

TIME-CO-ORDINATED PREFEEDING ACTIVITY IN FISH

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Introduction

Field and laboratory investigations have revealed numerous daily rhythms in the physiology and behaviour of fishes which parallel daily changes in natural light (e.g. Barlow, 1958; Carlander & Cleary, 1949; Harder & Hempel, 1954; Jones, 1956; Kawamoto & Konishi, 1955; Welsh & Osborn, 1937). The wide occurrence in other animals of circadian rhythms, which rely on a biological clock, has led to more closely controlled laboratory work on the role of exogenous and endogenous components of daily rhythms in fishes. A biological clock has been demonstrated in the sun orientation rhythm of fish (Hasler & Schwassman, 1960) and also in their responses to 24 hour periodicities of light and feeding in the laboratory (Davis, 1963). Bluegills and largemouth bass kept under alternating 12-hour periods of bright and dim light and fed daily at the start of the light period show a daily increase in locomotion 1 to 3 hours before light and feeding time in 10 to 20 days. Experimental changes in the light and feeding cycles suggested that the timing of the activity is regulated from within the fish by a time sense which itself is co-ordinated by the daily change from dim to bright light. The present paper reports the outcome of studies with marine and freshwater fishes which indicate that this daily pre-light-pre-feeding activity is a consequence of regular daily feeding.

Material and Method

Automatically Recorded Observations

Adult fishes of the species listed in Table I were stored in salt water tanks at 16 to 17°C for one week to several months. In storage the fish had irregular daily changes in artificial and diffuse natural light and they were fed several times a week. The experiments were conducted in a darkened room where the fish were confined individually or in groups of 2 or 3 to aquaria in 6 separate light-tight chambers. The 30 × 60 cm. aquaria were filled to 30 cm. with running sea water from a large tank above the chambers. Water temperature was regulated with heaters in the overhead tank, and a thermistor coupled

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with a chart recorder kept a continuous record of the water temperature in one of the 6 chambers; temperature varied between 19 and 23° during the months of testing without a detectable daily cycle. At the rear of each experimental tank there was an overflow pipe and 2 platforms under which the fish could hide. The front end of the tank was beneath a feeding hole recessed in the chamber door.

Daily light schedules will be described with abbreviated notations. For example, a daily cycle, of 12 hours of bright light and 12 hours of dim light (to be called 'darkness') is described as LD': 12-12. 'Darkness' (D') was given by an NE-2 voltage indicator which burned continuously with a dim red-orange glow; the intensity was not measured. In the light period (L) or in constant light (LL) a 25 watt, white incandescent lamp gave light of 50 to 100 lux at the water surface; this lamp was connected to a timer which regulated the LD' cycles.

During experiments the fish were fed a variety of fresh and frozen chopped fish, clam, and squid at specified times of day. Where feeding is noted to occur at the onset of the light period (onset L) it in fact was given 1-2 minutes later to avoid exciting fish recovering from the sudden increase in light intensity. Food was dropped through the feeding hole into the front end of the tank, and the response to feeding was observed through a small mirrored window beneath the door. After feeding the feeding hole and the window were covered and the recording instruments and water flow were inspected. Debris in the tanks was removed with a siphon just after a feeding on days when the chambers were opened for other repairs. Ordinarily feeding the fish and maintaining the instruments took less than 10 minutes, and other than at feeding times the room was rarely entered.

Activity Recording

The locomotion detector and the recording instruments were essentially the same as those described by Davis (1963). The detector was a network of rubber bands on a 10 × 30 cm. wire frame. It was suspended in the water from a rigid support with 2 rubber bands, one end above the water, the other end near the bottom of the tank. A silver wire contact on top of the frame

touched a second contact on the rigid support, and when the fish pushed the detector the contacts separated. Contact disturbances were relayed through a thyatron circuit to an Esterline-Angus operation recorder. Two locomotion detectors, wired to work as a unit, were placed at an angle to one another in the feeding area at the front of each fish tank.

The discharges of the individual thyatrons, representing the locomotion of fish in the feeding areas of different chambers, were recorded at a chart speed of 1.9 cm./hr. Continuous records were kept in each experiment. The daily records were placed one beneath the other on sheets of cardboard and photographically reduced.

