Growth-reproduction interaction in Salmonids

Pierre-Yves Le Bail

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P.Y. LE BAIL

INRA, Laboratoire de Physiologie des Poissons
Campus de Beaulieu, 35042 Rennes Cedex, France

Summary

In teleost fish, as in most vertebrates, reproduction cannot be dissociated from other functions, and in particular from growth, which interfer with it. We present here, the results concerning the most studied group in fish : the salmonids.

It appears that puberty is mainly dependent on the size of the animal. All factors which directly influence the growth before the puberty (nutrition, temperature...) modify the age at which it occurs. One the other hand, salinity and smoltification have a more complex influence and often delay puberty. The genetic control of puberty is well etablished but is not as important as the external factors.

During the first months of gametogenesis, growth is accelerated but is often strongly reduced around the spawning period. Modifications of growth rate appear to be directly dependent on the sex steroids. The results recently obtained in mammals, allow the proposal of an hypothesis concerning the actions of somatotropic axis hormones on the regulation of reproductive function in vertebrates.

GENERAL INTRODUCTION

Two of the main criteria in the choice of interesting species for aquaculture are :

- rapid growth or a large commercial size
- high fecundity associated with a precocious reproduction.

Increase in growth has been achieved either by genetic selection or better nutrition, revealing a correlation between reproduction and growth. This presently excludes, from an economical standpoint, an increase in one of these functions without depletion of the other. A better knowledge of the relationship between growth and reproduction and especially of the control mechanism is needed to increase productivity.

This review will focus on salmonids in which reproduction interfered with :

- growth rate
- muscular composition and the flesh quality
- survival during spawning

We will consider, in order to simplify the presentation, the effect of growth on puberty and during post puberal gametogenesis.

I - PUBERTY

The definition of puberty remains arbitrary (Levasseur and Thibault, 1980).Puberty in the male is defined by the appearance of the first spermatocytes, and in the female by the beginning of vitellogenesis,the detection of which remains relatively easy and reliable.

a) Relation between growth and puberty. The percentage of puberal fish increase with the size according to a sigmoïd curve (fig. 1). The size of puberty is defined as that at which 50 % of the population enter into puberty. The same relation has been found for all salmonids (Alm, 1959 ; Rahrer, 1965 ; Lusk, 1968 ; Utoh,1976 ; Kato, 1978 ; Bagliniere and Maisse, 1985) and for most teleosteen fish. However, these results must be modified in function of the period of the reproductive cycle during which it has been established. In general, puberal size of the female is larger than the male.

Age must also be taken into consideration, because it is correlated with growth. Thus some authors express puberty as a function of age. But the results appear more variable from one year to another within the same population because the growth rate is dependent upon numerous parameters such as temperature, food availability ... However, sexual dimorphism of puberal size gives rise to mature males one year before mature females.

Age cannot be totally excluded in the determination of puberty because sometimes the size at puberty appears to decrease with age (Wydoski and Cooper, 1966).Stearns and Grandal (1984) suggest that puberty depends on a size-age relation which it is possible to predict.

In salmonids, **the critical period** during which the growth influences puberty is at the beginning of spring. Under natural conditions, the percentage of maturation depends on the previous years growth (Maisse et al., 1987). In the hatchery, modifications of the growth rate before spring influences the percentage of maturing fish (Scott, 1962 ; Titarev, 1975 ; Mac Kinnon and Donaldson, 1976). On the other hand, modification of the growth rate after this period has no effect on the percentage of animals reaching puberty (Bagenal, 1969).

b) Factors influencing the age at puberty

The genetic component accounting for the variability of the age of puberty is less important than the environmental component but it must be considered (Gardner, 1976 ; Gjedrem, 1983 ; Peterman et al., 1986).

Genetic factors

Under similar environmental conditions, the percentage of mature fish in different strains of Atlantic salmon (Salmo salar) (figure 2) or Rainbow trout (Salmo gairdneri), varies greatly (Naevdal et al., 1981 ; Naevdal, 1983 ; Gjedrem, 1983 ; Burger, 1985). So, the hereditability of the age of the first maturation is high, around 0.4 (Burger, 1985 ; Gjerdem, 1984). But this hereditability is different between the parents. Puberty at one year of male Rainbow trout and parr Atlantic salmon, directly depends on the male parent. Later, both parents are involved in the genetic determination of puberty.

But it is clear that early puberty depends on a high growth rate,and the genetic selection of late puberty leads to the selection of a low growth rate strain (Gjedrem, 1983).

