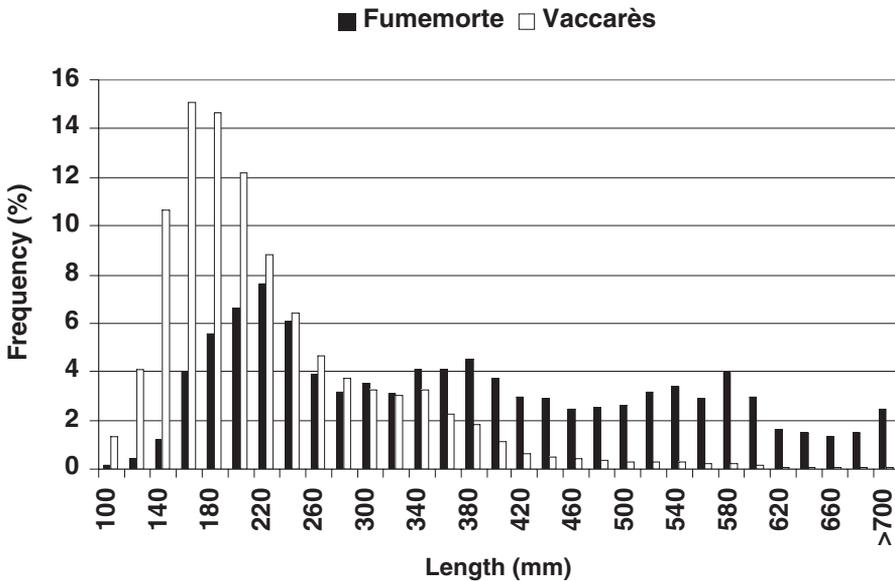


Figure 1  
Size distribution of eels captured during four years sampling in the Fumemorte drainage canal (N = 1350) and in Vaccarès lagoon (N = 8423).

Figure 1  
Distribution des tailles d'anguilles capturées pendant les quatre années d'échantillonnage dans le canal de drainage du Fumemorte (N = 1350) et dans l'étang du Vaccarès (N = 8423)

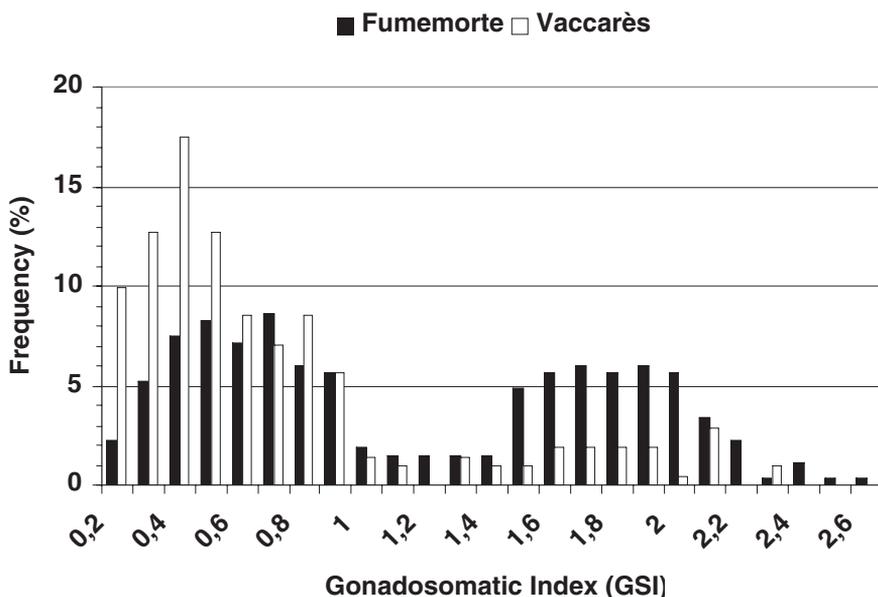
### Characterisation of the ecophases

#### Gonadosomatic index

The gonadosomatic indices of female eels varied from 0.08 to 2.53% in the Fumemorte and from 0.11 to 2.27% in the Vaccarès. The distributions of GSI of eels captured in the two sites were bimodal and were significantly different one from another (Figure 2) (Kolmogorov Smirnov test,  $df = 478$ ,  $p < 0.001$ ).

