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Daily and annual physiological and behavioural rhythms in fish: Implications for the domestication of bluefin tuna

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SUMMARY – Rhythms with a period of 24 h (daily) and one year (annual) represent one of the major components in the adaptation of organisms to their environment. Virtually all biochemical processes, physiological functions and behaviours are rhythmic. Photoperiod (i.e. the alternation of light and darkness over a 24 h cycle) and temperature play a major role in the synchronization of the daily rhythms (Falcón, 1999; Boeuf and Falcón, 2001). As a consequence of the seasonal variations in daylength and temperature, processes such as development, growth and reproduction, follow a seasonal pattern. One of the requirements to achieve domestication of any fish species, including bluefin tuna (BFT), is the elucidation of the mechanisms by which information from external cues is integrated; this remains far from clear. We want to emphasize here the importance of the melatonin system as a key component in the integration of external information into a temporal message involved in the synchronization of functions and behaviours (see Falcón, 1999, for extensive details).

Key words: Photoperiod, temperature, melatonin, rhythms, growth, reproduction.

RESUME – *"Rythmes physiologiques et comportementaux journaliers et annuels chez les poissons : Implications pour la domestication du thon rouge". Les rythmes sur une période de 24 h (journaliers) et d'une année (annuels) représentent une des composantes majeures de l'adaptation des organismes à leur environnement. Virtuellement tous les processus biochimiques, les fonctions physiologiques et les comportements obéissent à un rythme. La photopériode (c.a.d. l'alternance du jour et de la nuit sur un cycle de 24 h) et la température jouent un rôle majeur dans la synchronisation des rythmes journaliers (Falcón, 1999 ; Boeuf et Falcón, 2001). Comme conséquence des variations saisonnières de la longueur du jour et de la température, des processus tels que le développement, la croissement et la reproduction, suivent une tendance saisonnière. L'une des conditions pour la domestication de toute espèce de poisson, y compris le thon rouge, est la compréhension des mécanismes qui intègrent l'information provenant de signaux externes ; et ceci est loin d'être clair. Nous voulons souligner ici l'importance du système de la mélatonine comme composante clé de l'intégration de l'information externe dans un message temporel intervenant dans la synchronisation des fonctions et comportements (voir Falcón, 1999 pour plus de détails).*

Mots-clés : *Photopériode, température, mélatonine, rythmes, croissance, reproduction.*

Photoreception and melatonin production

Melatonin is produced by the photoreceptor cells of the retina and pineal organ (or epiphysis or "*third eye*"). The latter is organized as a simplified retina located above the brain hemispheres in a window below the skull and between the two eyes. Photoreceptors detect rapid changes in light environment [which results in the production of a neurotransmitter (glutamate)]. They also provide information on the respective duration of the light (L) and dark (D) phases through the rhythmic production of melatonin. This usually involves circadian clocks. In other words, each photoreceptor cell is a circadian system in which the LD cycle entrains the clock, which in turn drives the expression and activity of enzymes involved in the control of melatonin secretion. Temperature as well as internal chemical transmitters and hormones also modulate the shape of the daily oscillations. These include catecholamines, cortisol, sex-steroids, and peptides, which might represent elements of a feedback loop (Fig. 1). Melatonin levels in the pineal gland and blood are higher during night than during day, whereas a reverse pattern is observed in the retina. Retinal melatonin is produced and metabolized *in situ*. There is indication that retinal melatonin might regulate a number of daily retinal rhythms such as light sensitivity, adaptative retino-motor movements, and neurotransmitters release. Pineal melatonin is released in the blood, and the profile of the rhythm varies along the annual cycle. The nocturnal melatonin increase is of high amplitude/short duration during summer, and of low amplitude/long duration during winter. Nothing is known on the visual, circadian and melatonin systems in BFT.

Role of the pineal gland and melatonin in fish

As reviewed elsewhere (Zachmann *et al.*, 1992; Boeuf and Falcón, 2001) early physiological studies have involved the pineal gland and/or melatonin in the control of daily rhythms of: (i) metabolisms (electrolytes and glucose balance, hypothalamic monoamines, lipid content); and (ii) behaviours. The latter refer to skin pigmentation, shoaling behaviour, food intake, thermal preference, sleep-like status, locomotor activity and phototactic movements. Tagging studies (this meeting) indicated BFT go down at dawn and up at dusk. These dramatic daily vertical movements might reflect some special requirements of the BFT visual system, as also suggested from the observation that BFT larval mortality due tank bumping is higher at dawn (Kaji, pers. comm.).