Environmental factors

Feeding is one of the most important factors influencing the age of puberty. In nature, the increase in available food accelerates

growth and consequently the percentage of puberal animals (Woodhead, 1960 Mc Fadden et al., 1965 ; Bagliniere and Maisse, 1985). In the hatchery, where all environmental factors can be controlled, the results are more dramatic (Scott, 1962 ;Bagenal, 1969 ; Kato, 1975). Kato (1978) observed an increase of mature Sockeye salmon (Oncorhynchus nerka) from eighteen to eighty percent in males, and from zero to thirty three percent in fema-

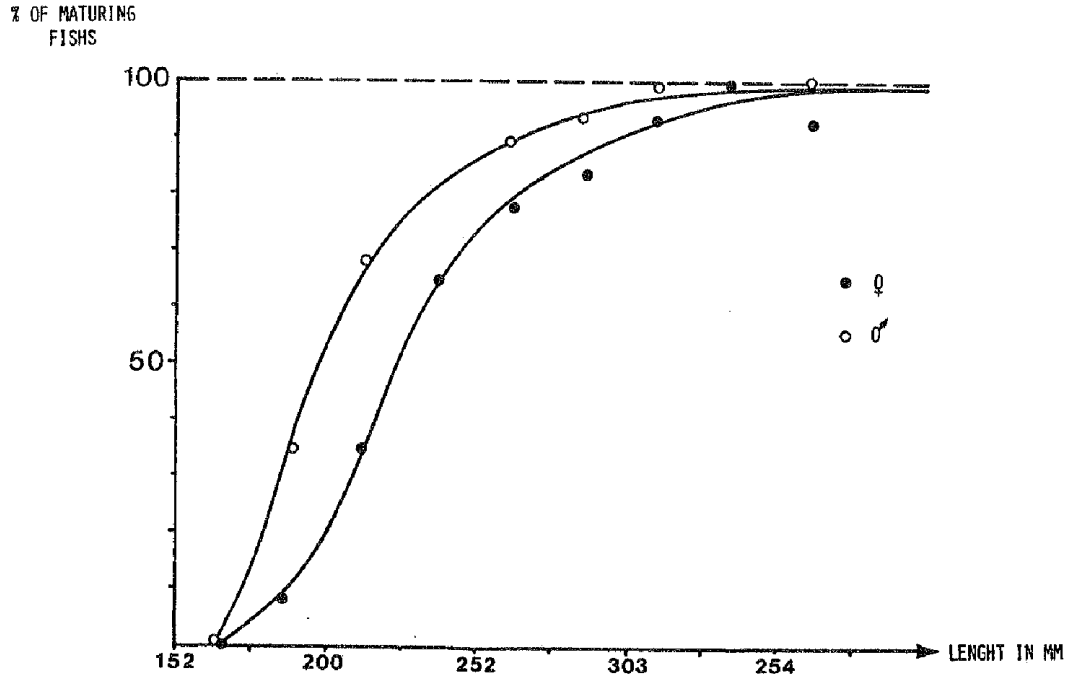

Fig 1 : Percentage of puberal fish in relation to the lenght in Salmo trutta (Taube, 1976)

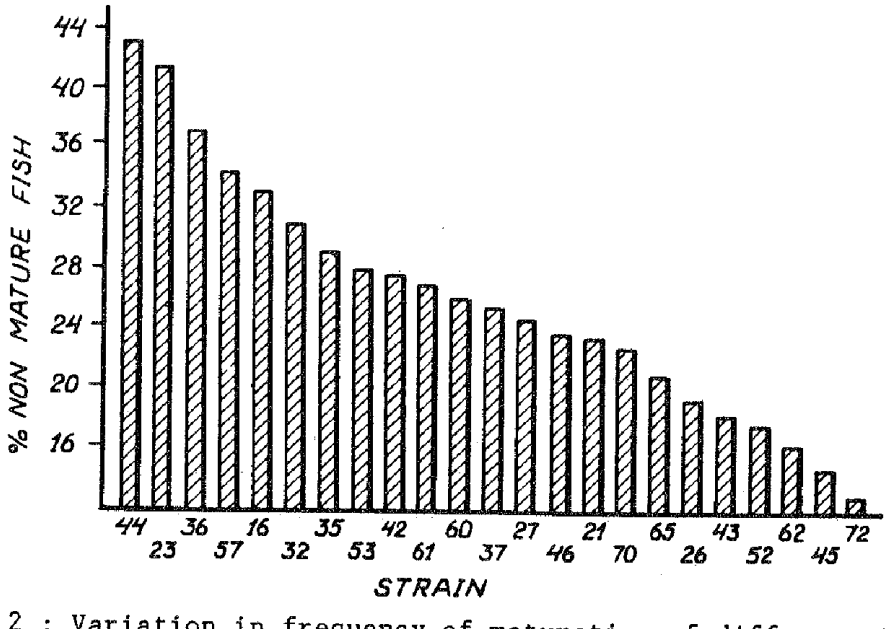

Fig 2 : Variation in frequency of maturation of different Atlantic salmon strains after two sea winters (Gunnes, 1979)

les when the feeding ratio increased from 1.5 to 3 percent.