The GSI distribution of female eels captured in the Fumemorte drainage canal was characterised by two modes peaking at 0.6 and 1.8%, respectively. In the eels from Vaccarès, there was a distinct first peak at 0.4%, but it was difficult to distinguish the second peak of higher values of GSI because of the small numbers of fish.

In any case, the number of eels with GSI values of between 1.0 and 1.4% was low in both types of environment, being only 7.8% of the eels captured in the Fumemorte and 4.7% of those from the Vaccarès (Figure 2). It therefore seems that the values of GSI can be used to differentiate between female eels with low ( $< 1.4\%$ ) and high ( $\geq 1.4\%$ ) gonadosomatic indices.



**Figure 2**

**Histogram representing the percentage of female eels ( $\geq 300$  mm) in relation to gonadosomatic index (GSI) for eels captured in the two sampling sites.**

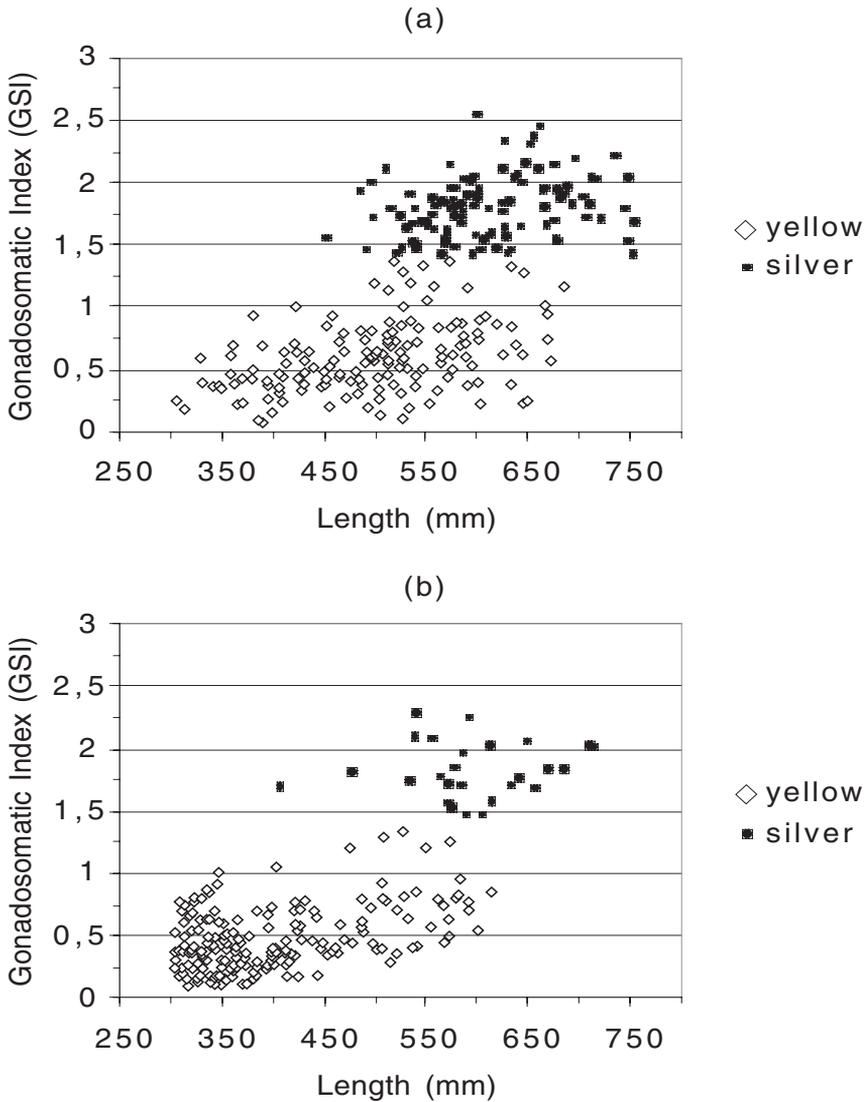
**Figure 2**

**Histogramme représentant les pourcentages d'anguilles femelles ( $\geq 300$ mm) en relation avec l'index gonadosomatique (IGS) pour les anguilles capturées sur les deux sites d'échantillonnage.**

According to MARCHELIDON *et al.* (1999), the bimodal distributions of GSI observed in the female eels from the Fumemorte and Vaccarès characterise yellow eels ( $GSI < 1.4\%$ ) and silver eels ( $GSI \geq 1.4\%$ ).

