



HAL
open science

DAILY FEEDING RHYTHMS AND FISH PHYSIOLOGY

Thierry Boujard

► **To cite this version:**

Thierry Boujard. DAILY FEEDING RHYTHMS AND FISH PHYSIOLOGY. *Vie et Milieu / Life & Environment*, 2001, pp.237-245. hal-03192521

HAL Id: hal-03192521

<https://hal.sorbonne-universite.fr/hal-03192521v1>

Submitted on 8 Apr 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

DAILY FEEDING RHYTHMS AND FISH PHYSIOLOGY

Thierry BOUJARD

Équipe Nutrition, Aquaculture et Environnement, Unité mixte INRA-IFREMER de Nutrition des Poissons, INRA Hydrobiologie, BP. 3, 64310 Saint-Pée sur Nivelle, France
E-mail: boujard@st-pee.inra.fr

FEEDING RHYTHMS
HUNGER
SATIATION
FOOD INTAKE REGULATION

ABSTRACT. – There is a considerable body of evidence demonstrating that hormones or metabolites involved in feeding, growth and energy partitioning show significant daily fluctuations suggesting that fish are in different physiological states at different times of the day. As such, they should respond differently to food depending on the time of feeding. It has been also demonstrated that the act of feeding periodically induce a pre-prandial locomotor activity. Thus, feeding time might have an influence on the phase or amplitude of some of the endocrine cycles involved in the physiological regulation of feeding. Nevertheless, data pertaining to the entraining effect of feeding time on endocrine cycles are scarce and results are equivocal. Although it is believed that feeding is required for the maintenance of a rhythmic pattern of circulating hormones and metabolites, the evidence for an effect of feeding time on the plasma profiles of hormones and metabolites involved in somatic growth is limited. It is concluded that daily rhythms in feeding activity may reflect adaptive responses to food availability and predators in the wild. It also depends upon endogenous mechanisms, and one might suppose that feeding activity occurs when the fish is physiologically best prepared to use nutrients efficiently. However the examination of plasma hormone profiles may not be particularly suitable for gaining information about the mechanisms involved in the effect of feeding time on growth of fish. Investigation of hormonal receptors, gene expression or enzymatic activity might provide more pertinent information to elucidate how feeding time affects metabolism and nutrient utilisation.

RYTHMES ALIMENTAIRES
FAIM
SATIÉTÉ
RÉGULATION DE L'INGESTION

RÉSUMÉ. – De nombreux travaux décrivent les fluctuations plasmatiques d'hormones et de métabolites impliqués dans la régulation de l'appétit, de la croissance et du métabolisme énergétique au cours du nyctémère. Ceux-ci suggèrent que les Poissons passent chaque jour par différents états physiologiques, et que l'utilisation des nutriments ingérés est affectée par l'heure d'alimentation. Lorsque les Poissons sont conditionnés à manger à heure régulière (une fois par jour), une activité locomotrice pré-prandiale quotidienne apparaît. L'heure des repas pourrait alors avoir une influence sur la phase et l'amplitude de certains cycles endocriniens impliqués dans la régulation de l'ingestion. Cependant les travaux portant sur la capacité de l'heure des repas à modifier des cycles endocriniens sont rares, et leurs résultats contradictoires. Bien qu'il soit largement reconnu que l'ingestion d'aliments participe au maintien des cycles des métabolites et de certaines hormones, la démonstration que l'heure d'ingestion affecte leurs profils reste peu probante. Les rythmes circadiens d'activité alimentaire sont probablement une des réponses adaptatives de l'animal aux cycles de disponibilité de la nourriture et de la présence des prédateurs dans le milieu naturel. Ils sont sous le contrôle de mécanismes endogènes, et on peut supposer que le pic d'activité alimentaire est synchrone avec la préparation physiologique à utiliser au mieux les nutriments ingérés. Cependant l'étude des récepteurs hormonaux, de l'expression de certains gènes ou des activités enzymatiques pourrait être plus pertinente que l'analyse des variations du profil plasmatique en hormones dans l'analyse des mécanismes impliqués dans l'effet de l'heure des repas sur la croissance.

INTRODUCTION

Fish are confronted, like other animals, to cyclical fluctuations of their environment. They have to be able to predict and respond to repetitive events, in brief, to develop capacities to evaluate cyclic changes in their environment and to adapt their behaviour. The capacity of the fish to respond behaviourally to these cyclic changes in a rhythmic way is well demonstrated for long (for review see Thorpe 1978), and the existence of rhythms of different periodicity (ultradian, circadian, tidally-synchronised, lunar, etc...), as well as the endogenous origin of some behavioural rhythms were discussed extensively in Ali (1992). In brief, in fish the suprachiasmatic nuclei of the hypothalamus, known as a major circadian oscillator in mammals, has never been identified but the circadian system, which is composed of circadian oscillators, includes the pineal organ and the lateral eyes (Falcon *et al.* 1992).

Feeding rhythm is a particular type of rhythmic behaviour. The first demonstration of the existence of a feeding rhythm under controlled conditions in fish was by Hoar (1942). He demonstrated that two salmonids, Atlantic salmon, *Salmo salar*, and brook trout, *Salvelinus fontinalis*, were eating less when feed was offered during the night than when it was offered during the day. Since then, rhythmic patterns of feeding activity have been described in many fish species, and the existence of not only circadian, but also seasonal rhythms in feeding activity is now largely recognised. In brief, fish are not eating all the time, and the temporal organisation of their feeding activity is under the influence of various factors of exogenous and endogenous origins:

Exogenous factors. It is evidenced that the light dark alternation is the main exogenous factor, but it should be reminded that any environmental factor, of either physico-chemical (t° , O_2 , turbidity, etc...) or biotic nature (predators, competition, etc...), may induce important changes in the profile of the feeding activity rhythm (for review see Spieler 1992, Boujard & Leatherland 1992a, Boujard & Luquet 1996, Boujard 1999, Bolliet *et al.* 2001b, Madrid *et al.* 2001).