Direct Observations

Thirty-two, newly captured, adult bluegill (*Lepomis m. macrochirus*) were placed in individual 19-litre tanks. The tanks were stacked in 4 rows of 8 in a constant temperature room (16°C). A wall of plywood with mirrored windows in front of the tanks isolated them from light in the room. Opaque partitions between the tanks prevented fish from seeing one another. Electric lamps lighted the front of the tanks continuously with light of 50 to 100 lux. The fish were fed earthworms and wet pellets of trout food mixed with fresh liver. Food was presented through opaque tubes which sloped down into the tanks from outside the plywood wall.

Levels of locomotion were evaluated by direct observation and recorded on tape during specified 1-hour periods prior to the daily feeding; 16 fish were fed in the morning (Group 1) and 16 in the evening (Group 2). The tapes were transcribed by 2 people independently to quantify the level of locomotion during the 1-hour periods. Where estimates differed, the mean score was taken. Six levels of activity were noted: Stationary fish scored 0, active fish were ranked from 1 to 5 with the nearly continuous and greatly active individuals receiving the highest score. The scores of the 2 groups were compared in a 2-way variance analysis and tests for least significant differences.

Results

1. Preliminary Studies

A variety of marine fishes were kept under LD' 12-12 with different feeding schedules for 1 to 2 months in a search for suitable experimental subjects. Some fish were fed daily at onset L throughout a test, and others were fed at

irregular times in L for the first 23 days and then daily at onset L. The period of irregular feeding was given in an attempt to control the influence of regular feeding on the establishment of the pre-light-pre-feeding activity. The results of some typical experiments are given in Table I. Tomcod, scup and killifish established daily pre-light-pre-feeding activity while flounder and cunner did not. The killifish was selected for further investigations.

2. Killifish Studies

Experiment No. 1: Pre-light-Pre-feeding Activity LD': 12-12

Two groups of 3 killifish were placed in LD': 12-12. Group 1 was fed daily on onset L and a persistent pre-light-pre-feeding peak of activity appeared in 12 days (Fig. 1). Group 2 was fed at an irregular time in L for 24 days and then daily at onset L. A pre-light-pre-feeding peak began for Group 2 on the first day after feeding at onset L was started (day 26; Fig. 2). When Group 2 was fed at irregular times prior to day 25, a feeding on one day was not noticeably correlated with the occurrence of a peak of activity near that time the following day. These results suggested that the establishment of the pre-light-pre-feeding activity depends on feeding at onset L, though there was an indication that during the first 24 days Group 2 was in some way preconditioned to respond to feeding at onset L but not elsewhere in the light period.

Experiment No. 2: Prefeeding Activity in LL

This experiment was undertaken to find out whether activity corresponding to the so-called pre-light-pre-feeding activity can be established in the absence of regular daily changes in light. Three groups of 3 killifish (Set A) in separate chambers were placed in LL and fed daily at 1200. To control the influence of factors other than regular daily feeding, a second set of three groups of fish (Set B) in LL were fed daily at a random time for 21 days and then daily at 1200 along with Set A.

Set A showed pre-feeding peaks of activity in 5 to 10 days (Fig. 3). Set B had pre-feeding activity beginning on day 23, the day after regular feeding at onset L was started, and Group 1 of this Set even showed a semblance of pre-feeding activity on day 22, (Fig. 4). Prior to day 22, some groups in Set B became active at 1200 when Set A was being fed (see days 7, 11, 12, 15; Fig. 4), the implication being that Set B responded to noises made in the room while

Table I. Summary of Studies with Marine Fishes.