A rise in **temperature** decreases the age of puberty (Titarev, 1975 ; Mc Kinnon and Donaldson, 1976). But a direct effect of temperature still requires verification because here feeding also increases (Brett and Groves, 1979).

The evidence for an effect of maturation upon smoltification, which depends on **salinity**, seems to vary according to the species. For example, in Atlantic salmon, a precocious maturation does not inhibit smoltification the following spring (Bagliniere and Maisse, 1985). Thus, in this species, puberty and smoltification appear to be relatively indepandant, and age of puberty in fresh water is not modified. In contrast, in Masou salmon (Onchorynchus masou), castration induces the parr-smolt transformation, so the maturation does seem to inhibit smoltification (Aida et al., 1984).

Salinity does appear to have a direct effect. In anadromous salmonids, growth is accelerated during the marine phase. One would expect diminution of the age of puberty, but this is not the case. In the same strain, the size at puberty is higher in sea water than in fresh water (figure 3). Maturing salmon during their first winter at sea have never been observed. This is also the case for the smolt which have matured precociously in fresh water (Sutterlin et al., 1978 ;Naevdal, 1983 ; Bagliniere and Maisse, 1985). The transfer into brackish water inhibits maturation strongly but not totally whereas fish in fresh water show normal maturation (Lundqvist and Fridberg, 1982). In conclusion, salinity appears to delay puberty. This is the result of a partial dissociation between puberty and growth.

c) Endocrinology of puberty

Puberty appears when the **gonadotrop axis** is "mature" (Magri, 1983). In the gonad the enzymes implicated in steroïdogenesis must be functional and the gonad must be receptive to gonadotropic hormone GtH. In male Rainbow trout, this is possible at five months old. Nevertheless, it is not sufficient to induce puberty. For example, castration does not modify the time at which the GtH secretion appears.

In the hypothalamo-pituitary system both GtH and GnRH (gonadotropic releasing hormone) synthesis and release must be active. GtH synthesis has been demonstrated to be under positive feedback control by steroïds. Futhermore, GnRH exists in the brain but there is no indication

about the factors stimulating its synthesis and release to the pituitary in order to stimulate GtH secretion. On an other hand, the pineal gland would be expected to exert an inhibitory effect on puberty (Breton et al., 1986).