Endogenous factors. Unequivocal results concerning the endogenous nature of the feeding activity rhythm in fish were obtained in European sea bass, *Dicentrarchus labrax* as well as goldfish, *Carassius auratus* (Sanchez-Vasquez *et al.* 1996), rainbow trout, *Oncorhynchus mykiss* (Sanchez-Vasquez & Tabata 1998, Bolliet *et al.* 2001a), and European catfish, *Silurus glanis* (Bolliet *et al.* 2001a) submitted to constant lighting conditions. The majority of the individuals studied displayed a free-running rhythm of feeding activity with tau (τ = the period of the biological rhythm) com-

prised between 22:15 h and 28:45 h. (for review see Madrid *et al.* 2001, Sanchez-Vasquez & Madrid 2001). The ability of fish to anticipate the time of feeding when food is given on a regular basis has also been recently demonstrated, but the location of a food-entrainable oscillator remains unknown (Sanchez-Vasquez *et al.* 2001).

It is of interest to investigate the link between these rhythms and the fluctuations over time of some metabolic and physiologic parameters. In this paper, we aim at reviewing the relationships between feeding and physiological rhythms in fish. In other words, one might wonder i) if some metabolic and physiologic parameters do also fluctuate in a rhythmic manner, and if so, ii) does the act of feeding influence these rhythms, and iii) is there any consequence of the time of feeding on the physiological state of the animal.

The cycle of hunger/satiety and the circadian rhythms of feeding

It is self-evident that the act of feeding has a physiological basis. This means that feeding activity should be triggered by internal signals, and the amount of food ingested within a period of time should be adapted to the metabolic needs of the organism.

The capacity of fish to adjust their feed intake in relation to the energy content of the diet has been demonstrated (Boujard & Médale 1994, Paspatis & Boujard 1996). It was therefore of interest to determine if circadian rhythm of feeding activity is influenced by the dietary energy levels. To that end, groups of European sea bass were fed on demand by means of self feeders, under Light: dark (LD) and constant light (LL) conditions, with a fixed or an unlimited amount of feed with variable lipid contents (Boujard *et al.* 2000a). Daily total feed intake, but not the feeding rhythm, was adjusted in relation to the energy content of the diet regardless of the lighting conditions (Table I). It was concluded that a satiation mechanism was likely responsible for the regulation of feed intake in relation to the dietary fat content but was not acting in itself on the mechanisms that drive the free-running rhythms of feeding activity. The same conclusion was also drawn from the study of Bolliet *et al.* (2001a), where rainbow trout and European catfish displayed free-running rhythms of feeding activity whether feed demand was rewarded by a distribution of food or not.

It is known in mammals that when the organism detect hunger signals to initiate another meal, the level of plasmatic free fatty acids increases rapidly and a short period of hypoglycemia occurs (Geiselman 1996). The existence of an increase in fatty acids in plasma of rainbow trout just before the time of feeding is demonstrated (Boujard &

Table I. – Voluntary feed intake (VFI, mean \pm SD), voluntary energy intake (VEI, mean \pm SD), and period lengths (τ , $P < 0.05$, values for each of the 3 replicates) of the circadian feeding rhythm of groups of sea bass fed on demand unrestricted amounts of diets with low (L), medium (M) or high (H) lipid content and submitted to LL conditions (from Boujard *et al.* 2000a).

		L	M	H	<i>p</i>
VFI (% biomass.24h ⁻¹)		1.06 \pm 0.04	0.99 \pm 0.05	0.80 \pm 0.03	< 0.001
VEI (kJ.kg ⁻¹ fish.24h ⁻¹)		206 \pm 8	214 \pm 11	196 \pm 8	not significant
τ (h)	replicate # 1	25:40	22:20	22:40	not significant
	replicate # 2	22:40	26:00	arrhythmic	
	replicate # 3	arrhythmic	21:20	22:40	

Leatherland 1992c, Boujard *et al.* 1993). There is also an increase in plasma concentrations of fatty acid in the late afternoon when fish are allowed to eat only in the morning (Fig. 1). It is well known that in fish, after the ingestion of food, plasma glucose concentrations increase during several hours (Bergot 1979, Brauge *et al.* 1995, Médale *et al.* 1999), and return slowly to their pre-prandial level. It has been shown recently that pre-prandial level of plasma glucose was negatively affected, and the plasma free fatty acids was positively affected, by the duration of feed deprivation. There was a correlation between these two parameters and the subsequent growth performance (Boujard *et al.* 2000b).

One might conclude that superimposed to the rhythm of feeding is the hourglass system regulating the cycle of hunger/satiety. In the homeostatic feedback model, hunger signals are generated when a critical level of depletion is detected for some of the regulated variables. Then, when the animals are eating, there is a monitoring of the total energy and the nutrients ingested until a critical level of repletion is reached (satiety) (See Geiselman 1996 for review on the control of food intake in mammals).

Although it seems reasonable to think that these cyclic changes in nutrient flow can act more or less directly as signals for hunger, satiety and satiety in the hypothalamus, as it is suggested in the glucostatic, lipostatic and homeostatic theories (see Geiselman 1996), it is also known that several peptides and hormones are involved in the regulation of feeding activity (Table II).