Preliminary Studies (Typical Experiments):			
<p>Flounder (<i>Pseudopleuronectes americanus</i>)—One fish in LD': 12-12, feeding every few days at an irregular time in L for 23 days and then daily on onset L; total 38 days (Dec. 1961-Jan. 1962). <i>Results:</i> No pre-light or pre-feeding activity; very low level of activity registered in L and in D'.</p>			
<p>Tomcod (<i>Microgadus tomcod</i>)—One fish in LD': 12-12 feeding every few days at an irregular time in L for 23 days and then daily at onset L; total 60 days (Dec. 1961-Jan. 1962). <i>Results:</i> Pre-light—pre-feeding peak of activity appeared one day after daily feeding at onset L was started (similar results were obtained with killifish); the fish was otherwise moderately active in L and D'. Tomcod frequently became ill in the experimental environment.</p>			
<p>Cunner (<i>Tautoglabrus adespersus</i>)—One fish in LD': 12-12, feeding every few days at an irregular time in L for 23 days and then daily at onset of L; total 60 days (Dec. 1961-Jan. 1962). <i>Results:</i> No pre-light or pre-feeding activity; the fish was most active in L but the level of activity was low. Cunner seldom fed, and would not tolerate companions in the experimental aquarium.</p>			
<p>Scup (<i>Stenotomus versicolor</i>)—Three fish in LD': 12-12, feeding daily at onset L; total 60 days (Feb.-March, 1962). <i>Results:</i> A pre-light - pre-feeding peak of activity appeared in 10 days and persisted for 34 days; thereafter the response was inconsistent. In repeated experiments scup always became excitable after a month of confinement.</p>			
Studies with Killifish (<i>Fundulus heteroclitus</i>):			
Experimental light and feeding schedules and the results are described in the text.			
Experiment no.	No. of fish	Total days	Dates
1	6	40	May-June, 1962.
2	18	32	August-September, 1962
3	9	122	May-August, 1962
4	18	100	Sept.-Dec., 1962

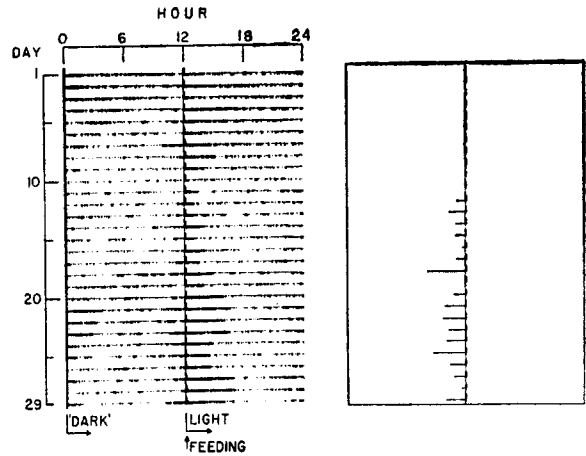


Fig. 1. Left: Activity in the feeding area registered by three killifish (Group 1) during the first 29 days of Exp. No. 1. The fish were held in LD': 12-12 and fed daily at onset L (vertical bars at 1200). Right: diagram of pre-light—pre-feeding activity which began on day 12.

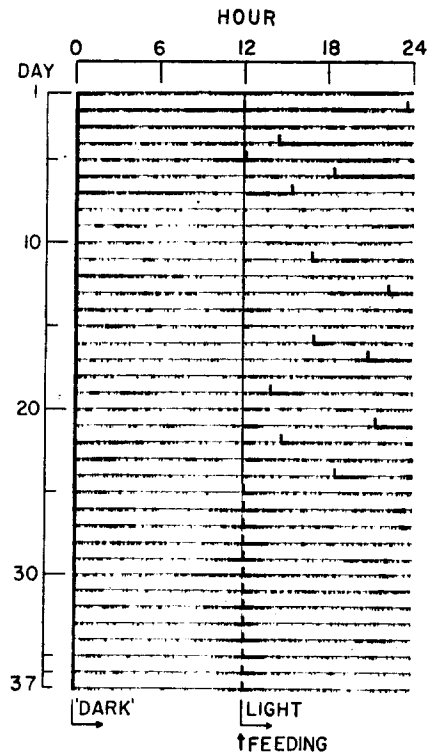


Fig. 2. Activity in the feeding area registered by three killifish (Group 2) during the first 37 days of Exp. No. 1. The fish were held in LD': 12-12 and fed at irregular times in L for 24 days and then daily at onset L (vertical bars). Pre-light—pre-feeding activity began on day 26.

Set A was being fed. Such stimuli may have pre-conditioned Set B to respond to daily feeding at 1200. Also, the activity just before feeding on day 22 shown by Group 1 of Set B (Fig. 4) may be pre-feeding activity evoked by the daily recurrence of noises of feeding Set A. Set A may have detected the noises of feeding Set B at random times of day. The records for the group of Set A shown in Fig. 3 reveal that the pre-feeding activity disappeared several days before day 22 and then reappeared when regular feeding at onset L was started for Set B; it was as though the food-related noises at random times of day disorganised the response of Set A to daily feeding at 1200.

