DAILY FEEDING RHYTHMS AND FISH PHYSIOLOGY
Thierry Boujard

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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.

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, O2, 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-Vazquez et al. 1996), rainbow trout, Oncorhynchus mykiss (Sanchez-Vazquez & 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) comprised 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 physiological 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 physiological 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 plasma free fatty acids increases rapidly and a short period of hypoglycaemia 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 ± SD), voluntary energy intake (VEI, mean ± 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).

<table>
<thead>
<tr>
<th></th>
<th>L</th>
<th>M</th>
<th>H</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>VFI (% biomass.24h⁻¹)</td>
<td>1.06 ± 0.04</td>
<td>0.99 ± 0.05</td>
<td>0.80 ± 0.03</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>VEI (kJ kg⁻¹ fish.24h⁻¹)</td>
<td>206 ± 8</td>
<td>214 ± 11</td>
<td>196 ± 8</td>
<td>not significant</td>
</tr>
<tr>
<td>τ (h)</td>
<td>replicate # 1</td>
<td>25:40</td>
<td>22:20</td>
<td>22:40</td>
</tr>
<tr>
<td></td>
<td>replicate # 2</td>
<td>22:40</td>
<td>26:00</td>
<td>arrhythmic</td>
</tr>
<tr>
<td></td>
<td>replicate # 3</td>
<td>arrhythmic</td>
<td>21:20</td>
<td>22:40</td>
</tr>
</tbody>
</table>

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 (satiation) (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, satiation 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, Cholecystokinin (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, Le Bail & Breuf 1997, DePetro & Björnsson 2001 for details).

<table>
<thead>
<tr>
<th>Stimulation</th>
<th>Suppression</th>
</tr>
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<tbody>
<tr>
<td>Aldosterone</td>
<td>Anorectin</td>
</tr>
<tr>
<td>Dynorphin</td>
<td>Bombesin</td>
</tr>
<tr>
<td>Beta-endorphin</td>
<td>Calcitonin</td>
</tr>
<tr>
<td>Beta-casomorphin</td>
<td>Cholecystokinin</td>
</tr>
<tr>
<td>Corticosterone</td>
<td>Corticotropin-releasing factor</td>
</tr>
<tr>
<td>Galanin</td>
<td>Enterostatin</td>
</tr>
<tr>
<td>Growth hormone-releasing hormone</td>
<td>Gastrin-releasing peptide</td>
</tr>
<tr>
<td>Insulin (short term)</td>
<td>Glucagon</td>
</tr>
<tr>
<td>Peptide YY</td>
<td>Insulin (long term)</td>
</tr>
<tr>
<td>Thyroid hormones (long term)</td>
<td>Neurotensin</td>
</tr>
<tr>
<td></td>
<td>Oxytocin</td>
</tr>
<tr>
<td></td>
<td>Somatostatin</td>
</tr>
<tr>
<td></td>
<td>Thyrotropin-releasing hormone</td>
</tr>
<tr>
<td></td>
<td>Vasopressin</td>
</tr>
</tbody>
</table>

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 where 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 influence nutrient metabolism, and plasma concentrations are affected by feed intake (for review see Mommsen & Plisetskaya 1991, Le Bail & Breuf 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 T3 and cortisol was at their lowest level at dawn, and reached their highest values 2 to 6 hours after dawn. Plasmatic concentrations in T4 was also very low at dawn but reached high values only 8 to 10 h after dawn.

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 (Tmin) and highest (Tmax) values respective to the prandial time. n.s. = not significant.

<table>
<thead>
<tr>
<th>significance of diel variations</th>
<th>Tmin</th>
<th>Tmax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Free access to food</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T4</td>
<td>P &lt; 0.001</td>
<td>Pre-prandial</td>
</tr>
<tr>
<td>T3</td>
<td>P &lt; 0.001</td>
<td>Pre-prandial</td>
</tr>
<tr>
<td>Cortisol</td>
<td>P &lt; 0.001</td>
<td>Pre-prandial</td>
</tr>
</tbody>
</table>

| Food access restricted to dawn  |      |      |
| T4                             | P < 0.001 | several | Post-prandial |
| T3                             | n.s.    | n.s.   | n.s.           |
| Cortisol                       | P < 0.01 | several | post-prandial |

| Food access restricted to midday|      |      |
| T4                             | n.s.  | n.s.  | n.s.           |
| T3                             | 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 synchronizers 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 T₄ 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 T₄ 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 clear effect was found with higher plasmatic T₃ 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 detail 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 T₄, and no peaks of T₃ 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 T₄ concentrations have been shown by other authors to have diel periodicity. For example, plasma T₄ 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 T₄ 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 T₄ 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 T₄ 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 T₄ 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 T₃ changes to be the more significant than those of T₄, because T₄ is generally considered to be the precursor hormone for the biologically active T₃. An effect of feeding time on plasma T₃ 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. Other studies in which diel profiles of plasma T₃ have been investigated in rainbow trout have revealed

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
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.

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