Among the peptides involved in the control of satiety, Cholecystinin (CCK) is probably the most studied and can serve as an example in this review. CCK is found in peripheral and central neurons and in endocrine cells throughout the gut in numerous species, including fish (Aldman & Holmgren 1987). Two pathways have been suggested for the inhibitory effect of CCK on food intake: the action at peripheral sites, mediated by CCK-A-type receptors, and the action at central

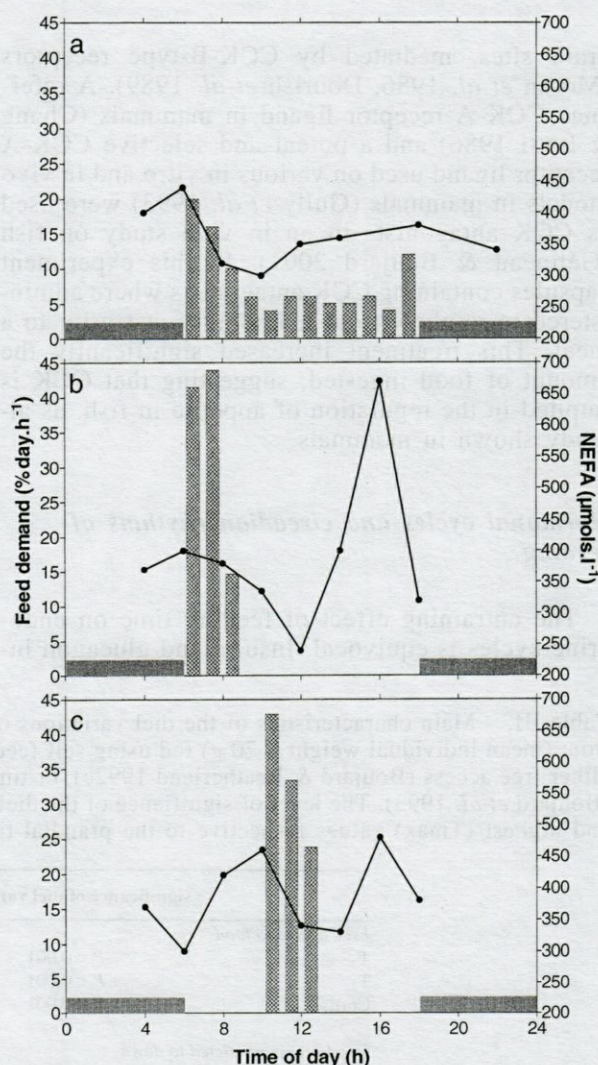


Fig.1. – Patterns of plasma non esterified free fatty acid concentrations (NEFA, full circles) and diel profile of feeding activity (histograms) in rainbow trout when food is available (a) 24h/24h, (b) between dawn and dawn +3h, and (c) between 12h and 15h. Redrawn from Boujard & Leatherland (1992c) and Boujard *et al.* 1993.

Table II. – Main hormones and peptides involved in the stimulation and in the suppression of food intake (see Geiselman 1996, LeBail & Bœuf 1997, DePetro & Björnsson 2001 for details).

Stimulation	Suppression
Aldosterone	Anorectin
Dynorphin	Bombesin
Beta-endorphin	Calcitonin
Beta-casomorphin	Cholecystokinin
Corticosterone	Corticotropin-releasing factor
Galanin	Enterostatin
Growth hormone-releasing hormone	Gastrin-releasing peptide
Insulin (short term)	Glucagon
Neuropeptide Y	Insulin (long term)
Peptide YY	Neurotensin
Thyroid hormones (long term)	Oxytocin
	Somatostatin
	Thyrotropin-releasing hormone
	Vasopressin

brain sites, mediated by CCK-B-type receptors (Moran *et al.* 1986, Dourish *et al.* 1989). A reference CCK-A receptor ligand in mammals (Chang & Lotti 1986) and a potent and selective CCK-A receptor ligand used on various *in vitro* and *in vivo* models in mammals (Gully *et al.* 1993) were used as CCK antagonists in an *in vivo* study on fish (Gélineau & Boujard 2001). In this experiment capsules containing CCK antagonists were administered to rainbow trout held singly just prior to a meal. This treatment increased significantly the amount of food ingested, suggesting that CCK is implied in the regulation of appetite in fish, as already shown in mammals.

Hormonal cycles and circadian rhythms of feeding

The entraining effect of feeding time on endocrine cycles is equivocal. Insulin and glucagon in-

fluence nutrient metabolism, and plasma concentrations are affected by feed intake (for review see Mommsen & Plisetskaya 1991, Le Bail & Bœuf 1997). Thyroid hormones (triiodothyronine [T₃], thyroxine [T₄]) are thought to play a permissive role in growth, by potentiating the effect of other anabolic hormones (Sumpter 1992). Growth hormone (GH) is considered to be a major hormone contributing to the regulation of somatic growth in teleosts (Björnsson 1997, DePedro & Björnsson 2001). Consequently, one might expect to find rhythms of these hormonal secretion that parallel those of the feeding activity. On the other hand, feeding time might have an influence on the phase or amplitude of some of these endocrine cycles, thereby affecting processes involved in energy use, and in nutrient partitioning and storage.

An effect of feeding time on circulating insulin has been reported in sea bass fed 2h or 7h after the onset of light (05:45) (Perez *et al.* 1988). A peak in plasma insulin concentration was observed around 15:00, but fish fed in the morning had their lowest plasma insulin concentration around midday, and those fed in the afternoon exhibited their lowest plasma insulin concentration around midnight. In addition, the fish fed early in the photophase had significantly lower plasma insulin concentrations than those fed later. However, according to the authors, the differences in hormonal levels might have been the result of quantitative differences in feed intake rather than to a direct effect of feeding time.

