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POISSONS
CROISSANCE
PHOTOPÉRIODE
GLANDE PINÉALE
MÉLATONINE

RESUMÉ. – La lumière représente un facteur écologique externe fort complexe incluant en fait divers aspects: le spectre de couleurs (qualité de la lumière), l'intensité (quantité) et la photopériode (périodicité). L'environnement aquatique est très particulier à ce sujet et les fluctuations de ces facteurs y sont extrêmement variables. En outre, la réceptivité à la lumière chez les Poissons varie considérablement d'une espèce à l'autre et, au sein de la même espèce, également au cours de la saison et en fonction du stade de développement. La revue proposée ici relate des données et discute sur l'aspect périodique de l'exposition à la lumière et les conséquences sur le développement et la croissance des Poissons. Non seulement la croissance, mais aussi tous les processus biochimiques, les fonctions physiologiques et les comportements sont rythmiques dans la nature et synchronisés par l'alternance jour/nuit. Les données de la littérature démontrent que le développement et la croissance des Poissons suivent des modalités saisonnières, liées aux fluctuations de la photophase. Généralement, les larves ont besoin d'un minimum d'intensité lumineuse pour pouvoir se développer et grandir, ceci en relation avec leur aptitude à détecter leurs proies et à s'alimenter correctement. Les longues photopériodes favorisent un développement harmonieux. Le rôle synergique longueur du jour/disponibilité en nourriture est l'un des points-clés. Chez les juvéniles et animaux plus âgés (Poissons marins et Salmonidés), la réaction à un allongement de la photophase est quasi-unanime, elle stimule la croissance. Seuls certains Poissons plats semblent moins réactifs, peut-être en relation avec leur comportement benthique. Le Saumon atlantique est tout particulièrement sensible, en eau douce et en eau de mer, et durant la smoltification. La question que nous posons est « Comment les effets de la photopériode sont-ils médiés » ? Les travaux menés en physiologie et endocrinologie suggèrent une influence de l'épiphyse. La glande pinéale chez les Poissons est directement photosensible. Chacune de ses cellules photoréceptrices de type cônes contient une horloge circadienne synchronisée par le rythme jour/nuit déclenchant la production de messages rythmiques. En fait, la pinéale ressemble à une rétine très simple sans réseau inter-neuronal organisé. Mais les photorécepteurs de l'épiphyse et de la rétine produisent le messager donneur de temps universel, la mélatonine. Celle-ci est synthétisée et utilisée « sur place » dans la rétine alors qu'elle est libérée dans la circulation par la pinéale. Notre revue synthétise également les informations disponibles sur le rôle de la mélatonine et de sa réceptivité chez les Poissons. Des données très récentes permettent d'imaginer une influence, soit directe via l'hypophyse, soit indirecte via l'hypothalamus, sur la synthèse et la libération d'hormone de croissance. La mélatonine peut aussi jouer un rôle sur le métabolisme thyroïdien et sur la prise alimentaire, deux aspects conditionnant la croissance. Les travaux futurs, combinant approches physiologiques « classiques » *in vitro* et *in vivo* et d'autres, pharmacologiques et moléculaires, permettront très probablement de mieux aborder ces questions du rôle de la photopériode sur la croissance. Tous ces travaux peuvent amener des applications fort prometteuses vers l'aquaculture.

FISH
GROWTH
PHOTOPÉRIODE
PINEAL GLAND
MELATONIN

ABSTRACT. – Light is a complex external and ecological factor whose components include color spectrum (quality), intensity (quantity) and photoperiod (periodicity). An aquatic environment has peculiar and extremely variable characteristics. Moreover, "receptivity" of fish to light changes profoundly from one species to another and, within the same species, from one developmental stage to another. The present review focuses on the periodic aspect of light supply and its consequences on fish growth. Not only growth, but virtually all biochemical processes, physiological functions and behaviors are rhythmic in nature and synchronized by the 24 h

light/dark (L:D) cycle. Available data indicate that fish growth follows a seasonal pattern which varies as a function of variations in daylength. Generally, larvae need a minimal threshold intensity to be able to develop normally and grow. This is probably related to the aptitude to localize, catch and ingest prey, and long daylength improves larval rearing quality. The synergistic effect of "food availability and daylength" appears to be determining at this stage. Older fish (marine and salmonid species), also react to photoperiod treatments and long daylength stimulates growth. The most studied species is the Atlantic salmon, which is very sensitive to changes in photoperiod, in fresh and seawater, and particularly during the parr-smolt transformation. Flatfish appear as a noticeable exception because growth was not affected by photoperiod in several cases in the species investigated. The question raises to know how are the effects of photoperiod mediated? Early physiological studies suggested a role for the pineal gland. The fish pineal organ is a light sensor. Each of its cone-type photoreceptor cells contains a circadian clock, synchronized by the 24 h light: dark cycle which, in turn, produces rhythmic messages. Actually, the pineal gland resembles a very simple retina with only very few interneurons. Pineal and retinal photoreceptors produce the "time-keeping molecule" melatonin. Retinal melatonin is used and metabolized *in situ*, whereas pineal melatonin has neurohormonal properties. The present paper reviews the information regarding the fish melatonin generating system and melatonin receptors. We also discuss recent evidence indicating the hormone might affect fish growth hormone secretion either directly (on the pituitary) or indirectly (hypothalamus). Melatonin may also influence thyroid hormone metabolism as well as food ingestion, two other factors that affect growth. Future studies combining "classical" physiological approaches (*in vitro* and *in vivo*) together with pharmacological and molecular approaches should provide insights into the mechanisms underlying the control of fish growth by photoperiod. This studies have great potential interest for aquaculture because they should provide indication on the best photoperiod conditions for optimizing fish "natural" growth all year long.

1. INTRODUCTION

From unicellular to vertebrates, environmental factors influence the activity of cells, organisms or populations. In fish, behavioral processes such as locomotor activity, skin pigmentation, thermoregulation, shoaling behavior, etc..., are under the influence of environmental factors. The same holds true for major physiological functions such as growth and reproduction.

Growth implies an increase in size or number of cells over time, with the important connotation of a positive energy balance (Mommsen 1998). Development and growth of teleost fish follows a pattern specific to each species. It differs from growth of birds and mammals in that it is a continuous process so that the older the fish the bigger (Boeuf *et al.* 1999). In fish the energy otherwise used to overcome the effects of gravity (reduced in an aquatic environment) and the energy cost of thermoregulation (required for endotherms) are available for growth. At hatching, fish are the smallest known vertebrates; therefore they will experience quite different metabolic scaling effects compared to other vertebrates. Another aspect contributing to the indeterminate growth pattern is the absence of calcified components with a definitive stop in growth layer increments (bone, otolith). The continuous growth of fish is mostly a consequence of cellular hyperplasia. Growth rates are

lower in adults for many reasons including the potential limitations of the intestinal system that scales differently than muscle to animal mass and diffusion rates in the white muscle itself (Mommsen & Moon 2001).

Growth is rather flexible because it depends on a number of factors. As ectotherms, fish are highly dependent on temperature, but many other factors are also known to play a major role on the capacity to develop and grow. These include salinity, pH, oxygen availability, and eventual presence of "natural toxicants" (Boeuf & Le Bail 1999), as well as food availability and developmental stage (Sumpter 1992). Finally another, but nonetheless important, factor controlling growth is light. The main natural source of light is the sun, but other secondary sources are also available originating from the moon, stars, and luminescent organisms. When talking about light, one must consider several aspects including quality (wavelength), quantity (intensity-irradiance) and duration (periodicity) (Boeuf & Le Bail 1999). This review focuses on the latter aspect, *i.e.*, in the effects of the alternating phases of light (L) and dark (D) during the 24 h cycle.