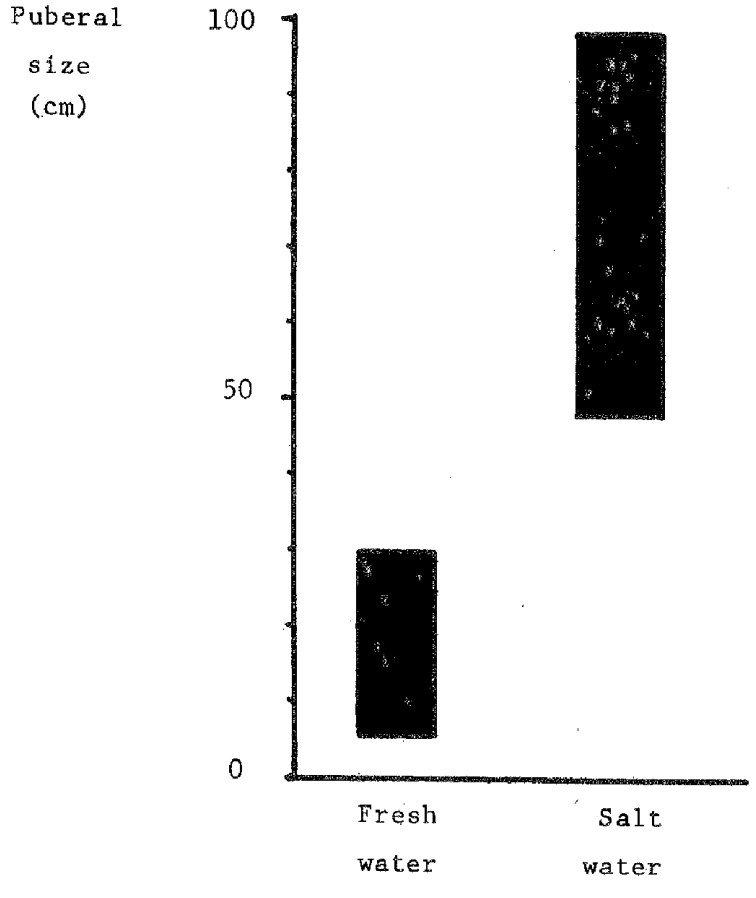

Fig 3 : Size of puberal Salmo salar in fresh or salt water (from Fontenelle et al., 1980, Prouzet et al., 1980, Baglinière et al., 1985)

There is at present no data indicating a direct involvement of **somatotrop axis** hormones on the maturation of the hypothalamo-pituitary axis. However, somatotrop axis hormones do act on mammalian gametogenesis :

Independantly of growth, the decrease of GH secretion delays the age of puberty in rat (Ramaley and Phares, 1983) ; GH regulates the levels of IGFs (Somatomedins or Insulin like-growth factors) in the granulosa (Hsu and Hammond, 1986) and Sertoli cells (Benahmed et al., 1985). In fact, IGFs are present in different compartments of the gonads like granulosa cells (Adashi et al., 1985), follicular fluid (Hammond et al.,1985 ;

Ramasharma et al., 1986), Sertoli cells, spermatocytes (Tres et al., 1986) and seminal plasma (Ramasharma et al., 1986). But only granulosa cells (Hammond et al., 1985), Sertoli and myoid cells (Tres et al., 1986 ; Benhamed et al., 1986) produce this factor.

The presence of IGF receptors have been demonstrated on granulosa (Baranao and Hammond, 1984 ; Davoran et al., 1986 ; Adashi et al., 1986), Leydig cells (Handelsman et al., 1985) and Sertoli cells (Borland et al., 1984). These data indicate that IGFs have an autocrine, paracrine and perhaps endocrine action. There are two types of action : firstly, IGFs have a mitotic effect and increase the differentiation of Sertoli, Leydig and granulosa cells (Borland et al., 1984 ; Adashi et al., 1985 Bernier et al., 1986). Secondly, IGFs increase the number of LH receptors and the steroidogenic activy of granulosa and Leydig cells, in synergy with FSH and oestradiol (Davoren et al., 1985 ;Adashi et al., 1986 ; Benhamed et al., 1986 ; Veldhuis et al., 1986)

In fish, the few avaible results would suggest an action of IGFs on the gonads. In trout testis cell culture, steroid production and their stimulation by GtH is increased in the presence of a steroid free serum (Loir, personal communication). On the other hand, in the hypophysectomized killifish, (Fundulus), the growth hormone alone stimulates gonial division, and with LH, increases cell differentiation and the activity of the steroidogenic enzymes (Pickford et al., 1972).

These results agree with those obtained in mammals and the following hypothesis is suggested to explain the action of GH on gonadal growth (figure 4) : In animals with a better growth rate which are supposed to enter into puberty earlier, the high production of GH stimulates the gonadal IGF action on steroidogenesis, gonial and cell differentiation, and so accelerates gametogenesis. However, the steroids amplify this phenomenon with a double positive feed back on the GtH and IGF secretion.

In conclusion, it appears that GH would not induce puberty,but accelerate it.

II - POST PUBERAL GAMETOGENESIS

The energetic theory explains that during the puberal period, the excess of energy which is not used for basal metabolism or activity,

