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The Neuroendocrine Control of the Gonadotropin (GTH2) Secretion in Teleost Fish

B. Breton, T. Mikolajczyk, and W. Popek

In fish the control of the pituitary maturational gonadotropin (GTH2) secretion is mainly under the influence of the gonadotropin releasing hormone (GnRH). This paper will deal with recent advances in the knowledge of the GnRH system in teleost fish, and on the other neuromediators which can modulate positively or negatively this system or act directly on the GTH2 secretion, hormone mainly involved in the control of the last phases of the reproductive cycle, from the end of the vitellogenesis to maturation and ovulation on which have been done most of the works to date.

THE GONADOTROPIN RELEASING SYSTEM

Characterization and biological activity

Until now 6 different forms of GnRH have been characterized from the vertebrate brain. At least 2 forms are generally present in teleost fish. The salmon GnRH form (sGnRH = Trp⁷ Leu⁸ GnRH), has been found in most species as well as the chicken GnRH II form (cGnRH II = His⁵ Trp⁷ Tyr⁸ GnRH). Other forms have also been demonstrated in fish, such as the chicken GnRH I form (Gln⁸ GnRH) in tilapia, hake and winter flounder, and the mammalian form in some species such as the eel and the sturgeon (reviewed by King and Millar 1987, Sherwood and Coe 1991). In the goldfish, sGnRH, cGnRH I and II are all biologically active on the *in vivo* stimulation of the GTH2 secretion (Peter et al. 1987), cGnRH II being even more active than sGnRH, may be demonstrating a possible physiological significance of the presence of these different GnRH forms in fish (Chang et al. 1990).

The biological effects of GnRH are dose dependent and related to the pituitary responsiveness. In salmonids this responsiveness increases with the advancement of the gametogenesis and becomes maximum during the spawning period (Weil and Marcuzzi 1990a and b). In the goldfish, the pituitary responsiveness to GnRH also varied with the gonadal stage (Sokolowska et al. 1985), but cannot be demonstrated without the removal of a dopamine inhibition over GnRH action on the pituitary (for review Peter et al. 1986). This problem will be discussed in more detail in another part of this paper. The biological action of the peptide can also depend upon the GnRH catabolism which can vary according to species. In the sea bream *Sparus aurata*, sGnRH is rapidly cleaved at the 5-6 and 9-10 bonds by pituitary endopeptidases. The modification of these two bonds blocked the cleavage sites, sGnRHa being only intensively cleaved at the unmodified bond (Zohar et al. 1990). In the rainbow trout, the 5-6 bond cleavage is on the contrary very weak and slow in the pituitary, GnRHa being not degraded *in vitro* by pituitary cells in culture (Weil et al. 1991). Thus there would be species differences in the endopeptidase GnRH cleaving activity according to species. The highest resistance of fish GnRH compared to mammals, could also be linked to a GnRH serum binding protein with a low affinity site ($K_a = 2,2 \cdot 10^{-6} M^{-1}$) and a high capacity ($R_o = 3,56 \cdot 10^{-10} M/mg$ of serum protein), as demonstrated in the goldfish, which would prevent clearance of GnRH by the kidney and protect GnRH against degradation by serum enzymes (Huang and Peter 1988).

Numerous works have been done using mammalian GnRH analogs (GnRHa) generally substituted in position 6 and 9 in order to investigate the structure activity relationships in fish. GnRHa generally induced a long lasting stimulation of the GTH2 secretion (Peter et al. 1987), in addition treatment by a sustained release form of GnRHa stimulated the GTH2 secretion for several weeks in the rainbow trout (Breton et al. 1990b), indicating that contrary to mammals there is no rapid down regulation of the GnRH action at the pituitary level (Breton et al. 1990). Because of their prolonged effect on the stimulation of GTH2 secretion, GnRHa are now widely used as potent maturation inducers in numerous cultured species.