Most of the fundamental rhythms in nature (diurnal or seasonal) are related to the periodicity of light (Edmunds 1988). They results from the rotations of the earth on its axis and around the sun. Many animals, including fish, exhibit a 24-hour cy-

cle in their activities (diel rhythm) which may be a matter of simple photokinesis (Clarke 1965). Fish are more active either during day or at night. For example, light-to-dark transitions are very important to synchronizing locomotor activity rhythms in the Atlantic salmon *Salmo salar* (Richardson & McCleave 1974), and fish feed actively during the day but not at night (Thorpe *et al.* 1988). Hence daylength may indirectly modify growth by increasing food intake or muscle mass by exercise. Most often, daily rhythms are driven by endogenous biological clocks, synchronized by the 24 h L: D cycle, and which would free-run under constant conditions (with a period approximating 24 h). Similarly, circannual rhythms are endogenous rhythms which fluctuate on an annual basis. Organisms with circadian clocks are able to predict and anticipate daily changes, so that the right event will occur at the right time. How do fish integrate the photoperiod information? Where are the biological clocks located? Does the photoperiod system modulates animal growth and how? These questions are also addressed in the present review. More precisely, we will focus attention on the melatonin generating system and its targets, because this molecule is now considered as the "hormonal messenger of photoperiod" in all vertebrates so far investigated (Zachmann *et al.* 1992a).

2. PHOTOPERIOD AND GROWTH

2.1. Larvae

Many studies have been carried out on cultured marine fish larvae, supplying light either continuously or over very long periods, compared to the natural conditions (rabbitfish (Duray & Kohno 1988); halibut (Hallaråker *et al.* 1995a), sole (Fuchs 1978); sea bass (Barahona-Fernandes 1979, Ronzani Cerqueira *et al.* 1991), green back flounder (Hart *et al.* 1996), gilthead sea bream (Tandler & Helps 1985, Ounais-Guschemann 1989), turbot (Person-Le Ruyet *et al.* 1991). Solberg & Tilseth (1987) demonstrated that yolk absorption was independent of the light regime in the cod *Gadus morhua,* except for larvae reared in the dark. In the sea bream *Archosargus rhomboidalis* (Sparidae), high levels of prey promoted good larvae growth under natural lighting conditions, but at low levels of prey growth increased with longer photoperiod (Dowd & Houde 1980). A "daylength-prey abundance" association is usable for the optimization of production cycles. For example, it was possible to produce juvenile halibuts from larvae, using a 6-month delayed photoperiod and ensure year-round production of juveniles (Naess *et al.* 1996). Hence, the "synergistic effect of food availability and light" is the most important factor acting on larval

growth; it allows the optimal exploitation of the trophic level. However, a high growth rate may not be good for a normal development as suggested from studies in the sea bass (Ronzani Cerqueira *et al.* 1991).

2.2. Juveniles

A few studies have concluded to a lack of effect of photoperiod on flatfish growth. For example, juvenile yellow tail flounder *Pleuronectes ferrugineus* had similar growth and survival rates under 24L:0D, 18L:6D and 12L:12D conditions (Purchase *et al.* 2000). Also, growth rate of halibuts reared from 5 to 20 g was not affected by light regimes changing from 7 to 12 h L and from 12 to 18 h L (Hallaråker *et al.* 1995b). However, with halibuts of 30 g maintained for 5 months under different photoperiod conditions, a high specific growth and survival rate was observed under a 24L:0D cycle, whereas a 8L:16D cycle gave the poorest results; intermediate values were obtained under natural conditions (Simensen *et al.* 2000). Moreover, fish first maintained under short daylength exhibited an increased growth rate 21 days after being transferred to continuous light (Simensen *et al.* 2000). Turbots, reared for at least 3 months (at 10 and 16°C) under continuous light had slightly higher growth rates than those maintained under natural or constant 16L:8D conditions; however, no difference was seen after 6 –months (Imsland *et al.* 1995). In another series of experiments it was shown that feeding was not affected in turbots maintained for 60 days under six different photoperiods (constant 8L:16D, 16L:8D, 12L:12D, 24L:0D; increasing 12-16L and decreasing 12-8L) (Pichavant *et al.* 1998). However, Imsland *et al.* (1997) observed a better long-term growth (18 months) in turbots exposed to extended daylength during the first winter.

Positive effects of photoperiod on growth have been recorded in other species. A constant 16L:8D cycle enhanced growth in *Sebastes diploproa* compared to a 12L:12D cycle, and this can probably be related to a greater scope for growth due to their lower standard metabolic rate (Boehlert 1981). In the gilthead seabream and sea bass, long photoperiod delayed spawning and increased somatic growth (Silva-Garcia 1996, Kissil *et al.* 2001, Rodriguez *et al.* 2001). The differences appeared after a long exposure time in the seabream (45-145 days depending on the light regime) (Silva-Garcia 1996), and were maintained up to 11 months (Kissil *et al.* 2001). Daily feed consumption was affected by the onset of spawning, and the efficiency of feed utilization and energy retention was also positively correlated with the long photoperiod (Kissil *et al.* 2001). A similar situation had been described in the green sunfish, *Lepomis*

cyanellus maintained for 6 weeks at four photoperiods (constant 8L:16D, 16L:8D, increasing 8-16L and decreasing 16-8L). In this species, food intake is directly correlated to the amount of light to which the fish were exposed (Gross *et al.* 1965). Fish growth and food conversion efficiency were closely correlated and were generally highest in the increasing photoperiod, even when temperature was the same in spring and autumn.

In salmonids, for which there is not a true larval stage, Brännäs (1987) failed to demonstrate an influence of photoperiod during the yolk sac phase or on behavior at emergence in the Atlantic salmon. In the same species, Berg *et al.* (1992) obtained a good relationship between the duration of lighting and growth after first feeding: growth decreased on reduced daylength. This species is particularly receptive to extended daylength and grows very well, even under continuous light, eating continuously during the photophase. In an experiment lasting 192 days after the first feeding, where both temperature and photoperiod were changed, Thorpe *et al* (1989) found that in late summer the greater the growth opportunity (°C X daylength hours), the greater the proportion of young salmon maintaining good growth and within the upper mode of the population (see also below).

In rainbow trout *Oncorhynchus mykiss,* maintained under a natural photoperiodic cycle a reduced rate of decreased daylength favored growth and food conversion efficiency (Mäkinen & Ruohonen 1992). A longer light phase favors food intake and also possibly food conversion (Mason *et al.* 1992). Better growth and food conversion efficiency rate have been observed under continuous illumination during the first year (Maisse & Le Bail unpubl results). In Arctic charr, Mortensen & Damsgård (1993) found that a long photoperiod increased the compensatory growth observed after a previous "warm" (11 °C) temperature and short days pre-treatment. Hence, it appears that growth of non-migrating salmonid species is sensitive to increasing daylength under artificial conditions. However, these results do not take into account any of the other endogenous growth cycles which have been described in these species (Jobling 1987, Saether *et al.* 1996, Noël & Le Bail 1997), and which could also be influenced by light.