These results suggest that in Experiment No. 1 the apparent facilitation of the pre-light-pre-feeding activity of Group 2 may have been caused by the noises made while feeding Group 1 at onset L each day. The same possibility holds for the results obtained with tomcod in the preliminary experiments (Table I), where pre-light-pre-feeding activity appeared the day after feeding at onset L was started; the room had been entered daily at that time of day to feed the other fish.

Experiment No. 3: Pre-feeding Activity in LD': 12-12

The foregoing results suggested that the pre-light-pre-feeding activity in LD' is caused by feeding at onset L. The relation between the activity and the periodicities of light and feeding was further studied by comparing groups of fish fed at 24-hour intervals but at different times in a 24-hour LD' cycle. Three groups of 3 killifish in separate chambers in LD': 12-12 were fed daily at 1200. The LD' cycles in the different chambers were phased so that feeding occurred at onset L for Group 1, at 6 hours after onset L for Group 2, and at 10 hours after onset L for Group 3. Group 1 showed a high level of intermittent and irregular activity in D' and no consistent peak of pre-feeding activity was discernable. It is to be emphasized that the results for Group 1 in this experiment were typical in work with killifish fed at onset L: Group 1 in Experiment No. 1 produced the clearest records of pre-feeding activity under these conditions (see Fig. 1). Group 2 established pre-feeding activity near the middle of the light period in 5 to 10 days (Fig. 5), and Group 3 showed pre-feeding activity near the end of the light period by day 15 (Fig. 6). Neither Group 2 nor Group 3 had a pre-light peak of activity supporting the

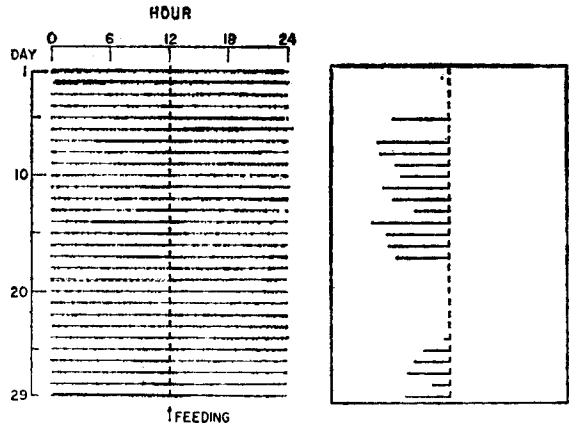


Fig. 3. Left: activity in the feeding area registered by three killifish (Group 1 of Set A) during the first 29 days of Exp. No. 2. The fish were held in LL and fed daily at 1200. Right: diagram of pre-feeding activity which began between days five to ten, disappeared on day 18 and reappeared on day 24.

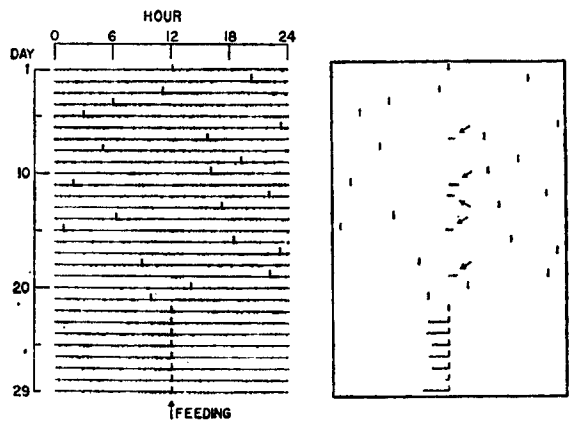


Fig. 4. Left: activity in the feeding area registered by three killifish (Group 1 of Set B) during the first 29 days of Exp. No. 2. The fish were held in LL and fed daily at a random time for 21 days and then daily at 1200. Right: diagram of pre-feeding activity which began on day 23; the arrows indicate activity coincident with the feeding of other fish (Set A, Fig. 3) in adjacent chambers.

conclusion that the pre-feeding activity is a consequence of regular daily feeding.