In the Fumemorte canal, the mean GSI values of yellow eels ( $GSI < 1.4\%$ ) and silver eels ( $GSI \geq 1.4\%$ ) vary respectively between  $0.60 \pm 0.28\%$  and  $1.78 \pm 0.24\%$ . In the Vaccarès lagoon, the mean GSI values of yellows eels and silver eels vary between  $0.48 \pm 0.24\%$  and  $1.81 \pm 0.22\%$  respectively.

The ovarian development that is characteristic of metamorphosis, and which takes place at a GSI  $\geq 1.4\%$ , started in eels of 453 mm in the Fumemorte (Figure 3a) and of 408 mm in the Vaccarès (Figure 3b). But in both sites, metamorphosis occurred at very variable body lengths varying between 400 and more than 750 mm.



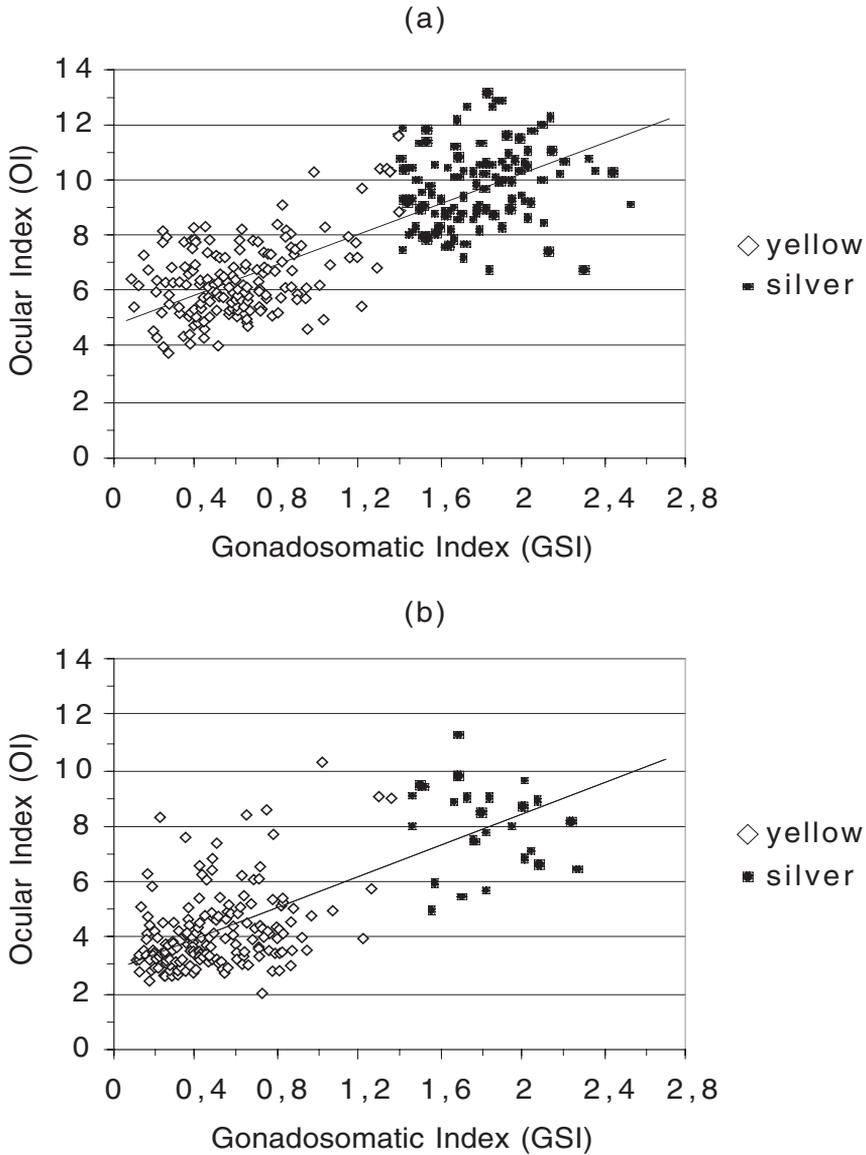
**Figure 3**  
Relation between the gonadosomatic index (GSI) and the body length (TL) for female eels  $\geq 300$  mm captured (a) in the Fumemorte canal (b) in Vaccarès lagoon.