A considerable amount of literature is dedicated to the effects of photoperiod on Atlantic salmon juveniles. Not all of these studies can be referred here, but the effects of photoperiod are so clear for this species that they merit special attention. The major difficulty in extrapolating results is the existence of the major developmental transformation from parr to smolt (see reviews in Fontaine 1975, Hoar 1988, Boeuf 1993). Photoperiod exerts an important role in salmon smoltification (Hoar 1988, Boeuf 1993, Saunders *et al.* 1994, Solbakken *et al.* 1994, Sigholt *et al.* 1995), and growth cannot be

dissociated from smoltification. At the end of the freshwater residence phase and just before migration, fish are euryhaline, and they grow very fast. During the first year, before completion of parr-smolt transformation, light stimulates growth. Lundqvist (1980) showed that a longer photoperiod (20L: 4D opposed to natural light or 6L:18D stimulated Baltic salmon growth during autumn. However, the "size-structure" of the experimental population was not considered in this study. The Atlantic salmon has a specific developmental strategy with two modes, weight and size, appearing in the population during the first year, 7 to 9 months before the completion of smolting. Thorpe (1987) proposed that photoperiod synchronises an endogenous rhythm, genetically determined, and regulates the time of the "switch" of the differentiation is made into two growth modes. Decreasing daylength may cause the appearance of bimodality: transfers of fish from continuous light to natural photoperiod (range 12-15 hours) are followed by a segregation in growth rates into lower and upper modes fish (Skilbrei 1991, Skilbrei *et al.* 1997). Under continuous light, bimodality is low or absent and the individual decision to enter the upper mode with fast growth is strongly dependent on the fish size at the time of winter light stimulus. Seven weeks of short-day treatment reduced growth in comparison with the continuous light exposed salmon (Sigholt *et al.* 1998). It is essential for completion of smolting to expose fish to an increasing photoperiod after short-day conditions (Kristinsson *et al.* 1985, Gaignon & Quemener 1992, Björnsson *et al.* 1995). In some cases, one was able to dissociate a pure growth effect of light from those linked to smolting: long term (a few months) constant long daylength stimulates growth, but is increasing daylength necessary for parr-smolt transformation? (Saunders *et al* 1985, Duston & Saunders 1992).

Feeding activity is fundamental, as salmon do not eat at all or at least very little during night time (Thorpe *et al.* 1988), even if they can do during very short photoperiods. Maybe, they can be looking for food at the bottom of the tank (olfactory sense?) during the night (Jorgensen & Jobling 1992). Villarreal *et al.* (1988) suggested that the delays observed in growth, after daylength reduction, reflected a synchronizing effect of photoperiod on an endogenous rhythm of appetite and growth. At present, it seems that growth, linked to daylength, is related to food intake.

All these data lead to the possibility of producing 0+-age smolts, and at present, an important part of smolt production makes use of light manipulations. One can produce 7-8 month old smolts, with a good growth, and ability to adapt to seawater (Saunders & Duston 1992, Thrush *et al.* 1994, Duncan & Bromage 1998). In the Ifremer laboratory of Brest, 0+-age smolts of different sizes have been produced using three photoperiod regimes

(16L:8D; 12L:12D and 8L:16D) for 5 months (following three months at 12L:12D; *in* Boeuf & Le Bail, 1999). Fish were reared in indoor 1 m^2 Swedish type tanks in constant light (L:L) and temperature conditions at densities of 15 kg.m^{-2}. They were fed dry commercial pellet (Aqualim) daily by an automatic feeder. Growth appeared related to both temperature and lighting conditions.

After seawater transfer, Atlantic salmon growth may also be influenced by daylength. Presently, many farmers in Norway and Scotland use continuous lighting during the autumn or winter (October-April in the North hemisphere) to improve growth: growth in fish subjected to natural daylight is depressed during the autumn and winter, while, conversely, no such growth depression in winter is observed under a continuous light regime (Forsberg 1995). Several authors, using photoperiod treatments, have experimentally demonstrated a substantial improvement of postsmolt growth in sea water (Saunders & Harmon 1988, Kråkenes *et al.* 1991, Hansen *et al.* 1992). However, in these experiments, such treatments not only stimulated growth, but also triggered earlier sexual maturation. It is known that somatic growth is accelerated during the first steps of the gametogenesis, an effect mediated by steroids (Le Bail 1988). Hence, it is possible that under these conditions, a great part of the light-promoted stimulation of growth is related to reproduction. However, in a recent study (Oppedal *et al.* 1997), it has been demonstrated that, if light intensity was sufficient, abrupt changes from natural short photoperiod to continuous additional light (January-June) promoted growth without triggering maturation.

Other studies have been carried out in Pacific salmon species, mainly coho *Oncorhynchus kisutch* and chinook *O. tshawytscha*. In 1978, Clarke *et al.* showed that the sensitivity of young fry to photoperiod varied seasonally. In 1986, Clarke & Shelbourn concluded that bimodal growth in juvenile salmon was a function of a photoperiod phase at the time of first feeding and it was possible to produce underyearling coho smolts. Extended daylength also stimulates growth for Pacific species (Thorarensen & Clarke 1989), as it does for Atlantic salmon. In fact, it is not the accumulation of light exposure that initiates smolting, but rather the time during the day when light is experienced. Moreover, responsiveness to inductive photoperiods depends on the initial photoperiod treatment (Thorarensen & Clarke 1989). Thorarensen *et al.* (1989) exposed young coho salmon to different levels of night illumination ranging from 0.0001 to 0.05 lux, after a first period at short-day (10L: 14D, during 12 weeks) and a second period under inductive lighting (9L: 9D: 1L: 5D or 24L: 0D): they observed slower growth rates for the fish exposed to nocturnal illumination. It seems that a period of total darkness is needed to obtain maximum growth.

In conclusion, increasing daylength exerts a greater influence on salmon smoltification than constant daylength. It seems important for freshwater fish to experience a few weeks of short-day conditions prior to transfer in increasing daylength conditions. Even if in nature this smolting phenomenon cannot be dissociated from somatic growth, the preceding data show that a long daylength (changing or constant) stimulates growth specifically. The observed great dependence of Atlantic salmon on photoperiod might be due to the strains used and high latitude conditions. It would prove interesting to compare the photoperiod responsiveness of northern and Southern strain.

3. THE ENDOLYMPH/OTOLITH SYSTEM

It is of relevant interest to discuss the possible role of the inner ear of teleost because fish otolith exhibits daily and annual rhythmic depositions in relation to photoperiod and light sensitivity. Furthermore, otolith increments have been used for a long time as indicators of life history, aging and somatic growth. They are composed of calcium carbonate crystals in the aragonite form, enmeshed in an inorganic matrix composed largely of a keratin-like protein (Wright *et al.* 1992). Accretion occurs through the alternate deposition of a mineral/matrix-rich layer with a mineral deficient layer. This is done on a daily basis in many species, so that a recognizable daily increment is produced (Pannella 1980).

