

Entrainment of the circadian rhythm of food demand by infradian cycles of light-dark alternation in *Hoplosternum littorale* (Teleostei)

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Abstract

Hoplosternum littorale (Hancock, 1828) shows a marked circadian rhythm of food demand. Feeding activity is mainly nocturnal, with two peaks, and is synchronized with the diel light cycle. We tested the effect of infradian (period > 28 h) light/dark cycles on this rhythm in fish with demand-feeders: fish subjected to a 13.5 L/22.5 D light/dark cycle for 8 days and a 25.5 L/10.5 D cycle for a further 8 days showed a strictly nocturnal feeding activity, a response that only passively reflected the cyclic alternation of light and dark.

Keywords : Siluriform, diel cycle, feeding rhythms.

Synchronisation du rythme circadien d'auto-distribution d'aliments par des cycles infradiens d'éclairage chez Hoplosternum littorale (Teleostei).

Résumé

Hoplosternum littorale (Hancock, 1828) présente un rythme circadien marqué d'auto-distribution de nourriture. Ce rythme, à acrophase nocturne, se caractérise par deux pics, il est synchronisé par l'alternance jour/nuit de la lumière. Nous avons mis à l'épreuve le caractère circadien (24 ± 4 h) de ce rythme à l'aide de distributeurs d'aliments « à la demande ». Les poissons soumis à un éclairage simulant la photopériode naturelle (13.5 J/10.5 N) ont un rythme circadien d'auto-distribution d'aliments. Lorsqu'ils sont sujets à un cycle d'éclairage infradien (période > 28 h) à longue scotophase (13.5 J/22.5 N) durant 8 jours, puis à longue photophase (25.5 J/10.5 N) durant 8 autres jours, ils ont un cycle d'auto-distribution d'aliments qui est entraîné sans délai par les changements successifs de cycles d'éclairage, et se nourrissent exclusivement durant les scotophases.

Mots-clés : Siluriforme, rythmes circadiens, cycles nyctéméraux, alimentation.

INTRODUCTION

A circadian rhythm (24 ± 4 hrs.) is characterized by its amplitude, mean value (or Mesor) and acrophase (Gwinner, 1986; Halberg *et al.*, 1977; Koukkari *et al.*, 1987). It is generally synchronized by photoperiod (or

alternation of day and night, or dawn, or dusk) or temperature (Randolph and Clemens, 1976). It may be endogenous, *i. e.*, persisting with its own period in constant environmental conditions, or exogenous if it only passively reflects the cyclic fluctuations of the environment. Circadian rhythms have been demon-

strated in a variety of eukaryotes, with most applications in the field of chronopharmacology. Spieler (1977), and later Parker (1984), suggested that such rhythms could be used to improve production efficiency in aquaculture.

The feeding periods of fish living in natural environments follow a marked diel cycle (Elliott, 1973; Müller, 1978; Jacob and Nair, 1983; Sagar and Glova, 1988; Walsh *et al.*, 1988). In artificial rearing conditions, and with the exception of Rozin and Mayer (1961) who found no circadian rhythm in the feeding activity of *Carassius auratus*, most other authors report strong circadian patterns of feeding in fish (Hoar, 1942; Adron *et al.*, 1973; Hirata, 1973; Landless, 1976; Grove *et al.*, 1978; Eriksson and Van Veen, 1980; Boujard *et al.*, 1990). Light/dark alternation is generally thought to be the main synchronizer (Gibson and Keenleyside, 1966; Chaston, 1968; Mantefel *et al.*, 1978; Müller, 1978; Molina Borja *et al.*, 1990), and in *Carassius auratus*, feeding rhythm is free-running for at least 5 days (Spieler and Clougherty, 1989). Meal times also affect growth rates (Ottaway, 1978; Greenland and Gill, 1979; Noeske *et al.*, 1981; Sundararaj *et al.*, 1982; Noeske and Spieler, 1984; Noeske-Hallin *et al.*, 1985), and can act as a synchronizer for several behavioural parameters (Weber and Spieler, 1987; Spieler and Clougherty, 1989) and for a large number of circulating hormones (Leatherland *et al.*, 1974; Spieler, 1977; Spieler *et al.*, 1977; Eales *et al.*, 1981; Spieler and Noeske, 1981, 1984; Perez *et al.*, 1988).

On the basis of these observations, and with the aim of improving the production of *Hoplosternum littorale*, a siluriform fish of economic interest for French Guiana (Boujard *et al.*, 1988), the circadian rhythm of food intake in this species was described using demand-feeders checked every 3 hours (Boujard *et al.*, 1990): food demand, synchronized by day-night shifts, was characterized by a nocturnal acrophase. Using the same device as in the previous experiment, but with automatic recording of the self-distributed food, we tested the effect of infradian (period > 28 hrs.) light/dark cycles on this rhythm.