**Figure 3**  
Relation entre l'index gonadosomatique (IGS) et la longueur du corps (TL) pour les anguilles femelles  $\geq 300$  mm capturées (a) dans le canal du Fumemorte (b) dans l'étang du Vaccarès.

Ocular index

The length of eels on its own is insufficient for determining whether metamorphosis has occurred, since a large proportion of eels  $> 500$  mm still have characteristics of yellow eels.

In the Fumemorte, yellow eels with GSI < 1.4% had OI that varied from 3.80 to 11.6 (mean value  $6.49 \pm 1.38$ ), whereas the ocular indices of silver eels (GSI  $\geq 1.4\%$ ) ranged from 6.72 to 13.13 (mean value  $9.71 \pm 1.40$ ) (Figure 4a).



**Figure 4**  
Relation between the gonadosomatic index (GSI) and ocular index (OI) for female eels captured (a) in the Fumemorte canal (b) in Vaccarès lagoon. Significant correlations were observed for eels ( $p < 0.001$ ).

**Figure 4**  
Relation entre l'index gonadosomatique (IGS) et l'index oculaire (OI) pour les anguilles femelles captures (a) dans le canal du Fumemorte (b) dans l'étang du Vaccarès. Des corrélations significatives ont été observées pour les anguilles ( $p < 0.001$ ).

The female eels captured in the Vaccarès had ocular indices that varied from 2.03 to 10.3 (mean value  $4.20 \pm 1.36$ ) for yellow eels and from 4.95 to 11.25 (mean value  $8.0 \pm 1.54$ ) for silver eels (Figure 4b).

There were significant correlations between OI and the GSI for all eels captured in the Fumemorte ( $p < 0.05$ ,  $r^2 = 0.61$ ,  $N = 267$ ) (Figure 4a) and in the Vaccarès ( $p < 0.05$ ,  $r^2 = 0.49$ ,  $N = 212$ ) (Figure 4b).

OI's threshold value of 8.0 proposed by MARCHEDIDON *et al.* (1999) for characterising silver eels, discriminated respectively 85.4% and 70% of the eels that had a  $GSI \geq 1.4\%$  in the Fumemorte and in the Vaccarès. The threshold value for OI of 6.5 proposed by PANKHURST (1982) only discriminated 62.4% and 64.7% of female eels with a  $GSI \geq 1.4\%$ .

The analysis of GSI and OI enabled us to discriminate between the yellow and silver ecophases. It appeared that the proportions of female silver eels ( $OI \geq 8.0$ ) in the Fumemorte drainage canal (23%) and in the Vaccarès lagoon (2.4%) differed significantly from one another ( $\chi^2 = 3903.05$ ,  $df = 1$ ,  $p < 0.000$ ).

#### Growth and age of female eels

Individual age was determined on a sample of 402 eels from the Fumemorte and 243 eels from the Vaccarès. The linear regressions between Length and Age were one of the models that explained most of the variance and were chosen for simplicity. Length-Age relations were therefore produced for the Fumemorte (Length =  $163.54 + 46.03 * \text{Age}$ ,  $r = 0.78$ ,  $N = 402$ ,  $p < 0.001$ ) and Vaccarès (Length =  $67.82 + 95.23 * \text{Age}$ ,  $r = 0.87$ ,  $N = 243$ ,  $p < 0.001$ ).

To compare growth rates between eels of Fumemorte and Vaccarès, an analysis of covariance was therefore conducted on the 2+ age-class because of the small sample size of the 0+ and 1+ age-classes in the Fumemorte samples. The growth rate of female eels from Vaccarès was much higher significantly than those from the Fumemorte (comparison of slopes  $F_{1,569} = 55.88$ ,  $p < 0.001$ ).

For example, at the age of 4 years, female eels from the Fumemorte measured 348 mm whereas those from the Vaccarès had a length of 427 mm. The annual growth rate was 90 mm for eels captured in the Vaccarès whereas this was only 46 mm for those from the Fumemorte.