A few scientists have questioned the role of photoperiod on otolith growth. In Atlantic salmon, deposition is regulated by an endogenous circadian rhythm synchronized to the 24 h L:D cycles (Wright *et al.* 1991). Otolith calcification declines at night and resumes lower levels at dawn: a diel fluctuation in net calcium accretion, linked to plasma calcium concentration, appears (Wright *et al.* 1992). A similar phenomenon is recorded in rainbow trout (Mugiya 1987), Arctic charr (Adams *et al.* 1992) and pike *Esox lucius* (Wang & Eckmann 1992). In embryonic and larval rainbow trout, photoperiod is a potent synchronizer of the daily rhythm of deposition, whatever the photoperiod conditions (6L:6D; 12L:12D; 24L:24D; 24L:0D and 0L:24D; Mugiya 1987). It is not so easy to correlate somatic growth and otolith growth, probably because numerous factors are involved in the control of each of them. Actually, incremental increases in otolith width appear to be linked to photoperiod, whereas increases in the number of rings appear to be related to feeding activity (Neilson & Geen 1982). Other external fac-

tors, such as temperature, may also modify the ratio between somatic and otolith growth, as shown in young turbot (Kossmann, Leroux & Boeuf unpublished observations).

Very little information is available concerning the physiology of the endolymph-otolith complex. The saccule has specialized small and big cells which display all the characteristics of gill ionocytes (Mayer-Gostan et al. 1997). The presence of a pH gradient in the inner ear of teleost is a unique common pattern among vertebrates. This is probably related to bio-calcification of otoliths. pH variations could be the major factor affecting the rate of the daily calcium deposition (Payan et al. 1997). The lack of spatial uniformity in both the otolith and the saccular endolymph must be taken into account when studying otolith and fish growth (Payan et al. 1999). It is not known whether the fine control of photoperiod on otolith growth involves a nervous and/or an endocrine signal. Interestingly, somatic and scale growths were totally inhibited in hypophysectomized goldfish Carassius auratus while otolith growth was only slightly reduced (Mugiya 1990); injections of pituitary extracts (GH) restored the normal conditions. On the other hand, starvation resulted in both somatic and otolith growth depression in rainbow trout (Mugiya & Oka 1991).

4. HORMONAL CONTROL OF GROWTH

4.1. Somatotropin

Somatotropin (or growth hormone) originates from the anterior pituitary gland and plays a major role in fish growth and adaptation (Le Bail et al. 1993, Sakamoto et al. 1993). As early as 1976, Komourdjian et al. suggested that somatotropin could play a role as a part of a "light-pituitary axis" in the growth of Atlantic salmon during smoltification. In fact, during this process, plasma GH levels increase "naturally" after the spring equinox, when photoperiod rapidly increases (Boeuf et al. 1989, Prunet et al. 1989). Generally, increased daylength accelerated the parr-smolt transformation and associated growth, and increased blood GH levels (Björnsson et al. 1989, 1995, Stefansson et al. 1991, McCormick et al. 1995). Exposure to continuous light in autumn and winter causes a "free-running" of an endogenous rhythm governing smolting and a subsequent phase-delay of the smoltification-related increase in circulating GH levels (Björnsson et al. 1995, 1998, Björnsson 1997). Similar results of somatotropin increase during smoltification completion have been obtained for masu salmon Oncorhynchus masou (Okumoto et al. 1989). However, outside of

the smolting completion period, increasing light does not necessarily increase GH levels, even if somatic growth is increased, as shown in three Pacific salmon species (Clarke et al. 1989). It is interesting to note that in the seabream, the seasonal increase of plasma growth hormone seems more related to daylength than temperature (Perez-Sanchez et al. 1994).

In mammals, circulating somatotropin is higher at night than during the day (Harvey & Daughaday 1995). In fish, the daily rhythms in GH content are related to feeding activity (Reddy & Leatherland 1994, Holloway et al. 1994) as well as to the L:D cycles (Bates et al. 1989, Boujard & Leatherland 1992). In a study of cannulated rainbow trout, Gomez et al. (1996) noted peaks in GH values, but they were irregular and asynchronous in individual fish; there was no clear-cut rhythm, but a trend to higher values at night. However, none of these studies provide a link between the daily rhythm and somatic growth capabilities.

It should also be mentioned that generally plasma GH levels were inversely correlated to growth performance in fish (Le Bail et al. 1993). GH receptivity studies should be useful to better understand how daylength may influence growth. Adelman (1977) did not observe growth differences between carp Cyprinus carpio reared at 9L: 15D and 16L:8D, after treatment with mammalian GH. IGFs are probably very important in the mediation of light influences on growth. Studies of IGFs and insulin have only been possible in fish for the last few years and further experiments will be needed to evaluate a possible direct action of GH and the role of IGFs in these pathways. Recently, Elies et al. (1996) cloned and sequenced an IGF1 receptor in two teleost species, turbot and trout. Insulin and IGF1 receptors have been cloned and sequenced and mRNA expression studied in the turbot (Elies et al. 1999) and GH receptor has been molecularly characterized (Calduch-Giner et al. 2000).

4.2. Thyroid hormones (TH)

The thyroid gland of fish produces high amounts of thyroxine (T_4) which is then transformed into tri-iodothyronine (T_3) in peripheral tissues. The same receptor binds the T_3 and T_4 molecules, but with much higher affinity for the former than for the latter (Eales 1985). T_3 and T_4 levels vary on a seasonal basis in fish sampled in their natural habitat (Osborn & Simpson 1978, Eales & Fletcher 1982); two optima were reached in winter and in summer.

Daily variations in T_4, and less pronounced or even undetectable variations in T_3 are usually described in laboratory fish (Cook & Eales 1987, Gomez et al. 1997, Noeske & Spieler 1983). In

rainbow trout, the T_4 rhythm resulted from an interaction between feeding and photoperiod regimes (Boujard & Leatherland 1992). It is noteworthy than in trout and other salmonids, growth rate is significantly correlated to the daily average T_3 value although a marked diurnal rhythm is observed only with T_4 (Eales & Shostak 1985, Boeuf & Gaignon 1989, McCormick & Saunders 1990, Gomez et al. 1997). Hence, T_3 levels appear to provide a good estimation of growth responsiveness to light. However, it cannot explain all of the effects of light on fish growth. Indeed, Okumoto et al. (1989) found that plasma TH were not affected by changing daylength in masu salmon, although growth was stimulated. In the killifish, *Fundulus heteroclitus* Brown & Stetson (1985) showed that long days (14L:10D) increased, and short days (8L:16D) diminished, the negative feedback sensitivity of the hypothalamus-pituitary axis to TH. They proposed that such a photoperiodically-induced change could aid in the year-round maintenance of thyroxine levels necessary for seasonal adaptation and survival.

The roles of TH during parr-smolt transformation have been reviewed by Boeuf (1993). In the Atlantic salmon, increasing daylength stimulated growth and plasma thyroxin levels, without affecting T_3 (Mc Cormick et al. 1987). Under continuous light, T_4 levels remained low, but only true smolts grew "normally" after transfer to seawater. It is hypothesized that under normal photoperiod, the high T_4 levels could act as a growth stimulator at the end of the fresh water stage, in spite of the fact that T_4 has lower affinity than T_3 for the nuclear receptor. However, it should also be noted that T_4 plays many other roles during this period. For example, Iwata et al. (1989) discovered that coho and chum salmon *Oncorhynchus keta*, treated with thyroxine changed their phototaxis. Finally, the changes in visual pigments composition observed in the retina during smoltification might reflect modifications in the thyroid function. Indeed, the visual response of the retina to TH is altered after treatment with TH blockers (Alexander et al. 1998).