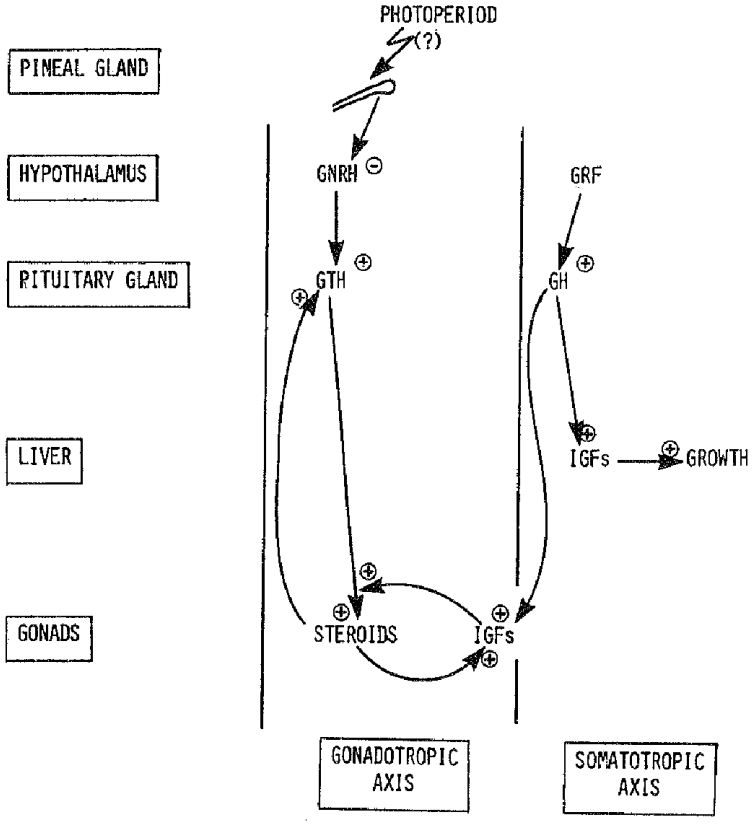

Fig 4 : Sheme of somatotropic axis action on puberty

is totally invested in growth. During gametogenesis, the gonads would take, for their recrudescence, a part or all of this energy (Wootton, 1979 ; Roff, 1983). In a first analysis, this is in accordance with experimental data. However, a more precise analysis indicates that the modification of growth is not just a simple derivation of energy to the gonads. During gametogenesis, three phenomenona related to growth can be observed : firstly, the fecundity growth relationship : secondly, the modifications of the growth rate and thirdly the relation between size and time of spawning.

a) Fecundity growth relation

As in all other teleost fish, there exists in salmonids a good correlation between size and eggs reproduction (Lusk, 1968 ; Bulkley, 1967 ; Blalckett, 1973 ; Gibson et al., 1976 ; Healey and Heard, 1984). However, this value varies and is not the same at the beginning and at the end of the reproductive cycle. In Atlantic salmon, fecundity is not correlated with the weight at the beginning of vitellogenesis, although it is a short time later. Thus, the fecundity which is 2300 oocytes/kg of

body weight between February and June, drops to 1600 oocytes/kg at the time of ovulation (Prouzet et al., 1984). These observations suggest that a regulation of the number of oocytes exists which depends on the growth rate. According to the literature,this regulation occurs during two critical periods (figure 5). Firstly, during the first year of life, at the time of gonial divisions : the modification of growth by nutritive restriction results in a decrease of fecundity, 1 year and a half later (Ivankov, 1983). Secondly, during the first part of vitellogenesis, restrictive nutrition also modifies the number of oocytes at the spawning period (Smith et al., 1979 ; Billard and de Fremont, 1980). After July, the number of oocytes remains stable until spawning even if the animal uses its body reserves to compensate a possible under feeding (Henderson, 1963). Genetics also influence fecundity (Kato, 1979).

The nature of an eventual endocrine regulation of fecundity, is not known.

b) Growth rate variation

In the same strain, if we compare the growth of animals starting gametogenesis with that of immature animals, two different phases can be distinguished (Lander and Tanonaka, 1964 ; Hunt et al., 1982 ; Tveranger, 1985 ; Burger, 1985) :

The **first**, from March to August, is characterized by an acceleration of growth. During this phase, fat accumulates around the guts and in the muscles, and the weight of the gonads increases slowly. The best growth rate of mature animals is not related to a larger size at puberty, because in animals of a calibrated size, the study of individual growth rates between April and August gives the same results (figure 6, Poquillon, 1984).

During **phase two**, there is a dramatic decrease of growth from September to the post spawning period. This corresponds to a rapid increase of gonad weight, during which the body fat decreases. A loss of body weight can occur in some species which experience starvation such as anadronous salmonids.

During the second reproductive cycle, the acceleration of growth during phase one is greater than that of the first reproductive cy-