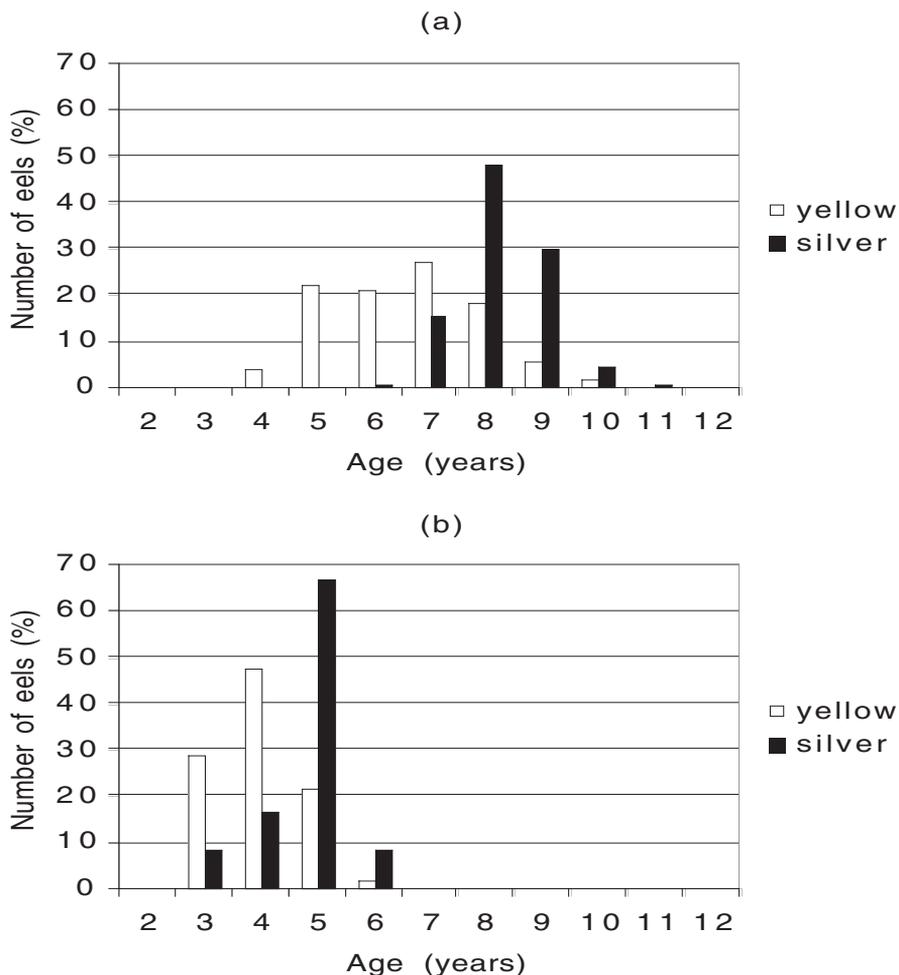
The ages of yellow female eels ( $OI < 8.0$  and  $TL \geq 300$  mm) in the Fumemorte varied from 4 to 10 years (Figure 5a), compared to 3 to 6 years in the Vaccarès (Figure 5b). The most abundant age-class in the Fumemorte was 7+ (27% of captures) and 4+ in the Vaccarès (47% of captures).

The average ages of yellow eels in the Fumemorte ( $6.07 \pm 1.32$  years) and Vaccarès ( $3.49 \pm 0.67$  years) differed significantly one from another (t-Test;  $p < 0.001$ ;  $df = 882$ ).

Female silver eels ( $OI \geq 8.0$ ) of Fumemorte were significantly older ( $7.75 \pm 0.82$  years) (Figure 5a) than those of Vaccarès ( $4.17 \pm 0.73$  years) (Figure 5b) (t-Test,  $p < 0.001$ ,  $df = 126$ ).

Eels from Fumemorte showed a wide range of age at metamorphosis that ranged from 6 to 11 years. For the entire sampling period, 94% of female eels  $\geq 300$  mm had an age at metamorphosis of between 7 and 9 years, age-class 8+ being the most abundant accounting for 48.3% of captures.

In the Vaccarès, female eels started metamorphosis much earlier. The age at metamorphosis varied from 3 to 6 years for the whole sampling period, 83.3% of female eels  $\geq 300$  mm metamorphosing between 4 and 5 years.