Localization

Immunoreactive sGnRH structures are localized along a column extending from the rostral olfactory bulbs to the pituitary. Cells bodies are observed within the olfactory nerves and bulbs, along the ventromedian telencephalon, the ventrolateral preoptic area and laterobasal hypothalamus. There are two main pathways reaching the pituitary, where GnRH has been localized in the neural tissue of the neurointermediated lobe (Kah et al. 1986). This has been confirmed using quantitative RIA determinations of both sGnRH and cGnRH II. In the goldfish, (Yu et al. 1988) and in the rainbow trout (Okusawa et al. 1990), cGnRH II is found in the same areas as sGnRH, but in addition it is preminent in the caudal brain (cerebellum, medula, spinal cord and optic tectum) in which no specific pathways leading to the pituitary

have been so far identified, making questionable the physiological role of GnRH contained in these structures. However, this suggests that cGnRH II and sGnRH immunocytochemical functions are anatomically separated, and that these peptides could have partially different physiological functions, at the pituitary level and also on other structures.

Involvement of GnRH in the control of gonadotropin secretion during the annual reproductive cycle

One of the main problem in studying GnRH secretion in teleost, is the lack of an hypothalamo-hypophysial system avoiding the possibility to measure GnRH blood portal levels in relation with GTH secretion. In mammals there is a correlation between luteinizing hormone (LH) and GnRH rhythms of secretion. In fish, it is thus questionable to know if the GnRH brain and pituitary contents could reflect a GnRH secretory activity, and be representative of a pituitary gonadotrophic activity in the absence of knowledge on such rhythms. However, seasonal variations of sGnRH brain and pituitary contents have been demonstrated in the rainbow trout (Breton et al. 1986) and the goldfish (Yu et al. 1987), but generally not correlated with GTH2 blood plasma levels, excepted the periovulatory period during which GTH2 secretion follows a circadian rhythm in both species (Montela and Peter 1980; Zohar et al. 1986b). In the goldfish the GTH2 ovulatory surge is accompanied by a dramatic decrease of the pituitary, telencephalon and olfactory bulbs sGnRH contents, may be corresponding to a sGnRH release inducing the gonadotropin surge. In a natural environment, in male and in female roach *Rutilus rutilus*, sGnRH contents were the highest, correlated with the lowest plasma GTH2 levels the day preceding fish gathering on the spawning grounds and the first ovulations. The following day, GTH2 blood plasma concentrations increased correlated with a decrease of brain and pituitary sGnRH contents. That occurred in all fish including male, ovulated and unovulated females exhibiting a spawning behavior (Breton et al. 1988a and b). This let suppose that, in natural populations, it would exist a synchronizing factor activating the hypothalamo-pituitary axis. In the goldfish, GnRH contents decreased in all parts of the rostral brain including the olfactory bulbs, providing evidence of functional relations between these structures and other brain areas (Yu and Peter 1990b). This could be an important link between environmental cues and the neuroendocrine system. Among the others, pheromonal stimulations certainly participate, because in the roach, in a natural environment, GnRH contents decreased in all fish independently of the maturational stage (Breton et al. 1988a and b), and in the goldfish exposure of male to a female exhibiting a prostaglandin induced spawning behavior, modified GnRH contents in the brain including in the olfactory bulbs (Yu and Peter 1990b). This situation appears original compared to mammals in which the olfactory bulbs tonically inhibited the gonadotropin secretion, by a mechanism which would not depends upon chemosensory signals as in the golden hamster (Pieper et al. 1990).

GnRH mechanism of action

The first step of GnRH action is the binding to GnRH pituitary receptors. They have been demonstrated in the winter flounder (Crim et al. 1988), the African catfish (de Leeuw et al. 1988) and the stickleback (Anderson et al. 1989) in which there are a single class of low affinity and high capacity binding sites. In the goldfish two classes of binding sites have been identified, a low affinity high capacity site, and a high affinity low capacity site (Habibi et al. 1987) which would be respectively 51000 M₁ and 71000 M₁ proteins (Habibi et al. 1990). There are seasonal variations in pituitary GnRH receptor activity in the catfish and the goldfish (Habibi et al. 1989), highest binding capacities occurring during the late stages of gonadal recrudescence when the pituitary responsiveness to exogenous GnRH stimulation becomes maximum. There is also a correlation between GnRH binding affinity and their functional ability to stimulate pituitary GtH secretion (Habibi et al. 1989).

Recent studies demonstrated a desensitizing effect of GnRH which depends upon the dose and the frequency of application of the decapeptide. This process is partly the result of a down regulation of the pituitary binding capacity (Habibi et al. 1991). A pulsatile GtH secretion exists in the rainbow trout (Zohar et al. 1986a), although GnRH pulsatility cannot be demonstrated in fish, it could be supposed that the GtH pulsatility would be the result of a GnRH pulsatile pituitary delivery, may be essential for the maintenance of a normal pituitary GtH release in fish as in mammals.