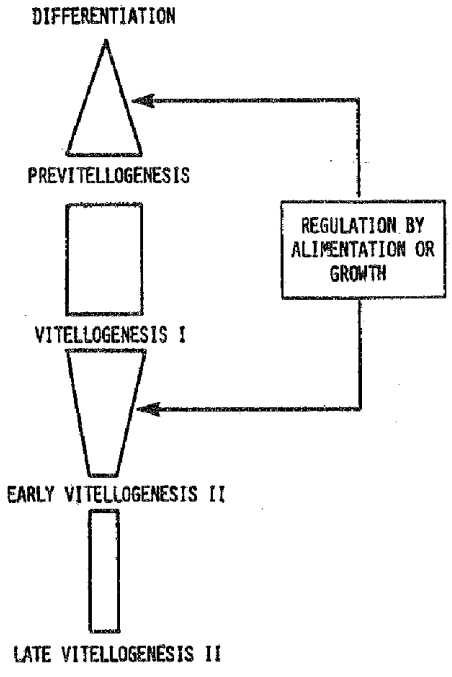

Fig 5 : Regulation of fecundity in Salmonids

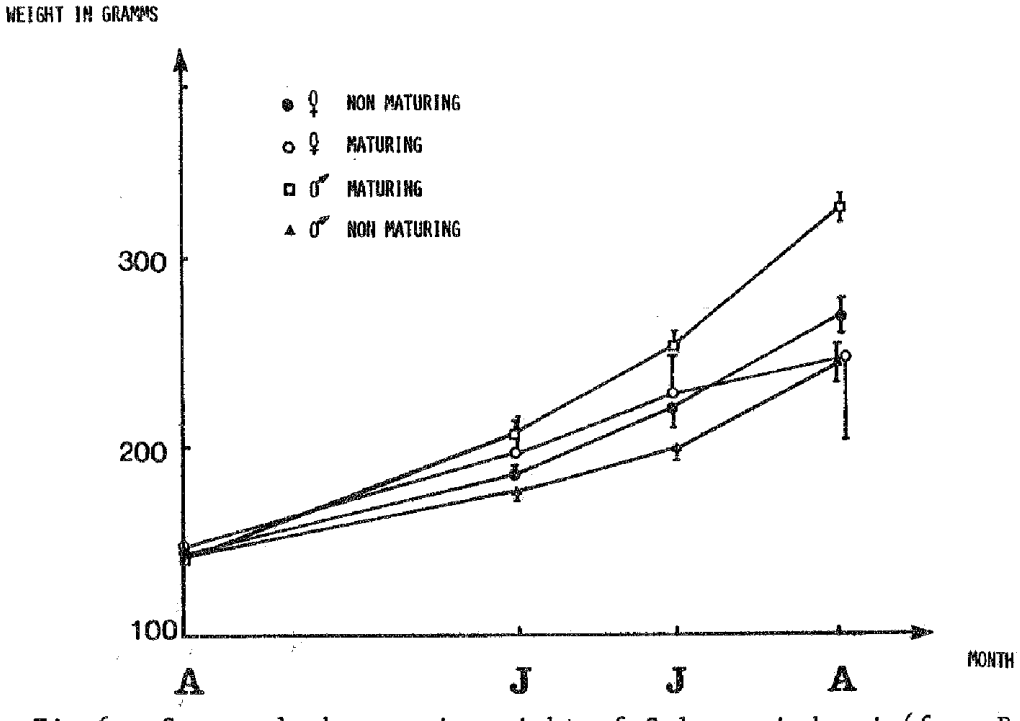

Fig 6 : Seasonal changes in weight of Salmo gairdneri (from Poquillon, 1984)

cle. However, it is not long enough to compensate the former retardation of growth.

We now have a good idea about the effect of **exogenous steroid hormones** in salmonids (Donaldson et al., 1979). Among the sexual steroids, the androgens have the most potent effect on growth. For example,

methyltestosterone results in a 150 % weight gain within nine months. Natural Salmonid androgens such as, 11-ketotestosterone and testosterone are also effective. There is a dose dependant effect when the dose does not exceed 10 mg/kg of food. Temperature increases the steroid action. With higher doses and after a long period of administration, growth is strongly depressed. This phenomenon is often correlated to an atypical process of maturation (Mc Bride and Fagerlund, 1973).It must be noted that the response to androgen treatment varies according to the species. It is maximum in Coho salmon (Oncorhynchus kisutch) and nearly zero in Atlantic salmon.

The levels of **endogenous sexual steroids** change dramatically during the reproductive cycle. In the male, two phases can be observed in steroid secretion (Sangalang and Freeman, 1974 ; Hunt et al., 1982 ; Baynes and Scott, 1985). During the first, their levels remain low and do not reach more than 10 ng/ml. This phase extends from March to July during the first reproductive cycle and is shortened during the following cycles (May to July). In July, at the beginning of the second phase, the levels rapidly increase and are the highest at the time of spermiation for 11-ketotestosterone, and for testosterone two or three months before . Their maximal levels vary according to the species. For example 11-ketotestosterone reaches 700 ng/ml in Coho salmon (Leatherland et al.,1982) and only 40 ng/ml in Atlantic salmon (Hunt et al., 1982).