In rainbow trout fed using self-feeders, under different photoperiod regimes (Boujard & Leatherland 1992c), plasmatic concentrations in T₄ and cortisol was at their lowest level at dawn, and reached their highest values 2 to 6 hours after dawn. Plasmatic concentrations in T₃ was also very low at dawn but reached high values only 8 to 18 h

Table III. – Main characteristics of the diel variations of plasma content in T₄, T₃ and Cortisol measured in rainbow trout (mean individual weight = 70 g) fed using self feeders. The self-feeders are computer controlled in order to give either free access (Boujard & Leatherland 1992c), or time-restricted access to the food (3h/24h) at dawn or at midday (Boujard *et al.* 1993). The level of significance of the diel fluctuations is given, as well as the time of the lowest (T_{min}) and highest (T_{max}) values respective to the prandial time. n.s = not significant.

	significance of diel variations	T _{min}	T _{max}
<i>Free access to food</i>			
T ₄	P < 0.001	Pre-prandial	Post-prandial
T ₃	P < 0.001	Pre-prandial	Post-prandial
Cortisol	P < 0.001	Pre-prandial	Post prandial
<i>Food access restricted to dawn</i>			
T ₄	P < 0.001	several	Post-prandial
T ₃	n.s.	n.s.	n.s.
Cortisol	P < 0.01	several	post-prandial
<i>Food access restricted to midday</i>			
T ₄	n.s.	n.s.	n.s.
T ₃	n.s.	n.s.	n.s.
Cortisol	P < 0.01	pre-prandial	several

after dawn (Table III). There was no clear trend in plasma GH fluctuations.

In another study the relative importance of the time of feeding and the light/dark alternation as putative synchronisers of endocrine parameters were investigated in rainbow trout (Boujard *et al.* 1993). The self-feeders were programmed in such a way that they could deliver food only at certain times of the day, i.e. during the first 4 hours of the photophase or between dawn + 4 h and dawn + 7 h. A significant effect of the time of feeding was observed. This effect was not only a shift in the acrophase of the measured parameters, but mainly a decrease in the amplitude of the rhythm in the animals fed in the middle of the photophase compared to the animals fed at dawn. As an example, the diel profile of plasmatic concentration in T_4 was similar in the fish fed at dawn in comparison with those fed on demand without time restriction, but in the fish allowed to feed only in the middle of the photophase the diel variations in plasma T_4 concentrations were not significant anymore (Table III).

In a study on the effect of nocturnal vs diurnal feeding in rainbow trout (Gélineau *et al.* 1996), a

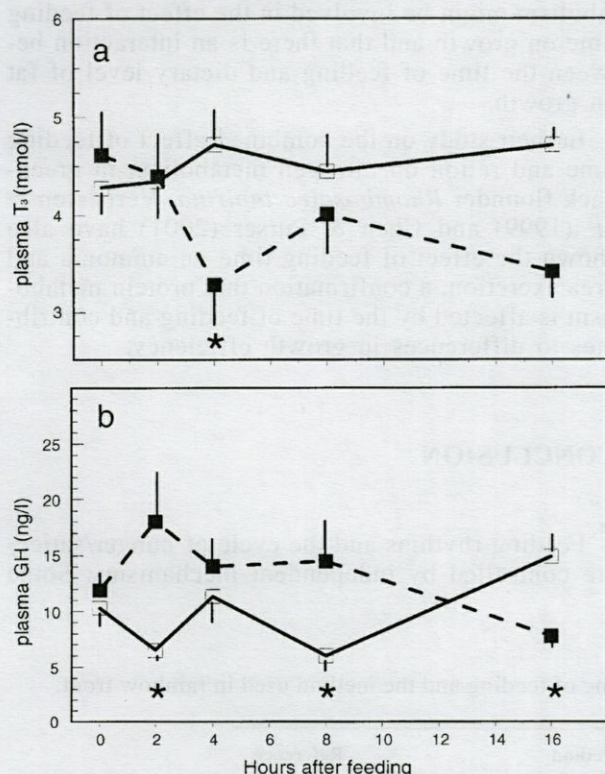


Fig. 2. – Post-prandial patterns of (a) plasma T_3 and (b) plasma GH concentrations in rainbow trout when food is distributed at dawn (full line and open squares) or at midnight (broken line and full squares). Stars indicate when differences are significant at $P < 0.05$ level and vertical bars = 1 SEM. Redrawn from Gélineau *et al.* 1996.

clear effect was found with higher plasmatic T_3 and lower plasmatic GH concentrations in fish fed at dawn than in fish fed at midnight (Fig. 2). However this result was not confirmed in another trial performed in order to characterise more in details the diel profile of GH and thyroid hormones in rainbow trout (Gomez *et al.* 1996, 1997), in relation with the time of feeding. In this additional study fish were sampled at one hour intervals during 24 consecutive hours the plasma of catheterised individuals held single. On average, two peaks of GH, three peaks of T_4 , and no peaks of T_3 were observed per 24 h. These peaks had very irregular patterns, thought more frequent during the scotophase in the case of GH, and they were not synchronised with the time of feeding.

Apart from the studies presented above, only in the work done by Reddy & Leatherland (1994, 1995) was observed a phase shift of the post-prandial peak of circulating GH related to meal timing. Studies on the diel variations of thyroid hormones are more numerous. In some species, plasma T_4 concentrations have been shown by other authors to have diel periodicity. For example, plasma T_4 concentrations in goldfish exhibited a peak at 16:00 h (Spieler & Noeske 1981). By shifting the light/dark alternation and feeding the fish always at the same time, these authors showed that the T_4 peak always appeared during the late photophase regardless of the feeding time even when fish were not fed during the sampling period (Spieler & Noeske 1984). In fact, with the exception of the study reported by Osborne and co-workers (1978), in which plasma T_4 peaked during the scotophase there seems to be a diurnal acrophase of circulating hormone regardless of feeding time.