**Figure 5**  
**Age distribution of female yellow (OI < 8) and silver (OI ≥ 8) eels as a % of those captured (a) in the Fumemorte canal and (b) in Vaccarès lagoon.**

**Figure 5**  
**Distribution des âges des anguilles femelles jaunes (OI < 8) et argentées (OI ≥ 8) en % de celles capturées (a) dans le canal du Fumemorte (b) dans l'étang du Vaccarès.**

**DISCUSSION – CONCLUSION**

The threshold value of GSI ≥ 1.4% that characterises the silver stage according to MARCHELIDON *et al.* (1999) provided a good discrimination between the two groups of eels that were in principle yellow or silver.

In both sites, metamorphosis occurred at very variable body lengths varying between 400 and more than 825 mm. It therefore seems that a minimum size would be a necessary but not exclusive factor for the start of metamorphosis, since eels do not all metamorphose at the same length.

In the Fumemorte canal, the mean GSI values were 0.60 ± 0.28% for the yellow stage and 1.78 ± 0.24% for the silver stage. In the Vaccarès lagoon, these values were 0.48 ± 0.24% and 1.81 ± 0.22% for yellow and silver stages respectively. These values are similar to samples of eels from northern France studied by MARCHELIDON *et al.*

(1999) where the mean GSI values were  $0.67 \pm 0.03\%$  for sedentary eels and  $1.74 \pm 0.03\%$  for eels migrating toward the sea.

The progressive increase in GSI with body length in yellow eels indicates that gonad development is a gradual phenomenon that starts in the yellow stage and is related to body growth (MARCHELIDON *et al.*, 1999).

The increase in eye diameter was evaluated by means of the ocular index (OI). MARCHELIDON *et al.* (1999) proposed a threshold OI value of  $\geq 8.0$  as being an external criterion for metamorphosis. 85.3% of silver eels (defined as having a  $GSI \geq 1.4\%$ ) had an ocular index  $\geq 8.0$  in the Fumemorte compared to 70% in the Vaccarès. This result confirms that the threshold values for metamorphosis of GSI and OI proposed by MARCHELIDON *et al.* (1999), who compared sedentary and migrating eels in northern France are also applicable to eels in Mediterranean freshwater and lagoon environments. The threshold value for metamorphosis of PANKHURST (1982) ( $OI \geq 6.5$ ) only discriminated 62.4% of female eels with a  $GSI \geq 1.4\%$  in the Fumemorte canal and 64.7% of those in the Vaccarès. This low threshold value therefore included eels that had low GSI values characteristic of eels that are in the process of metamorphosis or are still yellow, and whose ability to undertake the migration to the spawning areas in the Sargasso Sea would seem to be low (FONTAINE, 1994).

For the yellow female eels from the Fumemorte and Vaccarès, the significant positive correlation observed between OI and GSI indicates that the growth in eye diameter is a gradual phenomenon that starts in the yellow stage and is related to gonad development. A significant increase in ocular index was observed during metamorphosis, the mean value of OI increasing between the yellow and silver stages from  $6.49 \pm 1.38$  to  $9.71 \pm 1.40$  in the Fumemorte and from  $4.20 \pm 1.36$  to  $8.0 \pm 1.54$  in the Vaccarès lagoon.

DURIF *et al.* (2000) studied the changes in morphological and physiological variables during metamorphosis in eels from the Lac de Grand-Lieu (Loire-Atlantique, France). Their study confirmed the hypothesis of FONTAINE (1994) that metamorphosis takes place progressively. They were able to distinguish four distinct groups (A1 to A4) characterised mainly by their different mean GSI and OI values. Stage A4, that includes silver females, was defined as fish having a mean GSI of  $1.63 \pm 0.33\%$ . This result confirms that GSI values of the second peak in the Fumemorte canal and Vaccarès lagoon characterize silver eels which were ready to undertake their spawning migration.