Group 3 was discarded after 2 months. Group 2, which was being fed 6 hours after dawn, was kept for 4 months. During the last month a *pre-light* peak of activity appeared (day 87) and persisted concurrent with the *pre-feeding* activity. The pre-light activity was distinguishable on most days to the end of the experiment on day 122. The pre-feeding activity, on the other hand,

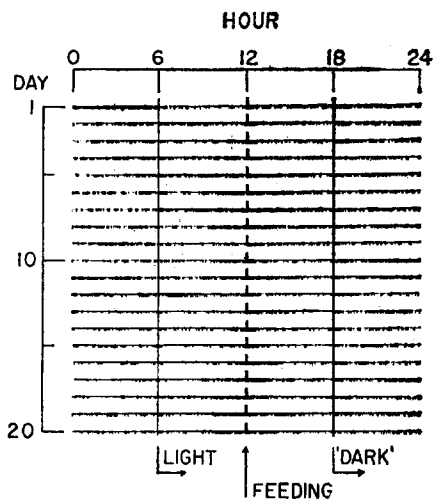


Fig. 5. Left: activity in the feeding area registered by 3 killifish (Group 1) during the first 20 days of Exp. No. 3. The fish were held in LD': 12-12 and fed daily 6 hours after onset L (1200). Right: diagram of pre-feeding activity which began between days 5 to 10.

disappeared on day 110 (Fig. 6) and thereafter the fish refused food at feeding time.

Fig. 6 also shows part of the results of an attempt to determine the role of the LD' cycle in co-ordinating pre-feeding activity occurring in the L period. During the second and third months Groups 2 and 3 were subjected to 2 10-day periods when onset L started 6 hours earlier in the day; the L period was increased from 12 to 18 hours and the D' period was decreased from 12 to 6 hours. On most but not all days during these 10-day periods the pre-feeding activity of both groups started several hours earlier in the day, and when the original LD': 12-12 cycle was restored, the pre-feeding peaks of activity shortened correspondingly. During the fourth month Group 2 was given a 10-day period where onset D' occurred 6 hours later in the day (days 90 to 99: Fig. 6). On the first day there was no pre-feeding activity and the fish refused food. It was as though the 6-hour delay in onset D' the previous day had caused a delay in the start of the pre-feeding activity. In succeeding days pre-feeding activity reappeared before the unaltered feeding time (1200) and the fish resumed feeding. When onset D' was subsequently advanced 6 hours, to restore the original LD'

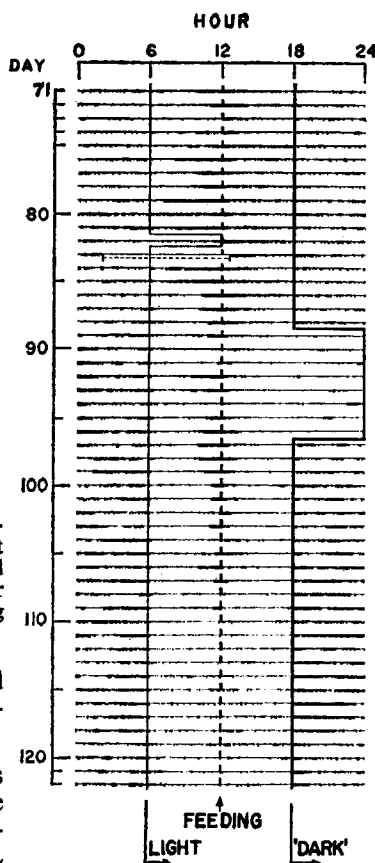


Fig. 6. Left: activity in the feeding area registered by 3 killifish (Group 2) during the last 52 days of Exp. No. 3. The fish were held in LD': 12-12 and fed daily six hours after onset L (1200). (Instrument failures delayed onset L 6 hours on day 82 and halted recording for a time on day 83). Right: diagram of pre-light activity which began on day 87, and of the previously established pre-feeding activity which disappeared on day 110. The outcome of the 6-hour shifts on onset D' on days 89 and 97 is discussed in the text.

cycle, there was no perceptible change in the timing of the pre-feeding activity (day 97; Fig. 6). It should be noted that Group 2 showed pre-light activity on days before the onset D' was altered (Fig. 6) and also that the activity was too irregular to tell whether it was influenced by the change in the LD' cycle.