Cook & Eales (1987) found in rainbow trout that while plasma T_4 concentration did not show a significant diel change when the fish were fasting, a diurnal acrophase was present when the fish were fed at dawn or at the middle of the photophase. However, when the same species was fed four times during the photophase, there was no evidence for a plasma T_4 diel rhythm (Leatherland *et al.* 1977). Other examples are also found in sea bass, sea bream, *Sparus auratus*, and red porgy, *Pagrus pagrus* (Pavlidis *et al.* 1997, 1999a).

If the feeding activity rhythms are driven by thyroid hormone activity rhythms, one might expect T_3 changes to be the more significant than those of T_4 , because T_4 is generally considered to be the precursor hormone for the biologically active T_3 . An effect of feeding time on plasma T_3 was reported in the goldfish (Spieler & Noeske 1981). Fish fed in the afternoon had a highly significant rhythm of circulating hormone, the highest concentration occurring at 16:00, whereas fish fed in the morning did not show any significant rhythm. Others studies in which diel profiles of plasma T_3 have been investigated in rainbow trout have revealed

either low or no fluctuations, and no effect of feeding time on the profile (Eales *et al.* 1981, Holloway *et al.* 1994, Reddy & Leatherland 1994, 1995).

Daily changes in plasma cortisol concentrations in fish appear to be related strongly to the feeding schedule in goldfish, with the peaks preceding the time of feeding by approximately 4 hours (Spieler & Noeske 1981) but not in Common dentex (*Dentex dentex*, Pavlidis *et al.* 1999b). A phase shift of light/dark alternation did not affect the timing of the peak, but it did affect the amplitude of the peak (Spieler & Noeske 1984). In rainbow trout, plasma cortisol concentrations peaked during the scotophase, but secondary peaks corresponded to the time of feeding (Bry 1982, Rance *et al.* 1982, Laidley & Leatherland 1988). A similar post-prandial peak in plasma cortisol concentrations was reported in brown trout, *Salmo trutta* by Pickering & Pottinger (1983). In brief, a peak in plasma cortisol has been observed 4h before feeding in the goldfish (Spieler & Noeske 1981, 1984), at feeding time in rainbow trout (Bry 1982, Rance *et al.* 1982, Laidley & Leatherland 1988, Boujard & Leatherland 1992c), and several hours after feeding in brown trout (Pickering & Pottinger 1983) and rainbow trout (Boujard *et al.* 1993). In goldfish and rainbow trout, it has been suggested that fluctuations in plasma cortisol concentrations might be entrained by both feeding and photoperiod (Spieler & Noeske 1984, Boujard *et al.* 1993). However, when synchrony is observed between the cortisol peak and feeding time it is difficult to know whether this is a response to feeding *per se* or whether it is an expression of stress resulting from competition for food (Boujard & Leatherland 1992c).

Time of feeding and nutrient metabolism

A series of experiments were performed in rainbow trout with the aim of studying the effect of the time of feeding on nutrient metabolism (Boujard *et al.* 1995, Gélineau *et al.* 1996, 1998, Bolliet *et al.* 2000). The better feed efficiency and nutrient retention observed in fish fed in phase with their natural feeding activity appeared to be related to protein synthesis and retention (Table IV). This was because ammonia excretion, thought to result from

a rapid oxidation of exogenous amino-acids (Brett & Zala 1975), was higher in trout fed at midnight than in those fed at dawn (Gélineau *et al.* 1998). Trout fed at dawn seemed to have a higher capacity for protein synthesis (assessed as RNA:DNA ratio, *cf.* Bulow 1987) in the liver than those fed at night (Gélineau *et al.* 1996). A reduced capacity for protein synthesis amongst fish fed at night would be expected to lead to amino acid deamination thereby leading to a less efficient use of protein for growth. In another study (Bolliet *et al.* 2000), the effect of feeding time in rainbow trout fed different dietary levels of fat on apparent digestibility efficiency and post-prandial protein synthesis was studied. Fish were fed either one hour after light on in the morning or one hour after light off in the evening with a low energy diet (LE, 6% lipid) or a high energy diet (HE, 23% lipid). Regardless of the diet, apparent digestibility and post-prandial protein synthesis were higher in fish fed in the morning than in those fed at the beginning of the night. In fish fed the LE diet in the morning, growth performance and nutrient retention efficiency tended to be higher than in those fed at the beginning of the night. In contrast, fish fed the HE diet in the morning had lower protein growth rate, protein content and protein retention efficiency than those fed in the evening. These results suggest that protein metabolism might be involved in the effect of feeding time on growth and that there is an interaction between the time of feeding and dietary level of fat on growth.

In their study on the combined effect of feeding time and ration on nitrogen metabolism in greenback flounder *Rhombosolea tapirina*, Verbeeten *et al.* (1999) and Chen & Purser (2001) have also shown the effect of feeding time on ammonia and urea excretion, a confirmation that protein metabolism is affected by the time of feeding and contributes to differences in growth efficiency.

CONCLUSION

Feeding rhythms and the cycle of hunger/satiety are controlled by independent mechanisms. Some

Table IV. – Summary of the studied variables affected by the time of feeding and the method used in rainbow trout.

	Method	Reference
Apparent digestibility	digestibility trial	Bolliet <i>et al.</i> , 2000
Ammonia excretion	indirect calorimetry measurements	Gélineau <i>et al.</i> , 1998
Capacity for protein synthesis	RNA/DNA ratio	Gélineau <i>et al.</i> , 1996
Post-prandial protein synthesis	³ H-phenylalanine injections	Bolliet <i>et al.</i> , 2000
Protein retention efficiency and protein growth rate	growth trials and carcass analysis	Boujard <i>et al.</i> , 1995 Bolliet <i>et al.</i> , 2000

metabolites, peptides and hormones appear to be directly involved in the hourglass mechanisms related to the cycle of hunger/satiety (CCK, Insulin, plasma levels of glucose, etc...). Other hormones are involved in feeding, growth and energy partitioning and they show significant daily fluctuations. But it remains very difficult to stress a clear and simple picture of the metabolic and physiological rhythms in fish. Indeed, the daily patterns of the studied parameters appears not to be consistent between the different studies. These differences may be related to the techniques used by the authors, the period of the year the experiment was performed, the age of the animal and its sexual state, etc... Further, no studies have been made in free-running conditions, so whether or not the studied parameters have endogenous rhythmicity and would continue to show diel variations in fish without food or under constant lighting conditions is not known so far.