In the female, the level of 11-ketotestosterone is low (Scott et al., 1980). However, the level of testosterone is similar to that in the male. It often peaks at more than 200 ng/ml. Testosterone is considered as the estradiol precursor (Scott et al.,1980 ; Sumpter et al., 1984).

It is tempting to correlate the two phases of growth with androgen secretion. This has been done in a population of Atlantic salmon where growth and androgens level were monitored (Hunt et al., 1982) (figure 7). It is noticeable that the low levels of androgen correspond to high growth rate and inversely, high levels of androgens correspond to a zero growth rate. Unfortunately, the effects on growth of endogenous androgens cannot be directly explained by the effects observed with exogenous steroids, because induced blood levels have not been measured in these experiments. This raises the following question : **Are the steroids directly active on the somatotrop axis ?**

In mammals at the time of puberty, GH and Somatomedins increase (Luna et al., 1983 ; Krabbe et al., 1984 ; Minuto et al. 1985) simulta-

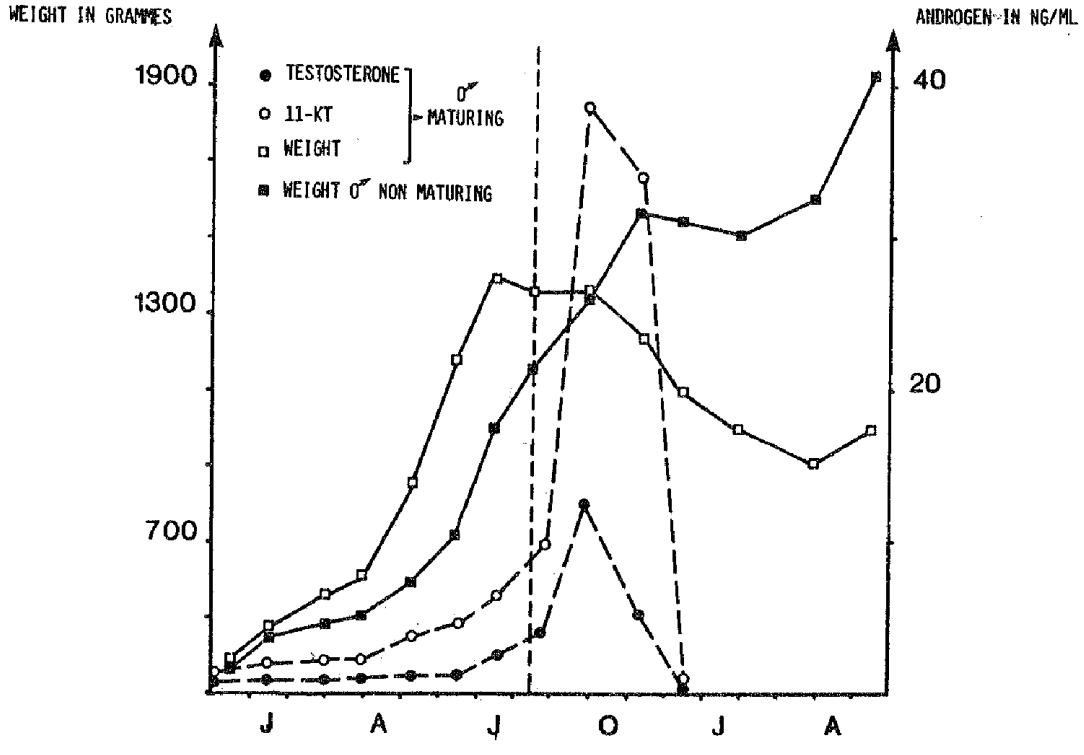

Fig 7 : Seasonal changes of mean weights and serum androgens in male Salmo salar (from Hunt et al., 1982)