The post membrane action of GnRH in fish is mainly mediated by extra cellular Ca⁺⁺ as second messenger, in catfish (Van Asselt et al. 1989), tilapia (Levavi-Shimoni and Yaron 1989) and carp (Mikolajczyk et al. 1990a). The entrance of Ca⁺⁺ into gonadotropes would be the result of the activation of voltage dependent calcium channels (VDCC), but in carp, contrary to mammals in which LHRH activated L types of VDCC, sGnRH activated N or T types of VDCC. On another hand, in carp the specific blockade of L type VDCC by nifedipine also induced an *in vitro* GtH2 release in absence of GnRH and their specific activation by Bay K8644, induced a dose dependent inhibition of GtH2 release (Mikolajczyk et al. 1990b), may be indicating that other mediators have a direct trophic effect on gonadotropes through the modification of L type VDCC. Other relays than Ca⁺⁺, have also been demonstrated in fish. This is the case of the protein kinase C (PKC) in tilapia (Levavi-Shimoni and Yaron 1989), which is also involved in LHRH action in mammals resulting of PKC intracellular redistribution following Ca⁺⁺ mobilization; and arachidonic acid (AA) in the goldfish (Chang et al. 1989). In this last species sGnRH and cGnRH II bind to the same receptors, but they could have different second intra cellular messengers, AA mediating more especially the action of cGnRH II (Chang et al. 1991).

OTHER NEUROMEDIATORS AND THEIR INTERACTION WITH THE GnRH SYSTEM

The dopaminergic system

The role of dopamine (DA) as a gonadotropin release inhibiting factor (GRIF) is well established in goldfish, in which its main action is the inhibition of GnRH stimulates GtH release as well *in vivo* as *in vitro*, depending on the gonadal stage of development. The inhibitory tone exerts by dopamine increased with the advancement of the gametogenesis, reaching a maximum level at the time of ovulation. As a consequence, in this species the artificial induction of ovulation absolutely requires a combined treatment using GnRHa and a DA antagonist such as pimozide (for review Peter et al. 1986). The DA inhibitory tone also exists in other teleost species (de Leeuw et al. 1986), but its intensity appears to depend on the species as indicated by the ovulatory response to GnRHa treatments. In salmonids for instance, 100% ovulations can be obtained using GnRHa alone (Breton et al. 1990), although it had been mentioned that pimozide potentiated GnRH stimulated GtH release in the coho salmon. Other species such as the chinese loach (*Paramisgurnus dabryanus*) present intermediary situation, in which DA antagonist also potentiated GnRH induced GtH release, but only increase the frequency of induced ovulation (Lin et al. 1986). This variability of the DA inhibitory tone may be representative of evolution throughout teleost fish, but could also depend on other factors, and among the more or less important dependence of final maturation process to strict environmental cues as in the goldfish, where the spontaneous GtH ovulatory surge cannot occur in absence of aquatic vegetation (Stacey et al. 1979). These include pheromonal interactions which could activate or inhibit neuronal circuits leading to dopaminergic inhibition or its removal as we already hypothesized in the roach (Breton et al. 1988a and b). see social factors.

There are also differences in the DA metabolic pathways according to species. In teleost, the main pathway for DA degradation is linked to the monoamine oxydase activity; in addition, in some species such as the rainbow trout and the catfish, a second pathway through catechol o methyl transferase (COMT) has also been demonstrated (Van Asselt et al. 1989, Saligault et al. 1990). By the way, there will be a competition between catechol estrogens and DA for COMT, leading to an additional modulation of DA degradation. This process depends upon estradiol levels and aromatase activity (Van Asselt et al. 1989). Research have failed to demonstrate such a mechanism in the goldfish (Trudeau et al. 1991). Thus it can be speculated that the metabolic pathway for DA degradation could be also part of the mechanisms which determine DA inhibitory tone on GnRH action, in relation with steroids.