MATERIAL AND METHODS

Four groups of 10 *Hoplosternum littorale* that had been hatched in the laboratory and reared in ponds (mean weight 49 g) in French Guiana at the Socoumou Farm (5°N, 52°30'W) were distributed into 200-l tanks, on the 18th of January 1990. The tanks were continuously supplied with recycled water (temperature 28 ± 2°C, oxygen at saturation) and held in a light-tight room with artificial lighting provided by four 50 watt neon tubes controlled by an electric timer. For a period of 12 days, the fish were subjected to a 24 hrs. light cycle that simulated the natural photoperiod (13.5 L/10.5 D). The light cycle was

thereafter changed to a 36 hrs. light cycle with a longer scotophase for a period of 8 days from the 30th of January 1990 (13.5 L/22.5 D), and subsequently to a cycle of 36 hrs. with a longer photophase for another period of 8 days, from the 7th of February 1990 (25.5 L/10.5 D).

Each tank was fitted with a metal rod which closed a 12 V circuit when a fish moved the rod. A 220 V feeder delivered 1 g of food via a relay. This device was coupled to a computer, which recorded the hour, date and tank number of each demand for food. In order to restrict unintentional triggering of the feeder by the fish, the rod was located 2 cm below the water surface, *i.e.*, far from the usual zone of activity of this bottom dweller fish. Furthermore, the tank design was such that unconsumed food pellets were constantly drained from the tanks with the water overflow. We therefore know that the consumption of food could take place only within a few minutes after demand-feeding. Operators entered the experimental room only every 3-4 days and hence the fish were disturbed very little during the experiment.

RESULTS

The timing of food demand during the three consecutive periods with different light cycles, from the 22nd January to the end of the experiment, is shown in *figure 1*. Regardless of the lighting cycle, self-feeding always took place throughout the phase of darkness and was infrequent during the light phases.

Figure 2 shows the distribution of food demand during the scotophases for each of the three conditions. When the lighting cycle simulated the natural photoperiod, food demand followed the same timing as that observed by Boujard *et al.*, (1990), *i.e.*, a significantly bimodal feeding activity ($p < 0.05$; sign-test) with a "dusk" peak and a second phase of self-feeding during the second part of the scotophase. When the fish were subjected to a 36 hrs. cycle of lighting with a longer scotophase, self-feeding remained constant throughout the nocturnal period. During 36 hrs. cycles of lighting with longer photophases, the "dusk" peak of feeding activity was again marked.

The amount of self-distributed food per hour varied during the scotophases of each situation. It was very high when the phase of light was prolonged and low with a longer phase of darkness. However, these differences were not significant ($p < 0.05$; sign-test) because the between-group variability was very high. Nevertheless, it can be interpreted as the expression of a compensation maintaining the 24 h-consumption (ranging between 3.4 and 4.0% of live weight) at a constant level (*table 1*). Similarly, the dusk peak of self-feeding observed after the long photophases might be the consequence of the long fasting observed during the light periods.

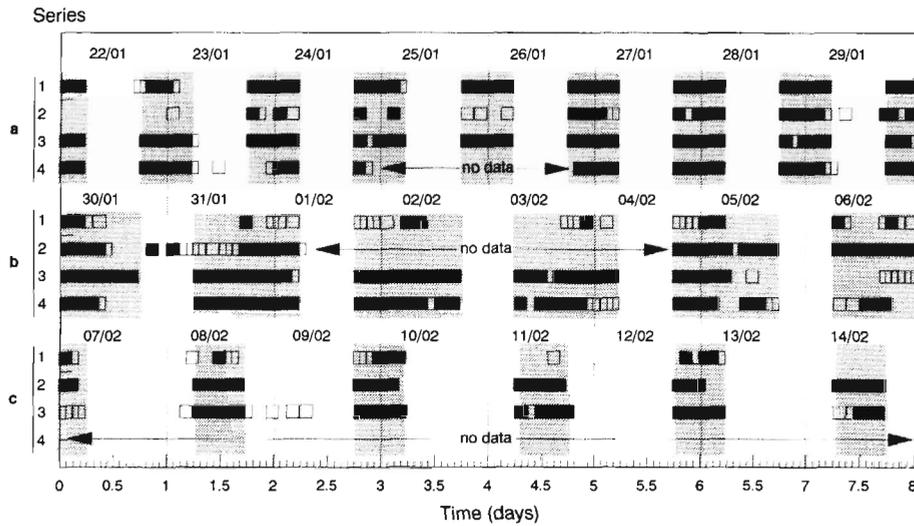


Figure 1. – Timing of the self-distribution of food during the different lighting regimes and for the 4 groups of 10 fish studied. Black squares indicate hours during which more than 1g was demanded, white squares indicate hours during which only 1g was demanded. Scotophase corresponds to the hatched parts of the graph.