Despite certain discrepancies, it seems that at least 2 synchronizers can be involved in the control of these fluctuations. Depending of the parameters studied, some are affected by the light/dark cycle, others by feeding-time and several appear to be under the control of both. These findings imply, as in mammals (Moore-Ede *et al.* 1976), a multi-oscillatory system in the temporal integration of fish with their environment.

If fish are in different physiological states at different times of the day, they should respond differently to food depending on the time of feeding (Spieler 1979). Accordingly, feeding fish in phase with their internal rhythms might provide the best conditions for nutrient utilisation (Bolliet *et al.* 2001 b).

Although it is believed that feeding is required for the maintenance of a rhythmic pattern of circulating hormones and metabolites (MacKenzie *et al.* 1998), the evidence for an effect of feeding time on the plasma profiles of hormones and metabolites involved in somatic growth is limited. Comparisons among studies are hampered by differences in experimental conditions; sampling interval, season, temperature, fish age and sex, reproductive stage and nutritional state. All are potentially confounding factors that may influence endocrine cycles (Perez-Sanchez *et al.* 1994).

This suggests that the examination of plasma hormone profiles may not be particularly suitable for gaining information about the mechanisms involved in the effect of feeding time on growth of fish. Investigation of hormonal receptors, gene expression or enzymatic activity might provide more pertinent information to elucidate how feeding time affects metabolism and nutrient utilisation.

REFERENCE LIST

- Aldman G, Holmgren S 1987. Control of gallbladder motility in rainbow trout, *Salmo gairdneri*. *Fish Physiol Biochem* 4: 143-155.
- Ali MA (ed) 1992. Rhythms in fishes. NATO ASI ser, Ser A, *Life Sci*, 236, Plenum Press, New York, 348 p.
- Bergot F 1979. Effects of dietary carbohydrates and of their mode of distribution on glycaemia in rainbow trout (*Salmo gairdneri* Richardson). *Comp Biochem Physiol* 64A: 543-547.
- Björnsson BT 1997. The biology of salmon growth hormone: from daylight to dominance. *Fish Physiol Biochem* 17: 9-24.
- Bolliet V, Cheewasedtham C, Houlihan D, Gélinau A, Boujard T 2000a. Effect of feeding time on digestibility, growth performance and protein metabolism in the rainbow trout *Oncorhynchus mykiss*, interactions with dietary fat levels. *Aquat Living Resour* 13: 107-113.
- Bolliet V, Aranda A, Boujard T 2001a. Demand-feeding rhythm in rainbow trout and European catfish. Synchronisation by photoperiod and food availability. *Physiol Behav* 73: 625-633.
- Bolliet V, Azzaydi M, Boujard T 2001b. Effects of feeding time on feed intake and growth. In D Houlihan, T Boujard & M Jobling eds: Food intake in fish. Blackwell Science Ltd, Oxford: 233-249.
- Boujard T 1999. Les rythmes circadiens d'alimentation chez les Téléostéens. In T Boujard & J-Y Sire eds: C r XXIIes journées de la société française d'ichtyologie. *Cybiun* 23 suppl: 89-112.
- Boujard T, Leatherland JF 1992a. Circadian rhythms and feeding time in fishes. *Env Biol Fish* 35: 109-131.
- Boujard T, Leatherland JF 1992b. Demand-feeding behaviour and diel pattern of feeding activity in *Oncorhynchus mykiss* held under different photoperiod regimes. *J Fish Biol* 40: 535-544.
- Boujard T, Leatherland JF 1992c. Circadian pattern of hepatosomatic index, liver glycogen and lipid content, plasma non-esterified fatty acids, glucose, T₃, T₄, growth hormone and cortisol concentrations in *Oncorhynchus mykiss* held under different photoperiod regimes and fed using demand feeders. *Fish Physiol Biochem* 10: 111-122.
- Boujard T, Luquet P 1996. Rythmes alimentaires et alimentation chez les siluriformes. *Aquat Living Resour* 11: 335-340.
- Boujard T, Médale F 1994. Regulation of voluntary feed intake in juvenile rainbow trout fed by hand or by self-feeders with diets containing two different protein / energy ratios. *Aquat Living Resour* 7: 211-215.
- Boujard T, Bett S, Lin L, Leatherland JF 1993. Effect of restricted access to demand-feeders on diurnal pattern of liver composition, plasma metabolites and hormone levels in *Oncorhynchus mykiss*. *Fish Physiol Biochem* 11: 337-344.
- Boujard T, Gélinau A, Corraze G 1995. Time of a single daily meal influences growth performance in rainbow trout. *Aquaculture Research* 26: 341-349.
- Boujard T, Gélinau A, Corraze C, Kaushik S, Gasset E, Coves D, Dutto G 2000a. Effect of dietary lipid