In the goldfish and the catfish, DA action is exerted through D₂ dopamine receptors (Olmejaniuk et al. 1986, Van Asselt et al. 1990), and results in several effects such as a down regulation of the pituitary GnRH receptors (de Leeuw et al. 1988, 1989), and the modification of GnRH contents in the brain structures excepted the pituitary in the normal

male goldfish. In male induced to spawning behavior following exposure to prostaglandin treated female, the increase in GnRH brain contents is abolished after DA antagonist treatment (Yu and Peter 1990b). All these data demonstrate the important role of the central dopaminergic system in fish as an important inhibitory component of the regulatory circuits of brain GnRH levels, GnRH release and GnRH action at the pituitary level.

Neuropeptide Y (NPY)

This 36 aminoacids peptide which, in the mammals, had very pleiotropic actions, is involved in the central regulation of the luteinizing hormone (LH) secretion. It had also been characterized in the goldfish (Pontet et al. 1989), and the rainbow trout (Danger et al. 1991). It had a widespread brain distribution. In particular, NPY immunoreactive neurons are located in the nucleus enteropeduncularis and the preoptic nucleus; but there is no colocalization with sGnRH. On the contrary in the pituitary, NPY immunoreactive fibers are in direct contact with gonadotrophs (Kah et al. 1989), may be indicative of direct action of the peptide at the pituitary levels and indirect effects at the upper level. In the rainbow trout, it modulated the *in vitro* GtH2 secretion from perifused pituitary fragments, being either inhibitory during vitellogenesis or stimulatory during the periovulatory period. This modulation of NPY action depends upon the *in vivo* estradiol levels. Indeed, the *in vitro* response to NPY of pituitary taken from vitellogenic females treated with ATD, an inhibitor of the aromatase activity, is similar to that of pituitary taken from ovulating females in which estradiol levels are very low (Breton et al. 1989). The NPY action at the pituitary level is certainly complex, because its action is inhibited in presence of a GnRH antagonist in pituitary fragments, may be indicating interaction between the two peptides. On another hand, it also stimulated GtH2 secretion from perifused dispersed pituitary cells indicating a direct effect on the gonadotrophs (Breton et al. 1990). It equally stimulates the *in vivo* GtH2 secretion either after intraperitoneal treatment in the rainbow trout or intraventricular infusion in the carp. In both species it potentiates the *in vivo* and *in vitro* action of GnRH α (Breton et al. 1991). Thus besides direct effects of NPY on the gonadotrophs, there are clear evidence of interaction between GnRH and this peptide at the pituitary level. The mechanisms by which NPY enhances GnRH action; and GnRH antagonist blocks its action is unsolved in fish. In mammals, it had been demonstrated that NPY increased GnRH binding to pituitary membranes, may be explaining in part the action of this neuropeptide to potentiate GnRH induced LH release (Parker et al. 1991), such a mechanism must be investigated in fish. In the rat, one of the action of NPY at the pituitary level is mediated through the activation of VDCC (Crowley et al. 1990). In the rainbow trout, NPY as well as GnRH do not activated the pituitary adenylyl cyclase activity (unpublished data), that let suppose that NPY action is mediated by another second messenger. The *in vivo* stimulation of the GtH2 secretion by NPY could be linked to its effects on the GnRH release at the central level as well in fish as in mammals (Khorram et al. 1987). The *in vivo*

demonstration of such a mechanism in fish is nearly impossible because the lack of hypothalamo-pituitary portal vessel system. However, in the rainbow trout, NPY stimulates the *in vitro* sGnRH release from slices of telencephalon but not from the pituitary (Breton et al. unpublished data). Thus one of the effects of NPY would be the stimulation of GnRH from telencephalon perykaryons, which in turn would stimulate the pituitary GtH2 secretion. We have recently completed these experiments and demonstrated that the *in vitro* action is blocked in presence of propanolol (unpublished data), a noradrenergic antagonist, indicating that NPY action could be mediated by norepinephrine as already demonstrated in the rabbit (Berria et al. 1991).

All these results show that NPY is an important component of an excitatory neural circuit involved in the control of the pituitary gonadotropin secretion.

Other neuromediators

There are scattered informations on the effects of other neurotransmitters on the control of GtH secretion, mainly obtained in the rainbow trout and the goldfish.