We found a large difference in the minimum age at metamorphosis of about 4 years between the female eels from the Fumemorte drainage canal (6 years) and from the Vaccarès lagoon (3 years). In the Fumemorte canal, 94% of female eels became silver between 7 and 9 years. In the Vaccarès lagoon, 83.3% of females metamorphosed between 4 and 5 years. The age of metamorphosis of the latter are among the lowest ever recorded in a natural environment. For example, ROSSI and CANAS (1984) mentioned that the average age of female silver eels was  $6.4 \pm 1.2$  years in a lagoon in southern Sardinia. Under fish-farm conditions, BEULLENS *et al.* (1997) observed silver females aged 3-4 years, at lengths of between 530 and 790 mm. This result must be linked to habitat productivity since many studies show intraspecific differences between populations in life-history traits, including age at maturity which can be related to food availability (JONSSON and SANDLUND, 1979).

Brackish environments like the Vaccarès lagoon are more favourable sites for growth than freshwater environments (PANFILI and XIMENES, 1994). An annual growth rate of 90 mm was recorded for female eels captured in the Vaccarès lagoon whereas this was only 46 mm in the Fumemorte canal. Temperature cannot explain the

differences in growth since water temperature patterns were similar in both environments. PANFILI (1993) suggested that the observed differential growth rate could be caused by (i) the densities of eels occurring in the environment, (ii) the food availability, (iii) the quality of food available (fish, invertebrates, etc.), (iv) the turnover of this food and finally (v) competition with other species. Our results seem to confirm the hypothesis of SVEDÅNG *et al.* (1996), who suggested that environmental properties could lead to major differences in the metabolism of lipid accumulation (*i.e.* growth rates). THORPE (1994) argued that age-at-maturity differences among salmonid populations suggested multiple solutions as evolutionary stable strategies within species. This strategy has the advantage of reducing the generation time and therefore the risks of mortality before reproduction. Such a turnover would not explain alone the different proportions of female silver eels captured in the Fumemorte canal (23%) and Vaccarès lagoon (2.4%) throughout our sampling period. However, silvering may probably vary according to local environment conditions (catchment's size, habitat productivity, etc.) since such parameters are known to influence sex ratio, population structure and size of population (FEUNTEUN *et al.*, 2000).

Our results confirm that the sub-populations of eels from the Fumemorte drainage canal and Vaccarès lagoon belong to two different groups, respectively freshwater and brackish water ecotypes (PANFILI and XIMENES, 1994).

Analysis of the length frequencies of eels captured in the Fumemorte drainage canal show a low proportion of elvers suggesting a recruitment failure and/or a delay caused by its relative inaccessibility. It seems that the colonisation of the Fumemorte by young recruits (< 160 mm) is relatively poor. This sub-population is characterised by a predominance of female eels (81.6%). This situation is similar to that found in headwater streams where the densities of eels are low (PARSONS *et al.*, 1997). DUPONT (1984) already reported similar sex ratios in this canal (79% females), suggesting that the structure of sub-population has been very stable for nearly 15 years. Size structure of eels in the Fumemorte canal suggest that mortality is low since fishes  $\geq 300$  mm accounted for 58.0% (N = 782) of the whole sample. Moreover, we can also suggest that settling of female eels is important in the Fumemorte drainage canal. FEUNTEUN *et al.* (2000) showed, in the Frémur dammed catchment, that at least 15% of the silver eels present in the catchment stayed in the system the following year. Factors determining the timing of the catadromous migration of the silver eels in the Fumemorte drainage canal are under study.

Recruitment in the Vaccarès lagoon is much higher than in the Fumemorte since its geographic situation allows a good colonisation for the elvers. The sex ratio is close to equality (54.4%) and as a result frequencies of female eels are less important than in the Fumemorte system. In most Mediterranean lagoons, silver males predominate (from 58 to 80%) (MALLAWA, 1987). CRIVELLI (1998) suggested that the productivity of the environment in which eels are sedentary is the fundamental factor determining sexual differentiation, productive environments leading to high densities and therefore a differentiation toward the male sex. Contrary to the Fumemorte canal drainage, mortality seems to be high for eels  $\geq 300$  mm. We can suggest that (i) emigration is easier in Vaccarès for silver eels (ii) harvest of yellow and silver eels by local fisheries in the Vaccarès lagoon play an important role on the survey of the subpopulation (ii) mortality caused by adverse environmental conditions such as anoxia or hypertrophy that occur in all Mediterranean lagoons (CRIVELLI, 1998).

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