Experiment No. 4: Co-ordination of Pre-feeding Activity in LL

Six groups of 3 killifish in separate chambers were placed in LL and fed daily at 1200 for 60 days preparatory to testing the effect on the timing of the pre-feeding activity of shifts in feeding time. Groups 1 to 4 established daily pre-feeding activity in 12 to 45 days (Fig. 7).

The records for Groups 5 and 6 were disregarded because pre-feeding activity was seldom distinguishable; on most days there was a high level of intermittent and irregular activity which could have obscured the pre-feeding activity. After 60 days, feeding time was shifted from 1200 to 1800 for 10 days. The day feeding was delayed to 1800 (day 60) the pre-feeding activity continued beyond 1200 and some fish were active to 1800 at which time food was presented. The next day the pre-feeding activity

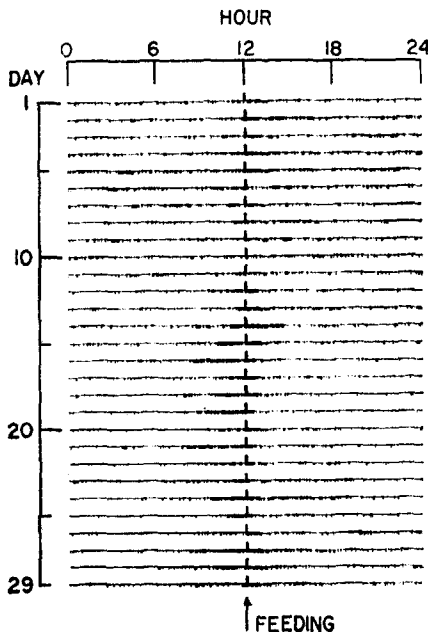


Fig. 7. Activity in the feeding area registered by 3 killifish (Group 1) during the first 29 days of Exp. No. 4. The fish were held in LL and fed daily at 1200. Pre-feeding activity began between days 10 and 15.

was delayed as though in compensation for the shift in feeding time (Figs. 8, 9).

When feeding time was advanced from 1800 to 1200 on day 70 Groups 1 and 2 showed a step-wise delay in the start of their pre-feeding activity on days 70, 71 and 72 which compensated for the 6-hour advance in feeding time (Fig. 8). Groups 3 and 4 responded differently: when feeding was advanced to 1200, activity continued to occur in the hours between 1700 and 2300, or near the old feeding time at 1800. While this semblance of a residual pre-feeding activity persisted on days 70 to 73 activity appeared before feeding at 1200 on day 71 for Group 3 and on day 73 for Group 4 (Fig. 9). The pre-feeding activity of Groups 3 and 4

seemed to go out of phase with the feeding cycle on days 76 and 77; there was no activity before feeding but prolonged intervals of activity occurred at another time of day.

3. Bluegill Studies

Direct observations of 32 individual bluegills given a regular daily feeding in LL showed that there was a daily increase in locomotion before feeding time. Sixteen of the fish (Group 1)

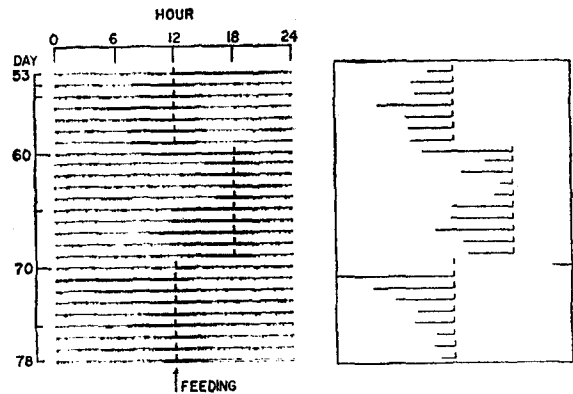


Fig. 8. Left: activity in the feeding area registered by 3 killifish (Group 1) in LL on days 53-78 of Exp. No. 4. Feeding time was delayed 6 hours, from 1200 to 1800, on day 60 and then advanced six hours on day 70. Right: diagram of changes in the timing of the pre-feeding activity following the shifts in feeding time (see text).