A few studies have noted a relationship between growth, TH levels and the phases of the moon (Grau et al. 1981, Farbridge & Leatherland 1987a b, Nishioka et al. 1989, Hopkins 1992). However, the effects of the moon would possibly be mediated by the lunar attraction rather than by the direct incident light (Noël & Le Bail 1997).

4.3. Other hormones

Other hormones such as insulin and steroids also have an effect on fish growth; however, information lacks in terms of their relation to the influences of light. Regarding sex steroids, the available

information is only related to reproduction and gonadal development. However, puberty is strongly dependent on photoperiod during this phase: the puberty dependent-androgen secretion increase has an influence on somatic growth (Le Bail et al. 1988, Le Gac et al. 1993). Somatostatin (SRIF) is also known for strongly inhibiting GH secretion in all vertebrates, including fish. McCormick et al. (1995) found higher levels of plasma somatostatin-25 in salmon reared under a 9L:15D cycle, but no variation after exposure to longer daylength. Plasma levels of both somatostatins 25 and 14 are higher in stunting coho than in smolts (Sheridan et al. 1998). One study, published in 1996 by Zhu & Thomas, demonstrated an influence of different backgrounds and altered illumination on red drum *Sciaenops ocellatus* plasma and pituitary somatolactin (SL, which is a member of the prolactin/GH family of proteins): they found that both plasma and pituitary SL levels were higher in fish exposed for one week to black background and that circulating SL was maximal one day after transfer to a black background tank without illumination. SL may be involved in the adaptation to colored surroundings. However, at present, little is known about a possible involvement of SL in growth regulation.

5. THE MELATONIN GENERATING SYSTEM AND MELATONIN RECEPTORS IN FISH

To synchronize rhythmic functions and behaviors to the daily and annual cycles, an organism needs photoreceptive organs which will transduce the photoperiod information and produce output messages to convey this information to target centers. Fish possess two such photoreceptive organs, the retina of the lateral eyes and the pineal gland. Melatonin is one of the different messages they elaborate in response to the alternation of light and dark (Falcón 1999). As reviewed below, melatonin is considered a "time-keeping" molecule. We will focus attention on the pineal gland because retinal melatonin is unlikely to be involved in the synchronization of rhythmic events outside the retina. Indeed, retinal melatonin is produced, used and metabolized *in situ* where it has autocrine or paracrine effects: it modulates the sensitivity to light, the release of neurotransmitters; also it coordinates retino-motor movements (of cones, rods and retinal pigment epithelium), and outer segment disk shedding (Wiechmann & Smith 2001). Conversely pineal melatonin is released into the blood and cerebro-spinal fluid, and acts through specific receptors on target sites. It is not unreasonable to believe that many of the effects of photoperiod on

physiological and behavioral processes, including growth, are mediated through melatonin.

5.1. The fish pineal gland resembles a simplified retina

The pineal is an evagination from the roof of the diencephalon located just below the skull and connected to the diencephalon by the pineal stalk (Collin 1971, McNulty 1984). In most cases, a lumen filled with cerebrospinal fluid is opened to the 3rd ventricle (Omura & Oguri 1969, McNulty 1984, Falcón et al. 1992). Three main cell types make up the pineal parenchyma: photoreceptor cells, neurons and glial (interstitial) cells. Glial cells occupy the full height of the pineal parenchyma and isolate the other cell types from the blood vessels surrounding the organ. The pineal photoreceptor cells resemble to the retinal cones of vertebrates. At one end of the cell, the photoreceptive pole (outer segment) protrudes in the pineal lumen. At the other end, one or several pedicles establish synaptic contacts with dendrites of the 2nd order neurons (Ekström & Meissl 1997, Falcón 1999). This organization much resembles the organization of the retina, however with a much lesser degree of complexity. For example, although few inter-neurons have been described, no rod photoreceptors, bipolar, amacrine and horizontal cells per se are seen in the pineal gland.

The 2nd order neurons send their axons to the brain via the pineal tract which runs dorsally to the pineal stalk. It is noteworthy that the central projections from the pineal organ and retina of fish partly overlap (e.g., pretectum, dorsal thalamus and preoptic area) (Ekström 1984, Ekström & Meissl 1997).

5.2. The fish pineal gland elaborates rhythmic messages regulated by light

The fish pineal gland elaborates at least two important messages, in a rhythmic manner, a nervous and a neurohormonal message.

5.2.1. The nervous message, an excitatory neurotransmitter

In response to light, a pineal photoreceptor behaves like a retinal photoreceptor, and the mechanisms of phototransduction are similar in both cell types, actually the two cell types are anatomically and functionally analogous (refs in Falcón 1999). The pineal photoreceptor is depolarized in the dark and hyperpolarized during day (Meissl & Ekström 1988a b, Ekström & Meissl 1997). A major difference between the retinal and pineal photoreceptor is that under prolonged illumination the latter maintains an intensity related membrane potential so that it acts as an indicator of gradual light intensity changes (Ekström & Meissl 1997). It cannot discriminate between rapid light changes as the retinal photoreceptor does. This is consistent with the idea that the pineal gland functions as a luminance detector (Meissl & Dodt 1981). Information is transmitted to the second order neurons via an excitatory neurotransmitter, the release of which is inhibited upon photoreceptor hyperpolarization (Ekström & Meissl 1997). As a result, the spike discharges by the axons of the pineal tract are inhibited by light and increased in the dark. Inhibition is directly related to the intensity of the stimulus. The organ can integrate variations in intensity up to a 9 log units range in the pike (Falcón 1999). It is noteworthy that, when studied in parallel, the pineal and the retina of the same species exhibit similar spectral sensitivity curves (Falcón & Meissl 1981). The two organ express similar but different photopigment molecules, most probably as a result of gene duplication (Mano et al. 1999). In the pineal gland, spectral sensitivity curves may be recorded at the level of the photoreceptor cells or second order neurons; they are identical in both cases. The responses are usually sensitive in the green range or less often in the green and red range of wavelengths (Meissl & Dodt 1981, Ekström & Meissl 1997, Falcón 1999). In pike, dark adaptation curves show a shift of sensitivity indicating there is a photopic and a scotopic range of sensitivity (Falcón & Meissl 1981). This provides the animal with a greater adaptive advantage compare to those with either one of the sensitivity types.

5.2.2. The neurohormonal message, melatonin

Melatonin is synthesized from tryptophane which is taken up from the circulation. Tryptophane is converted to 5-hydroxytryptophane, by means of the tryptophane hydroxylase (TPOH), and 5-hydroxytryptophane is decarboxylated by the aromatic amino-acid decarboxylase to produce serotonin. Melatonin is synthesized from serotonin by the action of two enzymes: the first one, the arylalkylamine N-acetyltransferase (AANAT), converts serotonin to N-acetylserotonin; the second one, the hydroxyindole-O-methyltransferase (HIOMT), methylates N-acetylserotonin to produce melatonin (Klein et al. 1981, 1997). A combination of methods (histochemistry and immunocytochemistry, radio-autography, etc.) allowed to demonstrate that this pathway is active in the photoreceptor cells (refs in Falcón 1999). Melatonin may be either released or deacetylated in situ to produce 5-methoxytryptamine and 5-methoxytryptophol (Falcón et al. 1985, Yañez & Meissl 1996). Because of its highly lipophylic character, the molecule crosses easily the cell membrane. Other serotonin derivatives,

such as 5-methotrytryptophol, are produced from serotonin by the photoreceptor cells. However, unlike melatonin, their physiological role has yet to be assessed.