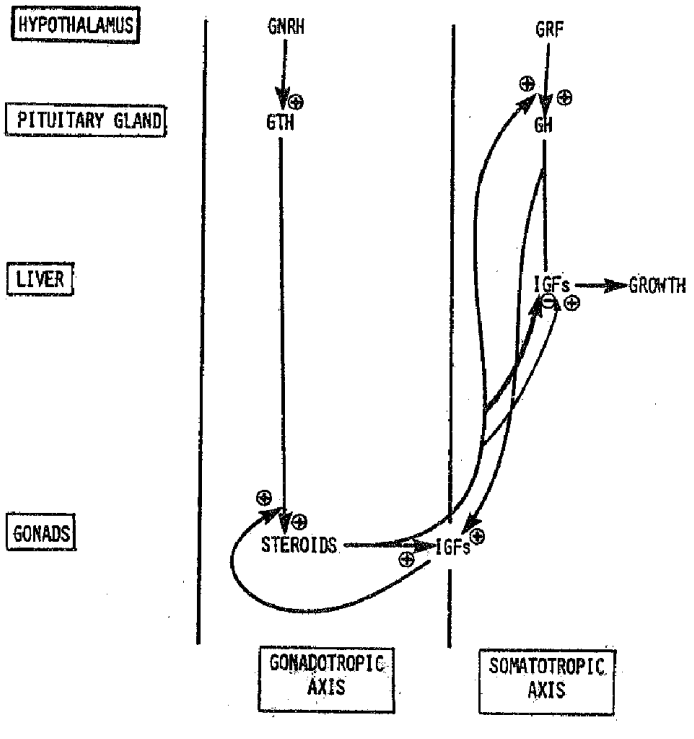

Fig 8 : Sheme of the endocrinology during the post-puberal growth

neously with blood androgens (Krabbe et al., 1984 ; Harris et al., 1985 ; Caufriez et al., 1986 a, b). On the other hand, injection of androgens increases the levels of circulating IGFs (Jasper, 1985 ; Caufriez et al., 1986 a) via stimulation of GH secretion (Jansson et al., 1983 ; Craft and Underwood, 1984 ; Link et al., 1986). This increase of GH secretion could be obtained by an increase of the somatotroph cell responsivness to the growth hormone releasing factor (Wehrenberg et al., 1985 ; Evans et al., 1985). Moreover, it is interesting to note that low levels of a steroid like estradiol can increase, the IGF secretion (Copeland et al., 1984 ; Caufriez and Copinschi, 1986), while at a high dose it blocks the stimulatary effect of the high level of GH on IGF secretion (Wiedemann and Schwartz, 1972 ; Janson et al., 1983). This leads to the paradoxal situation - a decrease of growth rate in spite of a high level of circulating GH (figure 8).

There is very little data in fish showing action of sexual hormones on growth. Estradiol can stimulate the activity of somatotroph cells (Olivereau and Olivereau, 1979). Morever, the injection of gonadotropin releasing hormone increases plasma GH levels in goldfish (Chang et al., 1982). So although these data are interesting, it is too early to propose a scheme in fish and further investigations are necessary to improve our knowledge of the endocrine effects of reproduction on growth.

c) Female size and time of spawning

In Kokane salmon and in Rainbow trout the largest females of a group of the same age spawn earlier in the season (Kato 1975, 1980).

In the turtle (Ho et al., 1985) and frog (Gobbeti et al., 1985), GH can enhance the secretion of blood vitellogenin. If this were the case in fish, a hypothesis could be put forward to explain the acceleration of vitellogenesis associated with a better growth rate.

CONCLUSION

It is clear that there is a strong relationship between growth and reproduction. Growth appears to be a modulator for puberty and fecundity,but does not seem to induce or directly control them.

The mechanisms involved in growth rate modulation, which are

still not clearly established in mammals, remain to be demonstrated in fish. On the other hand, the effects of steroids on the thyrotrop axis or directly on muscular growth make the problem more complex.

It now seems apparent that we must not try to correlate the criteria for growth with the plasma level of GH. An attempt to increase growth hormone levels either by an exogenous supply or by using transgenic animals is risky if we don't take into account the sexual cycle of the fish ; this could result in a zero or even negative effect on growth.

Résumé

Chez les poissons téléostéens, comme chez l'ensemble des vertébrés, la reproduction ne peut être dissociée des autres fonctions, et en particulier de la croissance qui interfère avec elle. Nous nous limiterons dans cette présentation aux données obtenues chez les salmonidés.

L'entrée en puberté apparait étroitement liée à la taille de l'animal. Tous les facteurs qui influencent directement la vitesse de croissance (nutrition, température...) modifient l'age de la puberté. L'effet de la salinité et de la smoltification est plus complexe et globalement tend à retarder son apparition. Le contrôle génétique de la puberté est bien établi mais se révèle secondaire par rapport à l'influence des facteurs externes.

Durant la gamétogénèse la croissance est vraisemblablement modulée par les stéroides sexuels. La fécondité et la date de ponte sont elles aussi corrélées à la vitesse de croissance. En se basant sur les résultats obtenus récemment chez les mammifères, un schéma hypothétique est proposé pour rendre compte de l'influence des hormones de l'axe somatotrope sur la fonction de reproduction des vertébrés.

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