Norepinephrine has been demonstrated to stimulate the GtH2 secretion in the goldfish (Chang and Peter 1984). We have already mentioned the possible involvement of the adrenergic system in the mediation of NPY stimulated GnRH release from telencephalon perykaryons in trout. Supporting this hypothesis, a direct effect of norepinephrine on the *in vitro* sGnRH release from slices of the preoptic anterior hypothalamic region had been demonstrated in the goldfish (Yu et al. 1991), in which, in addition it directly stimulated GtH2 secretion independently of sGnRH receptors (Chang et al. 1991). Thus this mediator could exert a dual control on the regulation of GtH2 secretion, having both a direct effect on the pituitary and indirectly modulating GnRH release from GnRH cell bodies.

Serotonin also stimulated *in vivo* and *in vitro* GtH2 secretion in the goldfish, probably through a direct action at the pituitary level (Somoza et al. 1988, Somoza and Peter 1991).

In the male goldfish naloxone (NAL), an opioid receptor antagonist caused an *in vivo* decrease in serum GtH2, it also blocked the stimulatory effect of GnRH during late gonadal recrudescence, whereas it stimulated GnRH induced GtH2 secretion during early recrudescence. Other experiments have shown that there is interaction between NAL and the dopaminergic system (Rosenblum and Peter 1989). These data suggest that opioids may also play an important role in the regulation of GtH2 secretion.

Direct treatment of goldfish with gamma amino butyric acid (GABA), induced an increase of GtH2 secretion depending upon the reproductive stage and the steroid environment (Kah et al. 1991). This action may be mediated by direct or indirect GABA influence on sGnRH release from pituitary peptidergic endings. In sexually mature carp, modifications of the GABA metabolism leading either to increase or decrease the endogenous GABA concentrations, had no effect on the GtH2 basal levels, but modified the response to GnRH treatment used alone or in combination with the DA antagonist pimozide. Thus in the female and male carp, 3 mercapto propionic acid (MPA), an inhibitor of GABA synthesis, enhances the response to GnRH-pimozide treatment, whereas the GABA mimetic compound valproic acid decreases the GnRH stimulated GtH2 levels in the male (Roelants et al. 1989). In mammals, GABA interacted with DA, especially in the control of LH secretion (Jason et al. 1980), on which GABA and DA had opposite effects (Elias et al. 1983). Our results suggest that GABA also interacts with DA in the control of gonadotropin secretion in fish, through an inhibitory tone. In the rainbow trout in which DA inhibition on GnRH action is low, the same kind of experiments did not modified either basal or GnRH stimulated GtH2 levels (unpublished data). This again point out the existence of species differences in the control of GtH2 secretion.

There are numerous works on the study of the role of the pineal on the control of the reproductive cycle in fish, but there is not clear conclusion on the relation between pineal and GtH secretion. Although pinealectomy could affected rythm of GtH2 secretion in the goldfish (Hontela and Peter 1980), until now there is no data on the effects of pineal secretions as elements involved in the regulation of gonadotropin secretion in fish. We have recently investigated the effects of melatonin on GtH2 secretion in the female carp. Melatonin intraperitonally injected or infused into the third ventricle induced a stimulation of the GtH2 blood plasma levels only if the treatments are done at the middle of the dark phase, treatments realized either at the beginning of the dark phase or during the light phase being ineffective. During the dark phase, these treatments also increase the response to GnRH injection, and their effects are suppressed in presence of apomorphine and enhanced with pimozide (unpublished data). These results clearly demonstrated that melatonin is involved in the control of GtH2 secretion in the carp, may be partially through the modulation of the dopaminergic inhibitory tone on GnRH action. The fact that melatonin is only effective during a short period of the nycthemer lets suppose that this mediator could have a permissive effect on the gonadotropin release and could play a role in the induction of the GtH2 ovulatory surge occuring during the last phase of the dark period in the goldfish (Stacey et al. 1979).