The production and release of melatonin by the pineal gland is rhythmic and synchronized to the 24 h L:D cycle. In fish as in all vertebrates classes so far investigated, production is higher during night-time than during daytime (Bolliet *et al.* 1995, 1996a, Falcón *et al.* 1987, 1989, Porter *et al.* 2001). AANAT is the key enzyme which expression and activity are regulated by the L:D cycle. AANAT activity increases after lights off and decreases late at night and early in the morning, as melatonin secretion does (Falcón *et al.* 1987, 1989, Morton & Forbes, 1988, Zachmann *et al.* 1992b). The increase in AANAT activity results, in pike and zebrafish *Danio rerio*, from an increase in AANAT gene expression which starts in the afternoon and decreases after midnight (Bégay *et al.* 1998, Coon *et al.* 1999, Klein *et al.* 1997). The decrease in AANAT activity results from both a decrease in AANAT expression and the light-dependent activation of enzyme proteolysis, as shown in seabream and pike (Falcón *et al.* 2001). In trout, AANAT gene expression is constitutive; variations in AANAT activity lie only upon AANAT protein proteolysis which is high during day and low at night (Bégay *et al.* 1998, Falcón *et al.* 2001). Unexpected illumination at night decreases AANAT activity as well as melatonin release, *in vitro* or *in vivo* (Falcón *et al.* 1989, Max & Menaker 1992, Bolliet *et al.* 1995). In the trout, the spectral sensitivity curves indicate a rhodopsin-like sensitivity (Max & Menaker 1992), as is the case for the release of the excitatory neurotransmitter in this species (Ekström & Meissl 1997).

Like the nervous message, the melatonin message also provides information on daylength, and this is achieved through its release in the blood (and may be in the cerebrospinal fluid). Variations in blood melatonin content are higher during night than during day *i.e.*, they mirror the variations in pineal melatonin production (Gern *et al.* 1978a, Falcón *et al.* 1987, Kezuka *et al.* 1988 1992, Zachmann *et al.* 1992b c, Iigo & Aida 1995, Randall *et al.* 1995, Pavlidis *et al.* 1999, Rebollar *et al.* 1999). As a consequence of the seasonal changes in daylength, the duration and amplitude of the plasma melatonin rhythm varies along with seasons in temperate regions (Kezuka *et al.* 1988, Randall *et al.* 1995), thus providing an accurate information on calendar time. Usually, the melatonin signal is of short duration and high amplitude in summer, and of long duration and short amplitude in winter (Kezuka *et al.* 1988). It has been suggested that duration is controlled by photoperiod, whereas amplitude is controlled by temperature (Garcia-Allegue *et al.* 2001, Samejima *et al.* 2000).

Results from *in vitro* studies support these conclusions.

Melatonin is also produced by the retina (see introduction). However, retinal melatonin does not contribute to the circulating levels for the following reasons: (1) only the pineal and plasma melatonin rhythms are in phase (Falcón & Collin 1991, Falcón *et al.* 1987, Zachmann *et al.* 1992b), and in many species (sea bass, pike, brook trout and rainbow trout) ocular melatonin levels are higher during day than during night, *i.e.*, in a 180° anti-phase with the blood rhythm (Falcón & Collin 1991, Zachmann *et al.* 1992b, Zaunreiter *et al.* 1998a b, Garcia-Allegue *et al.* 2001); (2) cultured sea bream, pike and white sucker retinas do not release melatonin into the culture medium (Molina-Borja *et al.* 1996, and unpublished observations); (3) pinealectomy, but not eyectomy, suppresses plasma melatonin in the goldfish and salmon (Kezuka *et al.* 1992, Iigo *et al.* 1997, Mayer 2000). The trout is the only fish species known where pinealectomy diminishes the nocturnal plasma melatonin surge without completely suppressing the L:D variations (Gern *et al.* 1978b).

5.3. The melatonin rhythm is driven by circadian clocks located within the pineal photoreceptors

Experiments conducted *in vivo* and *in vitro* provided indication, in most but not all (see below) of the species investigated, that the rhythm in melatonin secretion was not a simple passive response to the alternation of light and darkness. For example, whether light at night causes a rapid decline in AANAT activity and melatonin secretion, night during day does not necessarily induces an increase in pike (Falcón *et al.* 1987). Under experimentally manipulated photoperiods the melatonin rhythm follows the imposed L:D cycles, but this is achieved progressively (Bolliet *et al.* 1995, Molina-Borja *et al.* 1996). Moreover, the melatonin rhythms have been shown to persist in the pineal gland and blood of animals maintained under constant darkness (D:D), whereas a low-amplitude rhythm may be detected under L:L (Falcón *et al.* 1987, 1989, Bolliet *et al.* 1995, Porter *et al.* 2000). In culture, entire organs, pieces of glands, or dissociated cells maintain a rhythmic release of melatonin under D:D (Falcón *et al.* 1989, Ligo *et al.* 1991, Bolliet *et al.* 1994, 1996a b, Cahill *et al.* 1996, Okimoto & Stetson 1999a b). Altogether this indicates that multiple circadian oscillators drive the melatonin rhythm. Bolliet *et al.* 1996b provided definitive proof that these oscillators are located within the photoreceptor cells. The authors were able to monitor melatonin secretion from individual photoreceptors (using the reverse hemolytic plaque assay) or cultures made exclusively of

photoreceptors (using radioimunoassay); under L:D or D:D, both the amount of melatonin released and the number of melatonin producing photoreceptors, were higher during night (or subjective night) than during day (or subjective day).

Taken together, these findings indicate that single photoreceptor cells contain a circadian clock, a photoreceptive capacity and the ability to secrete melatonin. The L:D cycle synchronizes the clocks which in turn drive the melatonin rhythm. This is achieved through control of AANAT gene expression which is maintained rhythmic under L:L or D:D (Bégay et al. 1998, Coon et al. 1999).

Interestingly enough is the observation that the pineal gland of salmonids exhibits no rhythm under constant conditions (Gern & Greenhouse 1988, Iigo et al. 1997, Thibault et al. 1993). Under these conditions, AANAT activity and melatonin levels remain high in the dark and low in the light, independent on the duration of the light and dark phases (above refs). There is, to date, no explanation for these species-dependent variations.

5.4. Temperature modulates melatonin secretion by the fish pineal gland

In cultured pineal glands of pike, temperature cycles superimposed to photoperiod cycles enhance the amplitude of the rhythm when the cryophase coincides with the scotophase, and reduces the amplitude when the cryophase coincides with the photophase (Falcón et al. 1994). The opposite holds true in the white sucker (Zachmann et al. 1991, 1992c). Temperature cycles are able to synchronize the clocks that drive the rhythm in melatonin secretion. In D:D, melatonin peaks with the cold phase in the white sucker, and with the warm phase in the pike. However, temperature cycles are unable to entrain the circadian clocks, and temperature pulses cannot shift the phase of the clocks as light does (Falcón et al. 1994). Moreover, temperature does not affect the period of the free running rhythm under D:D in the sailfin molly and pike (temperature-compensation), but the oscillations are no more seen below a threshold level (Bolliet et al. 1994, Okimoto & Stetson 1999a b), consistent with the observation that blood melatonin rhythm is of higher amplitude at 12 °C than at 4 °C in juvenile salmon (Porter et al. 2001).