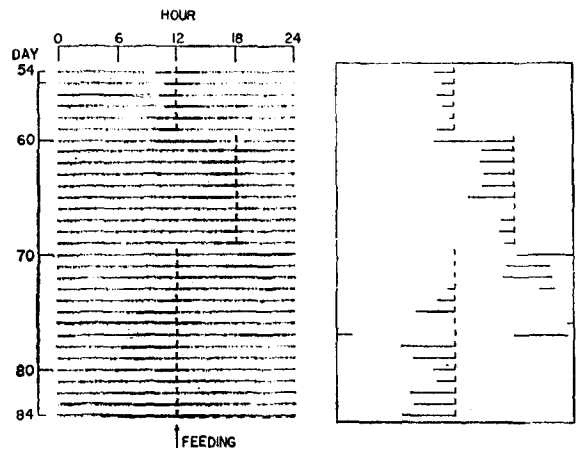


Fig. 9. Left: activity in the feeding area registered by 3 killifish (Group 3) in LL on days 54 to 84 of Exp. No. 4. Feeding time was delayed 6 hours, from 1200 to 1800, on day 60 and then advanced 6 hours on day 70. Right: diagram of changes in the timing of the pre-feeding activity following the shifts in feeding time (see text).

were fed at 1030 and the other 16 (Group 2) were fed at 1700. After 4 weeks of this regime daily observations were made for 2 weeks in which the level of activity of all fish was recorded during the hour preceding the 2 feeding times and half-way between the 2 feeding times. Group 1 was more active than Group 2 during the hour before its feeding time (1030), and Group 2 was more active than Group 1 during the hour before it was fed (1700). For both Groups the mean level of activity in the hour before feeding was higher ($P < .01$) than at the other 2 periods of observation, the indication being that during the last 2 weeks of the 6-week training period each of the 2 groups showed daily pre-feeding activity.

Discussion

The daily onset of the pre-feeding activity was not paralleled by detectable changes in the physical environment suggesting that the activity was timed in relation to a past event such as a feeding time or a change in light. The effect of light changes on the timing of a pre-feeding activity may depend in part on the phase relation between the periodicities of light and feeding. For example, in previous work with bluegills and bass (Davis, 1963), where feeding was at onset L, 6-hour shifts in the light transitions showed that the pre-light-pre-feeding activity was co-ordinated by onset L, and not by onset D' or by feeding time. On the other hand, the present results with killifish suggest that when feeding occurs near the middle of the light period both L-to-D' and D'-to-L transitions affect the timing of the pre-feeding activity. In LL the timing of the pre-feeding activity of killifish and bluegills is coupled with the periodicity of feeding. The coupling, however, is such that the activity rhythm can at times be out of phase with the feeding periodicity. This phase independence was manifest when the time of feeding of killifish in LL was advanced 6 hours. For several days periods of activity corresponding to the pre-feeding activity recurred at intervals different from 24 hours and then resynchronised with feeding at the earlier time of day (Fig. 8). The activity rhythm of bluegills and bass in LD' shows similar phase independence following a 6-hour delay in the onset of light (Davis, 1963). The stepwise shifting of a biological rhythm, in the absence of parallel changes in the external environment is one indication of an internal regulation by a biological clock. Irregularities in the timing of the pre-feeding activity from day to day are assumed here to be caused

by phase variations in the biological clock. The variations could be spontaneous or they could be induced by some uncontrolled timegiver in the external environment. Unaccustomed loud noises in the building, fighting or other social interaction might delay or advance or obliterate the pre-feeding activity on one day without influencing the clock. If the phase of the clock varies uncontrollably, a regular daily feeding would occur at different times in the clock cycle and presumably elicit compensatory changes in the cycle length. This effect was suggested in the oscillation of the start of the pre-feeding activity following a shift in feeding time (days 60 to 69; Fig. 9). Experiment No. 4, with killifish in LL, shows that it cannot be predicted whether a 6-hour advance in feeding will advance or delay the phase of the clock. Also in Experiment No. 4, following the 6-hour advance in feeding time, 2 groups of fish seemed to show a residual peak of activity near the old feeding time (days 70 to 73; Fig. 9). It is possible that the clock in some fish in the 2 groups failed for a few days to respond to the shift in feeding; the stimulus of feeding may be a weak timegiver or, in this instance, some uncontrolled timegiver recurring near the old feeding time at 1800 may have temporarily dominated over feeding at 1200.