There is also indication that melatonin synchronizes annual variations in fish reproduction and growth, although contradictory results were very often obtained even within the same species. For example, pinealectomy may have pro- or anti-gonadal effects or no effect at all, depending on the season the experiments were done. Similarly, growth rates are accelerated or reduced by pinealectomy, depending on the time of the year. Spawning in BFT occurs on an annual basis, but the modalities of this control are not known.

The identification and characterization of the melatonin binding sites, as well as the cloning of melatonin receptors provided a new step forward in the understanding of how external cues may affect daily and annual rhythms. Thus, it appears that the receptors display a widespread distribution in the fish brain. Brain melatonin receptors are seen in areas involved in the integration of sensory inputs (olfaction, vision, audition) and coordination of adaptative movements (cerebellum). Regarding the control of neuroendocrine functions, of great interest is the observation that functional melatonin binding sites were seen in the pituitary as well as in the hypothalamus of fish (Fig. 1). In the former, melatonin modulates the production of second messengers; we are currently investigating its involvement in the control of pituitary hormone production. In the latter, the pre-optic nuclei appear as a "key centre" because they contain melatonin receptors, receive neural input from both the retina and the pineal gland, and they send projections to the pituitary (Fig. 1).

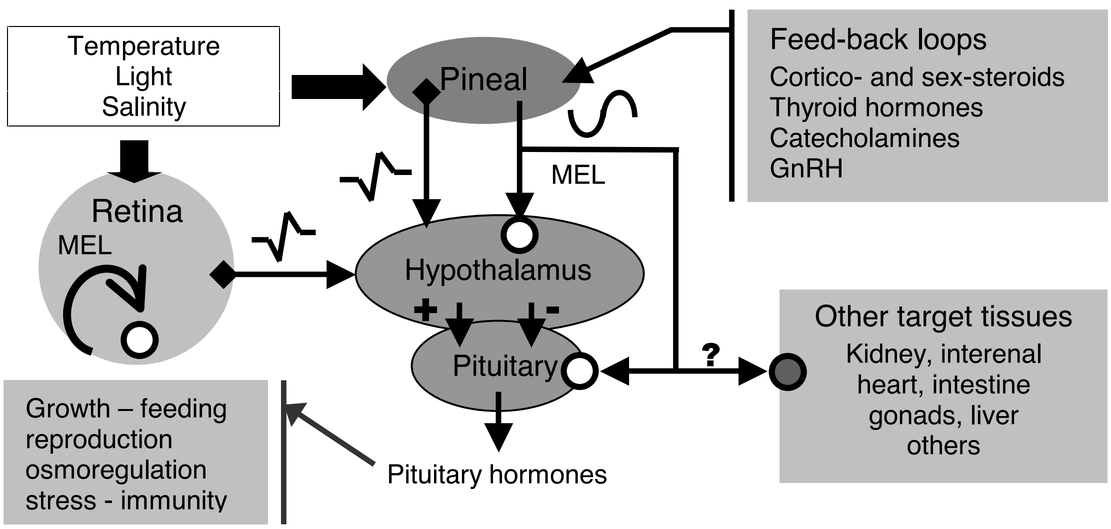

Fig. 1. Known and hypothetical (?) pathways of neuroendocrine functions control by external factors in fish. MEL = melatonin; diamonds with arrows = pineal and retinal ganglion cells; empty circles = identified melatonin receptors; filled circles = hypothetical melatonin receptors.

Conclusions and implications for the domestication of bluefin tuna

The idea that melatonin is a "conductor" that triggers the timing of daily and annual functions in fish is gaining interest (Fig. 1). However, its modes of action are far from being clearly understood and concern a very limited number of freshwater species. In addition, considering that very little is known on the physiology of BFT, and that there are great species-dependent variations, we believe there is an urgent need for basic investigations on the organization and function of the visual, circadian and melatonin systems in BFT. Such studies are of crucial importance to help defining the best photoperiod and temperature conditions for optimizing larval development, as well as adult growth and reproduction. To tackle this problem, we need to investigate, during development and along the daily and annual cycles: (i) the structure and function of the pineal gland and retina (spectral sensitivity, circadian organization, regulation of melatonin production); (ii) the factors and hormones of the hypothalamus-pituitary system (e.g. FSH, LH, GH, prolactin, and corresponding receptors); and (iii) the melatonin targets and modes of action.

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