In brief, photo- and thermo-period interact in fish to determine the amplitude and duration of the melatonin rhythm. The effects of temperature cycles are complex, and vary from a species to another. Differences result probably from variations in the metabolisms proper to each species. In cultured pineal glands, cyclic AMP accumulation AANAT activity peak at 12-15 °C in trout, and 18-25 °C in the pike (Thibault et al. 1993). AANAT activity from recombinant proteins as well as from gland homogenates exhibit the same maximum, indicating that this is a property of the AANAT protein. Under a 12 °C/20 °C temperature cycle melatonin would peak with cold temperature in the trout, and warm temperature in the pike.

5.5. Melatonin receptors in fish

Melatonin acts through specific membrane bound receptors which belong to the seven transmembrane domain G-protein coupled receptors (Reppert et al. 1995). The receptors are usually coupled negatively to the cAMP pathway, but effects on other second messengers have also been reported (Vanecek 1998). Three receptor subtypes have been identified to date in vertebrates: MT1 (Mel1a), MT2 (Mel1b) and Mel1c (Dubocovich et al. 2000, Reppert et al. 1995, Shiu & Pang 1998). In fish, the full length cloning of a melatonin receptor has been obtained only in pike (Gaildrat et al. 2001); partial cloning has been achieved in zebra fish (the three subtypes), trout (Mel1a, Mel1b), and pike (Mel1a) (Gaildrat & Falcón 2000, Mazurais et al. 1999, Reppert et al. 1995).

Distribution of melatonin receptors has been investigated using in situ hybridization in trout (Mazurais et al. 1999), RT-PCR in pike (Gaildrat & Falcón 1999, Gaildrat et al. 2001), and binding of 2-[^{125}I]-iodomelatonin (^{125}I-Mel) on tissue sections and membrane preparations from goldfish, pike, skate, seabream, salmon and trout (Martinoli et al. 1991, Ekström & Vanecek 1992, Davis et al. 1994, Iigo et al. 1994, Pang et al. 1994a, Falcón et al. 1996, Gaildrat et al. 1998, Mazurais et al. 1999). In the brain, the receptors exhibit a widespread distribution which differs, in terms of intensity, between the Mel1a and Mel1b receptors. The highest expression is consistently found in the optic tectum of all fish studied including deep sea gadiform fish (above refs and Priede et al., 2000). Other areas include the olfactive bulbs, telencephalon, preoptic area, thalamus, pretectal area, and cerebellum. Actually, brain melatonin receptors are seen in areas involved in sensory (visual, olfactive, auditive) integration. Melatonin receptors are also expressed in the retina (Gaildrat & Falcón 1999, 2000, Gaildrat et al. 2001, Iigo et al. 1997). This is consistent with the observation that retinal melatonin has auto/paracrine effects (see above). Studies in the Xenopus have indicated the receptors are expressed in photoreceptor and ganglion cells, as well as some unidentified cells of the inner nuclear layer (Wiechmann & Smith 2001). In peripheral tissues, melatonin receptors have been evidenced in fish heart (Pang et al. 1994b).

Of great interest is the observation that melatonin receptors are also found in the pituitary gland of pike (Mel1b>Mel1a) and trout (Gaildrat & Falcón 1999, 2000). The number of sites is less

than in the brain, but the affinity for melatonin is the same. As evidenced by *in vitro* autoradiography on tissue sections, the binding of ^{125}I-Mel is located in the antero-ventral part of the organ, an area known to contain gonadotropines (GtHs), prolactin (PRL) and growth hormone (GH) producing cells. Furthermore, melatonin modulates cAMP levels by cultured pike and trout pituitary organs indicating these receptors are functional (above refs).

The binding of ^{125}I-Mel to brain sections or membrane preparations exhibits daily changes in pike, seabream and goldfish (Gaildrat *et al.* 1999, Falcón *et al.* 1996, Iigo *et al.* 1994), but not in salmonids (Ekström & Vanacek 1992, Pang *et al.* 1994a). However, further studies are necessary in salmonids because (1) there were only two sampling times a day, and (2) experiments on whole brain homogenates may obscure variations in restricted areas. It is noteworthy that in the pike, the rhythm in the number of binding sites (high during daytime and low during night-time) is 12 h out of phase when compared with the rhythm in plasma melatonin content (Gaildrat *et al.* 1999). This might reflect a down-regulation of melatonin receptors at night, induced by melatonin itself, as suggested from preliminary unpublished experiments. Interestingly, the variations reported above are maintained in pike under constant conditions. The chronograms obtained under L:L or D:D displayed a slight phase advance when compared to the chronograms obtained under L:D. Altogether, these results support the idea that in fish, photoperiod mediates part of its effects through both the rhythmic production of melatonin by the pineal and the rhythmic expression of the melatonin binding sites in the brain.

6. HOW DOES THE PINEAL GLAND MEDIATE THE EFFECTS OF PHOTOPERIOD ON FISH GROWTH?

As the transducer of the photoperiod information in the organisms, there is indication that the pineal gland, through its output melatonin, might mediate the effects of photoperiod on fish growth. However, investigations on this matter are more than scarce, probably because physiological studies dealing with the effects of pinealectomy on physiological functions often ended with contradictory results. This is reviewed and discussed in the excellent review of Ekström & Meissl (1997). An early physiological study in the goldfish had shown photoperiod-dependent effects of pinealectomy on growth (De Vlaming 1980). Removal of the pineal gland resulted in a reduced growth rate under short, but not long, photoperiod; and melatonin administration reversed the effect under short photoperiod

only. A similar experiment was conducted 20 years later in the Atlantic salmon parr (Mayer 2000). In this case, pinealectomy resulted in lower specific growth rates during the period of lengthening photoperiod until summer solstice; but thereafter, *i.e.*, during the decreasing photoperiod, pinealectomized fish exhibited higher growth rates. This indicates that the mechanisms by which the pineal gland may modulate growth are complex. Such a complexity is emphasized by the observation that pinealectomy also affected, in a photo-dependent manner, body lipid content in the golden shiner *Notemigonus crysoleucas* and longnose killifish *Fundulus similis* (De Vlaming 1975, De Vlaming *et al.* 1974). However, melatonin injections exerted almost identical effects than pinealectomy, when one would expect opposite effects.

Although the effects of the pineal gland and melatonin are not yet elucidated, there is evidence suggesting that it participates in the control of fish growth. There are several direct and indirect ways through which melatonin could act. These include a control at the level of the hypothalamus-pituitary axis and/or of peripheral tissues involved in energy supply and food intake. Also, melatonin may be acting either on growth itself or on food intake and food conversion.

