FEEDING-ENTRAINED CIRCADIAN RHYTHMS IN FISHES

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INTRODUCTION

There has been sufficient work done in fishes to warrant a review of feeding-entrained rhythmicity, if only for comparative reasons. Relative to the extensive work with laboratory mammals, however, information on this topic in fishes is meager. An attempt at a broad overview at this point is fated from the outset to be data poor and speculation rich; hopefully this paper will, nevertheless, serve a heuristic role. Specifically, the paper addresses five questions regarding feeding entrainment of circadian rhythms in fishes: Does feeding entrain rhythms in fishes? How? Why? So what? and What next?

DOES FEEDING ENTRAIN CIRCADIAN RHYTHMS IN FISHES?

The answer is a qualified yes; in some fishes meal-feeding can entrain some rhythms. Like other vertebrates, most fishes have a circadian locomotor activity rhythm; and, it has been established that for a number of species, this rhythm is under endogenous control and entrainable by the light-dark cycle (i.e. Schwassmann 1971, Nishikawa and Ishibashi 1975, Kavaliers 1981, Spieler and Noeske 1984). There are some early studies (Spencer 1939, Spoor 1946) which examined the effects of meal-feeding on activity rhythms of individual goldfish, *Carassius auratus*. Spencer (1939) related that feeding produced a prolonged bout of activity directly after feeding, but Spoor (1946) did not find a consistent effect of feeding, or the timing of feeding, on activity rhythms. The first in depth examination of feeding entrainment in fishes was, however,the work of Davis and Bardach in the early 1960s. They examined the effect of feeding a single daily meal on locomotor activity rhythms in five species of marine fishes. Three species, tomcod (*Microgadus tomcod*), scup (*Stenotomus versicolor*) and mummichog (*Fundulus heteroclitus*), entrained to the feeding time with a prefeeding bout of activity. In mummichog, this activity could be entrained under constant light conditions (Davis and Bardach 1965).

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Since that landmark report, feeding-entrained activity rhythms have been reported for several other species. Winslade (1974) found an endogenous rhythm of activity in the lesser sandeel, *Ammodytes marinus*, which was reinforced by feeding. Nishikawa and Ishibashi (1975) reported that feeding one or two meals a day entrained crawling activity of mud-skippers, *Periophthalmus cantonensis*. Activity clustered within a few hours prior to the feeding time, and this pre-feeding activity persisted, under constant light conditions, even after the daily feeding ceased.

The activity rhythms of several species of cyprinids have been reported to be entrained to meal feeding. Both silver carp, *Hypophthalmichthys molitrix*, and common carp, *Cyprinus carpio*, were entrained to a single daily meal. Both species displayed either a prefeeding peak or ramping increase in activity and the common carp maintained the feeding entrainment under constant light conditions (Warthold 1980, Lange 1980, Robel 1981; cited in Zabka and Siegmund 1983).

Likewise with goldfish, the author and collaborators, have demonstrated that meal feeding a single daily meal is a potent entraining stimulus for a group of fish. Groups of goldfish (12 per feeding regime) fed at one of four times during the light-dark cycle entrained to the feeding time and maintained that entrainment through a ten-day fast (Spieler and Noeske 1984). When fed on a similar schedule, but allowed to free-run on constant light or dark, most groups remained entrained to the time-of-feeding for several days of fasting (Spieler and Clougherty 1989).

In addition to generalized locomotor rhythms, several specific behavioral rhythms in fishes have been demonstrated to be entrained by feeding. Pradhan and coworkers (1989) found a circadian rhythm of phototaxis in a cave fish, *Nemacheilus evezardi*; this rhythm was phase shifted by a period of restricted feeding (4h). With medaka, *Oryzias latipes*, meal-feeding readily entrained a circadian rhythm of agonistic behavior that remained fixed to the feeding time through a three-day fast (Weber and Spieler 1987). In the same study, however, the daily rhythms of courtship and egglaying did not phase-shift in response to meal-feeding but remained fixed to the light-dark cycle.

This latter report highlights an important cautionary note concerning work on entraining stimuli, feeding or otherwise, of circadian activity rhythms. Most researchers are dealing with locomotor activity in fishes as a single circadian rhythm. Yet there are multiple behavioral components of that rhythm (i.e. feeding, reproduction, territoriality, etc) that may be connected to different oscillator systems and which can be entrained by different stimuli (eg. light-dark or eat-fast cycles).

There are several physiological variables in fishes which are apparently also entrained by feeding. Most notable among these is the daily rhythm of circulating cortisol. With goldfish, a series of studies has demonstrated that this rhythm, similar to locomotor activity rhythms, is entrainable to the light-dark cycle if the animals are held on a random feeding regime (Noeske and Spieler 1983). If, however, feeding is restricted to a single daily meal the animals will entrain to the feeding time regardless of the phase angle of this time to the light-dark cycle (Spieler and Noeske 1981,1984). With goldfish, the acrophase of the cortisol rhythm usually occurs about 4-6 h prior to the feeding time (presumably directly prior to the pre-feeding activity) (Delahunty et. al. 1978, Spieler and Noeske 1981, 1984). A similar acrophase (5-9 h before feeding) is apparent in a seasonal study of brown trout, *Salmo trutta* (Pickering and Pottinger 1983). This pre-feeding acrophase timing (but not the feeding entrainment per se) differs from two reports in rainbow trout, *Oncorhynchus mykiss* (= *Salmo gairdneri*) which describe peaks of circulating cortisol about the time of feeding (Bry 1982, Laidley and