STEROID HORMONES

Feedback effects of steroids on the GtH2 secretion in fish was first demonstrated after castration experiments in the male (Billard et al. 19776) and the female rainbow trout (Bommelaer et al. 1981). Steroid hormones do not seem to have similar effects on the hypothalamo-pituitary axis in salmonids and cyprinids. A positive feedback of steroids on GtH2 synthesis had been demonstrated in immature fish in both species (Crim and Evans 1979, Crim et al 1981), but in goldfish only aromatisable androgens were active, whereas non aromatisable steroids were also effective in the rainbow trout (Goverdina et al. 1983), may be suggesting that testosterone acted differently or its action was differently modulated in these two species (see Peter et al. 1991 for review). This was confirmed by the long term effects of testosterone implantation in immature fish, which stimulated GtH2 secretion in trout (Crim et al 1982, Gielen and Goos 1984) but not in goldfish, may be resulting of a DA inhibition on spontaneous GtH2 secretion in the goldfish (see Peter et al. 1986 for review). We have reinvestigated this problem using a triploid rainbow trout model, in which testosterone and estradiol blood plasma levels are still undetectable in two years old fish, when normal fish of the same strain undergo gonadal recrudescence (unpublished results). As in normal juvenile fish, testosterone and estradiol stimulate the GtH2 synthesis, testosterone being more potent than estradiol, but only testosterone specifically stimulates GtH2 secretion in a dose dependent manner. In addition we have determined the effects of steroids on sGnRH synthesis and accumulation in the brain and the pituitary. testosterone and estradiol also increase sGnRH contents in areas containing sGnRH perikaryons (telencephalon and preoptic area), Testosterone being anew more potent than estradiol. There is no change in the hypothalamus sGnRH contents, whereas testosterone induces a rapid pituitary sGnRH accumulation, occurring less than a month after steroid implantation, and a month earlier than the stimulation of the GtH2 secretion, although the pituitary GtH2 synthesis was already stimulated (Breton et al. unpublished data). That might be indicative of other mechanisms, depending or not upon steroids, occurring progressively during the brain sexualization, and which could be involved in the determinism of GnRH release from pituitary peptidergic endings or in that of the pituitary sensitivity to GnRH for instance.

This last process had been demonstrated to be influenced by steroids in the goldfish, where testosterone implants increased the pituitary GnRH responsiveness at all stages of gonadal development, whereas estradiol exerted a similar effect only in sexually regressed fish (Trudeau et al. 1991a). Although this action could be mediated through the modulation of DA turnover in the goldfish (Trudeau et al. 1991b), in the rainbow trout, using pituitary cells cultures, Weil and Marcuzzi (1990a andb), demonstrated direct effects of steroids on the pituitary responsiveness to GnRH. These direct effects could be partly mediated by the effects

of steroids on the regulation of GnRH pituitary receptors as shown in the goldfish and the catfish.

From all these results, it is clear that steroids can act at multiple hypothalamic pituitary sites, and differently according to species. This is equally true for DA, and moreover they can interact together. This points out the necessity to develop comparative studies on different fish models.

SOCIAL FACTORS

In the male goldfish, exposure to a sexual stimulus resulted in a stimulation of the GtH2 secretion and an increase of the milt volume (Kyle et al. 1985). In the rainbow trout GtH2 plasma levels were also higher in males in contact with ovulated females exhibiting a spawning behavior (Liley et al. 1986). In the goldfish, it has been further demonstrated that these effects were mediated by a sex hormone originated from maturing females (Dulka et al. 1986, Kobayashi et al. 1986), which has been identified as the maturation inducing steroid (MIS), 17 hydroxy 20 β dihydro progesterone released in the water by ovulating females (Stacey and Sorensen 1986, Sorensen et al. 1987). The effect of the MIS on the GtH2 secretion is not a direct feedback on the pituitary, but results from the activation of neuronal circuits leading to GtH release, in which the olfactory system might play a key role, MIS activating the electrical activity of the olfactory epithelium (Sorensen et al. 1987). On the other hand, olfactory tract lesions inhibited MIS induced - GtH2 surge (Dulka and Stacey 1991). As we already mentioned, in spawning male goldfish, GnRH contents decreased in all part of the brain including the olfactory bulbs (Yu and Peter 1990b), may be as the results of MIS action on these structures.

In conclusion the neuroendocrine control of the gonadotropin secretion in fish is a multicomponent system in which each factor interacts with others. Besides GnRH, according to species other neuromediators do not seem to have the same importance. This is especially the case of dopamine which strongly inhibits GnRH action in some species such as the cyprinids, but has only a weak influence in others such as the salmonids. This raises the problem of the choice of the experimental model according to the factors to study, and the type and the strength of their interactions. For that reason it is now nearly impossible to draw a general model of the neuroendocrine regulation on gonadotropin secretion in which all components would have the same importance in all species. In our opinion comparative studies must be developed in other species than cyprinids and salmonids, in which most of the results have been obtained to date. Fish diversity offers such an opportunity.

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