6.1. Melatonin and food intake

A recent study by Pinillos *et al.* (2001) has shown that melatonin administration inhibited food intake in the goldfish. Interestingly, the effects were observed after peritoneal injection, not after intra-cerebral injection, precluding a centrally-mediated action. Melatonin effects were antagonized by luzindole, a specific melatonin receptor antagonist in homeotherms. This is consistent with the idea that melatonin and melatonin receptors are found in the gastro-intestinal tract of birds and mammals (refs *in* Pinillos *et al.* 2001). However, although melatonin was found in the gastro-intestinal tissues of sturgeon, trout and carp (Bubenik & Pang 1997), melatonin binding sites could not be clearly identified in the gut of seabream and pike (Falcón *et al.* 1996 & unpubl results) and the MT1 and MT2 melatonin receptor subtypes could not be evidenced in the pike intestine using a PCR approach (Gaildrat & Falcón 1999, 2000, Gaildrat *et al.* 2001). The possibility remains that a melatonin metabolite was acting instead of melatonin. Indeed, in the goldfish serotonin (a melatonin precursor) had similar anorectic effects as melatonin (Pinillos *et al.* 2001) which can be de-acetylated in the liver and pineal to give, among other products, 5-methoxytryptamine a compound closely related to serotonin (Falcón *et al.* 1985, Yañez & Meissl 1996).

It is well known that the fish pineal organ mediates locomotor activity rhythms (refs in Zachmann *et al.* 1992a, Ekström & Meissl 1997), sleep like states (Zhdanova *et al.*,2001) and thermal preference (refs *in* Underwood 1989, Zachmann *et al.* 1992a, Ekström & Meissl 1997). All three behaviors may affect food intake. It was recently shown that trout and catfish display a rhythm in demand-feeding when maintained under normal L:D cycles (Bolliet *et al.* 2001). Under L:L, food availability by itself was able to synchronized rapidly the demand-feeding rhythm to the period of food availability. However, the L:D cycle was a master synchronizer of the demand-feeding rhythm compared to food availability in trout. Finally, as reviewed elsewhere (Spieler 2001), fish grow differently depending on the circadian time feeding. This may have potential implications for aquaculture, but obviously our knowledge on the relationships between behavioral rhythms and food intake and digestion is still at its beginnings.

6.2. Melatonin and the control of hormones involved in fish growth

The evidence that melatonin receptors are present in the antero-ventral part of the pike and trout pituitary glands, and that melatonin modulates cAMP levels in cultured organs indicates that some hormonal output(s) is (are) under melatoninergic control. Preliminary investigations in trout indicate that GH is one possible candidate. Indeed, the release of GH by dissociated and cultured trout pituitary cells was increased in the presence of different melatonin concentrations. As observed for cAMP, the adenyl cyclase stimulator forskoline induced increases in GH release; under these pharmacological conditions melatonin effects are rather inhibitory. These results, although preliminary, are a good indication that melatonin may affect fish growth by a direct action on the GH producing cells of the pituitary. There is to date not enough data to explain why melatonin exerted two opposite effects. The presence of two melatonin receptor subtypes within the somatotrophs might be one requisite (Gaildrat & Falcón 1999, 2000).

The control of GH secretion by the fish somatotrophs is a process that involves both stimulatory (*e.g.*, dopamine, thyrotropin releasing hormone [TRH], GH-releasing factor) and inhibitory (*e.g.*, norepinephrine, serotonin, somatostatin [SRIF], GH) agents (Peng & Peter 1997, Agustsson & Bjornsson 2000, Agustsson *et al.* 2000). It is not unreasonable to believe that melatonin may affect GH secretion indirectly through controlling upstream regulatory factors. Dopamine and serotonin are two good candidates. Indeed, recent studies demonstrated that melatonin injections reduced dopamine content in trout hypothalamus and pituitary

(Hernandez-Rauda *et al.* 2000). Previous investigations had shown that melatonin was able to modulate serotonin metabolism in the fish hypothalamus (refs in Zachmann *et al.* 1992, Ekström & Meissl 1997). Future studies should aim to investigate whether these hypothalamic effects of melatonin are directed on dopaminergic and serotoninergic neurons that innervate the GH secreting cells.

Another possible way through which melatonin could influence fish growth is the pituitary/thyroid axis. In mammals, a type II iodothyronine deiodinase expression and activity has been evidenced in the pineal gland (Smith *et al.* 2001 and refs). In frogs and tadpoles melatonin is a potent inhibitor of T_4 secretion by the thyroid (Wright *et al.* 2000). In fish, little information is available regarding the interactions between melatonin and the thyroid. In catfish, pinealectomy reduces ^{131}I uptake by the thyroid, it increases plasma levels of T_3 and decreases those of T_4, but increases both T_3 and T_4 levels in the thyroid gland (refs in Ekström & Meissl 1997). The effects depend on the reproductive status.

6.3. What role for the nervous message?

When considering the effects of the pineal gland of fish, one must consider not only melatonin, but also the nervous message which is conveyed through the pinealofugal innervation to the brain centers. Unfortunately, virtually nothing is known on the role the nervous innervation plays. The only available information was obtained from neural tract tracing methods which made possible to delineate the brain areas innervated by the pinealofugal ganglion cells (for refs see Ekström & Meissl 1997). The most striking observation lies in the fact that many of these areas are also innervate by retinofugal projections. The pre-optic nuclei of the hypothalamus seem to occupy a key position for what concerns pituitary function (Holmqvist *et al.* 1994). Indeed, it receives projections from both the retina and pineal gland, it expresses melatonin receptors, and contains dopaminergic neurons that innervate the pituitary gland. This emphasizes that the hypothalamic optic nucleus constitutes a photo-neuroendocrine control center, activated by light, which probably plays an important role during growth and parr-smolt transformation by modulating the release of pituitary hormones. The lateral habenular *nuclei* are other putative dopaminergic nuclei that also receive innervation from the pineal gland and retina. The pretectal area, like the optic nuclei, also receive inputs from both the retina and pineal gland and posses melatonin receptors. Other areas of interest include the dorsal and ventral thalamus and the periventricular hypothalamus.

7. CONCLUSIONS

Many living species depend on the diurnal and annual lighting cycles for normal development, growth and reproduction. Daylength appears to be an important *"zeitgeber"* in fish. Many studies have demonstrated the positive influence of long daylength on growth and a few species, such as the Atlantic salmon, are extremely sensitive to it. Today, all this knowledge is used in salmoniculture, photoperiod manipulations being easily applied and not overly expensive. Long photoperiods or continuous daylight appear as a palliative for the compensation of low winter temperatures in highest latitude countries. This approach, however, may not be applicable to all species. Some fish do not respond and others need a (very) long time before expressing better growth. Research will have to be pursued in this area in the future to obtain more determining responses. Physiological mechanisms are not yet elucidated. How does photoperiod directly affect fish growth through a putative role of melatonin? During the last two decades, there has been a lack of interest, due to the difficulty to obtain clear-cut effects of pinealectomy or/and melatonin administration. Among different reasons, the experimental paradigms did not considered the respective roles of both the pineal and retina, the multiplicity of the messengers elaborated and released by these two organs and the fish seasonal physiological status. An issue to the elucidation of light receptivity and subsequent physiological responsiveness will come from studies combining "classical" physiological approaches (*in vitro* and *in vivo*) together with pharmacological and molecular approaches.

List of abbreviations: AANAT: arylalkylamine (serotonin) N-acetyltransferase; cyclic AMP: adenosine cyclic 3': 5'-monophosphate; ^{125}I-Mel: 2-[^{125}I]-iodomelatonin; HIOMT: hydroxyindole-O-methyltransferase; L:D: light/dark; L:L: constant light; RT-PCR: reverse transcription-polymerase chain reaction; SL: somatolactine; SRIF: somatostatin; T$_3$: tri-iodothyronine; T$_4$: thyroxine; TRH: thyroid hormones; TRH: thyrotropin releasing hormone.

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