- content on circadian rhythm of feeding activity in European sea bass. *Physiol Behav* 68: 683-689.
- Boujard T, Burel C, Médale F, Haylor G, Moisan A 2000b. Effect of past nutritional history on feed intake and growth during re-alimentation challenges in rainbow trout *Oncorhynchus mykiss*. *Aquat Living Resour* 13: 129-137.
- Brauge C, Corraze G, Médale F 1995. Effect of dietary levels of lipid and carbohydrate on growth performance, body composition, nitrogen excretion and plasma glucose levels in rainbow trout reared at 8 or 18 °C. *Reprod Nutr Dev* 35: 277-290.
- Brett JR, Zala CA 1975. Daily pattern of nitrogen excretion and oxygen consumption of sockeye salmon (*Oncorhynchus nerka*) under controlled conditions. *J Fish Res Bd Can* 32: 2479-2486.
- Bry C 1982. Daily variations in plasma cortisol levels of individual female of rainbow trout *Salmo gairdneri*: Evidence for a post-feeding peak in well-adapted fish. *Gen Comp Endocrinol* 48: 462-468.
- Bulow FJ 1987. RNA-DNA ratios as indicators of growth in fish: A review. In R C Summerfelt & G E Hall eds: *The age and growth in fish*. The Iowa State University Press, Ames: 45-54.
- Chang RSL, Lotti VJ 1986. Biochemical and pharmacological characterization of an extremely potent and selective non-peptide cholecystokinin antagonist. *Proc Natl Acad Sci USA* 83: 4923-4926.
- Chen WM, Purser GJ 2001. The effect of feeding regime on growth, locomotor activity pattern and the development of food anticipatory activity in greenback flounder. *J Fish Biol* 58: 177-187.
- Cook RF, Eales JG 1987. Effects of feeding and photoperiod on diel changes in plasma thyroid hormone levels in rainbow trout, *Salmo gairdneri*. *J Exp Zool* 242: 161-169.
- DePetro N, Björnsson BT 2001. Regulation of food intake by neuropeptides and hormones. In D Houlihan, T Boujard & M Jobling eds, *Food intake in fish*. Blackwell Science Ltd, Oxford: 269-296.
- Dourish CT, Rycroft W, Iversen SD 1989. Postponement of satiety by blockade of brain cholecystokinin (CCK-B) receptors. *Science* 245: 1509-1511.
- Eales JG, Hughes M, Uin L 1981. Effect of food intake on diel variation in plasma thyroid hormone levels in rainbow trout, *Salmo gairdneri*. *Gen Comp Endocrinol* 45: 167-174.
- Falcon J, Thibault C, Begay V, Zachmann A, Collin JP 1992. Regulation of the rhythmic melatonin secretion by fish pineal photoreceptor cells. In M A Ali ed, *Rhythms in fishes*. Plenum Press, New York: 167-198.
- Gélineau A, Boujard T 2001. Oral administration of cholecystokinin receptor antagonists increase feed intake in rainbow trout. *J Fish Biol* 58: 716-724.
- Gélineau A, Mambrini M, Leatherland JF, Boujard T 1996. Effect of feeding time on hepatic nucleic acid, plasma T₃, T₄ and GH concentrations in rainbow trout. *Physiol Behav* 59: 1061-1067.
- Gélineau A, Médale F, Boujard T 1998. Effect of feeding time on postprandial nitrogen excretion and energy expenditure in rainbow trout. *J Fish Biol* 52: 655-664.
- Geiselman P 1996. Control of food intake. A physiologically complex, motivated behavioral system. *End Met Clin North Am* 25: 815-829.
- Gomez JM, Boujard T, Fostier A, Bail PY 1996. Characterization of growth hormone nycthemeral plasma profiles in catheterized rainbow trout (*Oncorhynchus mykiss*). *J Exp Zool* 274: 171-180.
- Gomez JM, Boujard T, Bœuf G, Solari A, Le Bail PY 1997. Individual diurnal plasma profiles of thyroid hormones in rainbow trout (*Oncorhynchus mykiss*) in relation to cortisol, growth hormone and growth rate. *Gen Comp Endocrinol* 107: 74-83.
- Gully D, Fréhel D, Marcy C, Spinazzé A, Lespy L, Neliat G, Maffrand JP, Le Fur G 1993. Peripheral biological activity of SR 27897: a new potent non-peptide antagonist of CCK_A receptors. *Europ J Pharmacol* 232: 13-19.
- Hoar WS 1942. Diurnal variations in feeding activity of young salmon and trout. *J Fish Res Bd Can* 6: 90-101.
- Holloway AC, Reddy PK, Sheridan MA, Leatherland JF 1994. Diurnal rhythms of plasma growth hormone, somatostatin, thyroid hormones, cortisol and glucose concentrations in rainbow trout, *Oncorhynchus mykiss*, during progressive food deprivation. *Biol Rhythm Res* 25: 415-432.
- Laidley CW, Leatherland JF 1988. Circadian studies of plasma cortisol, thyroid hormone, protein, glucose and ion concentration, liver glycogen concentration and liver and spleen weight in rainbow trout, *Salmo gairdneri* Richardson. *Comp Biochem Physiol* 89A: 495-503.
- Leatherland JF, Cho CY, Slinger SJ 1977. Effects of diet, ambient temperature, and holding conditions on plasma thyroxine levels in rainbow trout (*Salmo gairdneri*). *J Fish Res Bd Can* 34: 677-682.
- LeBail PY, Bœuf G 1997. What hormones may regulate food intake in fish? *Aquat Living Resour* 10: 371-379.
- Madrid JA, Boujard T, Sanchez-Vasquez J 2001. Feeding rhythms in fish. In D Houlihan, T Boujard & M Jobling eds, *Food intake in fish*. Blackwell Science Ltd, Oxford: 189-215.
- MacKenzie DS, VandenPutte CM, Leiner KA 1998. Nutrient regulation of endocrine function in fish. *Aquaculture* 161: 3-25.
- Mommsen TP, Plisetskaya EM 1991. Insulin in fishes and agnathans: history, structure and metabolic regulation. *Rev Aqua Sci* 4: 225-259.
- Moore-Ede MC, Schmelzer WS, Kass DA, Herd JA 1976. Internal organization of the circadian timing system in multicellular animals. *Fed Proc* 35: 2333-2338.
- Moran TH, Robinson PH, Goldrich MS, McHugh PR 1986. Two brain cholecystokinin receptors: implications for behavioral actions. *Brain Res* 362: 175-179.
- Médale F, Poli JM, Vallée F, Blanc D 1999. Comparaison de l'utilisation digestive et métabolique d'un régime riche en glucides par la carpe à 18°C et 25°C. In T Boujard & J-Y Sire eds, *C r XXIIes journées de la soc française d'ichtyologie*. *Cybium* 23 suppl: 139-152.
- Osborn RH, Simpson TH, Youngson AF 1978. Seasonal and diurnal rhythms of thyroidal status in the rainbow trout, *Salmo gairdneri* Richardson. *J Fish Biol* 12: 531-540.