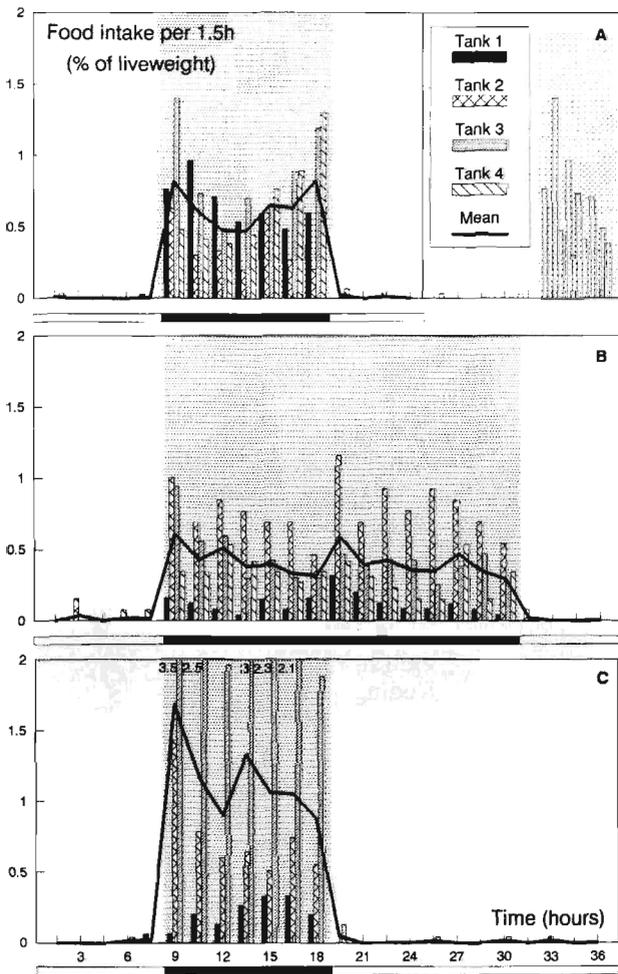


Figure 2. – Quantity of food self-distributed in each series expressed in % of live weight per 1.5hrs. during: A) 24hrs. cycle; 13.5L/10.5D; tanks 1, 2, 3, 4. B) 36hrs. cycle; 13.5L/22.5D; tanks 1, 2, 3, 4. C) 36hrs. cycle; 25.5L/10.5D; tanks 1, 2, 3.

Table 1. – Mean amounts of self-distributed food expressed as % of live weight per unit time.

Total duration of the light/dark cycle (hrs.)	24.0	36.0	36.0
Length of the scotophase (hrs.)	10.5	10.5	22.5
Food-demand per hours during the scotophase	0.37	0.57	0.24
Food-demand/24 hrs.	3.9	4.0	3.4

The high variability in food demand between tanks and days was caused by moisture in the device, which happened in tank 4 on 25th and 26th January, in tank 2 on 2nd and 3rd February, and in tank 4 between 7th and 14th February. During these periods, the fish were not able to obtain food on demand. The observed differences of food demand between tanks were high, especially during the last phase of the experiment. This was probably also caused by moisture in the device, making it more or less difficult for the fish of the different tanks to close the 12 V line. However, if these experimental failures restrict the significance of the results in terms of amount of food demand, they do not affect at all the significance of the temporal variations of the demand.

DISCUSSION

The endogenous aspect of a diel cycle is generally tested with isolated individuals in a constant environment (Millet and Manachere, 1983; Koukkari *et al.*, 1987). In such a “free-running” situation, endogenous rhythms are revealed by their specific periodicity, each individual within a given species tending to exhibit a slightly different periodicity. In the case of *Hoplosternum littorale*, individuals isolated from their congeners did not use the rod to demand food and

starved (unpublished data). Moreover, social interactions appear to be important in *Callichthyidae* (Kramer and Graham, 1976). In *Hoplosternum littorale* reared in ponds, one can see air-breathing fish moving in shoals of 10 to 25 individuals, swimming close to the bottom, and periodically moving up to the surface one after the other (unpublished data).

In our experiment, in the case of an endogenous rhythm a decrease in self-feeding was expected to be observed during late scotophase when the latter is prolonged, or an onset of self-feeding was expected during late photophase when that phase is prolonged. Neither of these two responses were obtained, and

the circadian rhythm of food intake was synchronized by an external and periodical stimulation, the light. As a result, in *Hoplosternum littorale*, feeding activity might be an exogenous rhythm, and if not, it is only weakly coupled to an endogenous oscillator, with a masking effect of the photophase. The strong relationship between scotophase and feeding emphasize the fact that this species is truly nocturnal, and in rearing conditions, feeding the fish by night might improve survival or growth, but this hypothesis remains to be tested in ponds. Nevertheless, our results show that artificially increasing the scotophase length does not increase daily food consumption.

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