Phase independence is also characteristic of the sun orientation rhythm of fishes and of the circadian rhythms which occur in many other organisms. In contrast to circadian rhythms, which are defined as being innate (Pittendrigh, 1960), the pre-feeding activity rhythm of fishes is learned in response to regular daily feeding. Time-co-ordinated pre-feeding activity has been shown in bees (Beling, 1929), birds (Wagner, 1956) and in rats (Reid & Finger, 1955). These animals also possess circadian activity rhythms. The relation between a rhythm caused by regular feeding and the circadian rhythm in the same animal needs investigation. Regular daily feeding can greatly alter the normal daily pattern of metabolism in rats (Werthessen, 1937) and activity in birds (Wagner, 1956). The co-ordination of pre-feeding activity, however, has apparently not been extensively studied.

What does the fish learn when it acquires the pre-feeding activity response? The existence of a biological clock predicates that time-co-ordinated stimuli arise from within the organism. It can be proposed that the pre-feeding activity is a consequence of conditioning the act of eating to an endogenous cue. Acquisition of the response would depend on repeated presentations of food

at the same time of day (it seems likely that feeding periodicities other than 24-hours would also be effective). The phase of the rhythm is susceptible to shifts in feeding time, therefore the presentation of food also acts as a timegiver, or regulates the timing of the endogenous cue. The occurrence of this cue prior to feeding time coupled with the failure of food to appear would promote restlessness having one expression in food-seeking approaches to the feeding area which register as pre-feeding activity.

The role of the LD' cycle is the acquisition of the pre-feeding activity response remains undetermined. The LD' cycle acts as a timegiver and it may therefore assist in establishing the response to regular feeding by stabilizing the phase of the biological clock. In Experiment No. 3, killifish in LD' for several months acquired a pre-light peak of activity while they were showing a pre-feeding peak in the middle of the light period (Fig. 6) as if the prolonged pairing of light and feeding conditioned the act of feeding to light, with the light period itself being conditioned to an endogenous cue. The dwindling and eventual disappearance of the pre-feeding peak in the light period suggests that the response to food as distinct from light was extinguished. When the pre-feeding activity disappeared, the fish refused food at feeding time, in fact they were startled by the presentation of food. But from day to day less food collected on the bottom than was presented indicating that some was eaten at times between daily feedings. Fish accustomed to being fed at a regular time of day are commonly disturbed when feeding time is advanced or delayed a number of hours; on the other hand fish fed at random times are seldom startled by the appearance of food at any time after the first few days.

There has apparently not been a unequivocal demonstration of a circadian rhythm in fishes, although they have been shown to possess a biological clock. In learned rhythms, such as (daily) pre-feeding activity, an environmental periodicity causes the rhythm and at the same time co-ordinates it by regulating the clock. Such rhythms therefore provide a means of investigating the properties of time-co-ordinated behaviour in fishes.

Summary

1. Fish fed daily at a regular time under (controlled) artificial illumination became active daily for a number of hours just before feeding time.

2. Tomcod, scup, and killifish held under alternating 12-hour periods of bright and dim light with feeding at the onset of bright light acquired pre-light-pre-feeding activity resembling the "predawn" activity previously found in bluegills and largemouth bass.

3. Killifish and bluegills established pre-feeding activity under constant illumination.

4. The timing of the pre-feeding activity of killifish was influenced by shifts in the light cycle and feeding time; when feeding time in constant light was advanced or delayed 6 hours, the pre-feeding activity shifted approximately 6 hours in 1 to 3 days.

5. The conclusion was reached that the pre-feeding activity is a consequence of conditioning the act of feeding to an endogenous cue which itself is co-ordinated by the time of feeding or daily changes in light.

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ABSTRACT

Fish fed daily at a regular time under controlled artificial illumination became active daily for a number of hours just before feeding

time. Experiments with killifish (*Fundulus heteroclitus*) in constant light and under alternating 12-hour periods of bright and dim light showed that the timing of the pre-feeding activity is influenced by shifts in the light cycle and feeding time; when feeding time in constant light was shifted 6 hours, the pre-feeding activity shifted approximately 6 hours in 1 to 3 days. The conclusion was reached that the pre-feeding activity is a consequence of conditioning the act of feeding to an endogenous cue which itself is coordinated by the time of feeding or daily changes in light.