- Paspatis M, Boujard T 1996. comparative study of automatic feeding and self-feeding in juvenile Atlantic salmon (*Salmo salar*) fed diets of two different energy levels. *Aquaculture* 145: 245-257.
- Pavlidis M, Berry M, Divanach P, Kentouri M 1997. Diel pattern of haematocrit, serum metabolites, osmotic pressure, electrolytes and thyroid hormones in sea bass and sea bream. *Aquac Int* 5: 237-247.
- Pavlidis M, Paspatis M, Koistinen M, Paavola T, Divanach P, Kentouri M 1999a. Diel rhythms of serum metabolites and thyroid hormones in red porgy held in different photoperiod regimes. *Aquac Int* 7: 29-44.
- Pavlidis M, Greenwood L, Paalavuo M, Mölsä H, Laitinen JT 1999b. The effect of photoperiod on diel rhythms in serum melatonin, cortisol, glucose, and electrolytes in the common dentex, *Dentex dentex*. *Gen Comp Endocrinol* 113: 240-250.
- Perez J, Zanuy S, Carrillo M 1988. Effects of diet and feeding time on daily variations in plasma insulin, hepatic c-AMP and other metabolites in a teleost fish, *Dicentrarchus labrax* L. *Fish Physiol Biochem* 5: 191-197.
- Perez-Sanchez J, Marti-Palanca H, Le Bail PY 1994. Seasonal changes in circulating growth hormone (GH), hepatic GH-binding and plasma insulin-like growth factor-I immunoreactivity in a marine fish, gilthead sea bream, *Sparus aurata*. *Fish Physiol Biochem* 13: 199-208.
- Pickering AD, Pottinger TG 1983. Seasonal and diel changes in plasma cortisol levels of the brown trout, *Salmo trutta* L. *Gen Comp Endocrinol* 49: 232-239.
- Rance TA, Baker BI, Webley G 1982. Variations in plasma cortisol concentrations over a 24-hour period in the rainbow trout *Salmo gairdneri*. *Gen Comp Endocrinol* 48: 269-274.
- Reddy PK, Leatherland JF 1994. Does the time of feeding affect the diurnal rhythms of plasma hormone and glucose concentration and hepatic glycogen content of rainbow trout? *Fish Physiol Biochem* 13: 133-140.
- Reddy PK, Leatherland JF 1995. Influence of the combination of time of feeding and ration level on the diurnal hormone rhythms in rainbow trout. *Fish Physiol Biochem* 14: 25-36.
- Sánchez-Vázquez FJ, Madrid JA 2001. Feeding anticipatory activity in fish. In D Houlihan, T Boujard & M. Jobling eds, Food intake in fish. Blackwell Science Ltd, Oxford: 216-232.
- Sánchez-Vázquez FJ, Tabata M 1998. Circadian rhythms of demand-feeding and locomotor activity in rainbow trout. *J Fish Biol* 52: 255-267.
- Sánchez-Vázquez FJ, Madrid JA, Zamora S, Iigo M, Tabata M 1996. Demand feeding and locomotor circadian rhythms in the goldfish, *Carassius auratus*: Dual and independent phasing. *Physiol Behav* 60: 665-674.
- Sánchez-Vázquez FJ, Madrid JA, Zamora S, Tabata M 1997. Feeding entrainment of locomotor activity rhythms in the goldfish is mediated by a feeding-entrainable circadian oscillator. *J Comp Physiol* 181A: 121-132.
- Sánchez-Vázquez FJ, Aranda A, Madrid JA 2001. Differential effects of meal size and food energy density on feeding entrainment in goldfish. *J Biol Rhythms* 16: 58-65.
- Spieler RE 1979. Diel rhythms of circulating prolactin, cortisol, thyroxine, and triiodothyronine levels in fishes: a review. *Rev Can Biol* 38: 301-315.
- Spieler RE 1992. Feeding-entrained circadian rhythms in fishes. In M A Ali ed, Rhythms in fishes. Plenum Press, New York: 137-148.
- Spieler RE, Noeske TA 1981. Timing of a single daily meal and diel variations of serum thyroxine, triiodothyronine and cortisol in goldfish, *Carassius auratus*. *Life Sci* 28: 2939-2944.
- Spieler RE, Noeske TA 1984. Effects of photoperiod and feeding schedule on diel variations of locomotor activity, cortisol, and thyroxine in goldfish. *Trans Am Fish Soc* 113: 528-539.
- Sumpter JP 1992. Control of growth of rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 100: 299-320.
- Thorpe JE (ed) 1978. Rhythmic activity of fishes, Academic press, London, 312 p.
- Verbeeten BE, Carter CG, Purser GJ 1999. The combined effect of feeding time and ration on growth performance and nitrogen metabolism of greenback flounder. *J Fish Biol* 55: 1328-1343.

Reçu le 9 mai 2001; received May 9, 2001

Accepté le 11 juin 2001; accepted June 11, 2001