

The Light Intensity as a Key Factor Controlling Nocturnal Action in the Catfish, *Pseudobagrus aurantiacus*

Kazuo Mashiko

(Received August 7, 1978)

Abstract Nocturnal action of the catfish, *Pseudobagrus aurantiacus*, was investigated with an actograph recording the movements into and out of a nest-hole in an aquarium. The nocturnal action commenced in dependence on fall of external light intensity in the evening, and the action commencement climaxed at 10^{-3} order in lux at water temperatures between 11° and 20°C , and at 10^{-2} order in lux at between 25° and 30°C . From the results of feeding experiments, the remarkably strict correspondence of nocturnal action commencement with the change of external light intensity is suggested to be concerned with a high degree of feeding intensity at that time. The catfish became active without periodicity for a whole day of continuous darkness (lower than 2×10^{-4} lux), and action was constantly depressed with the continuous illumination (1000 lux). Light intensity of the surroundings is considered to be a key factor in switching the activity of this catfish between day and night.

Pseudobagrus aurantiacus is a freshwater catfish distributed discontinuously in the north-eastern part of Honshū and Kyūshū, in Japan. According to Okada and Shiishi (1937) and Okada (1960), this catfish usually rests in shady sites during the day, and becomes active at night to forage for larvae and pupae of aquatic insects, crustaceans and small fishes. In catfishes such nocturnalism is common (Darnell and Meierotto, 1965; Scott and Crossman, 1973; Miyadi et al., 1976; Moyle, 1976). However, analytic investigations on their nocturnalism have been scarce. According to Miyadi et al. (1976) *P. aurantiacus* go to action not only at night but also during the day when water is muddy. Their observation proposes the idea on the mechanism of this fish's nocturnalism that its movement is controlled directly by the external light intensity of its surroundings. In the present study *P. aurantiacus*'s nocturnal action was investigated in the laboratory with special reference to the external light intensity under various water temperatures.

Materials and Methods

Experimental fish were collected from a tributary of the Tama River in Tokyo in the autumn of 1976, and were kept in an aquarium in the laboratory until the summer of 1977. Adult fish, which ranged in body length from

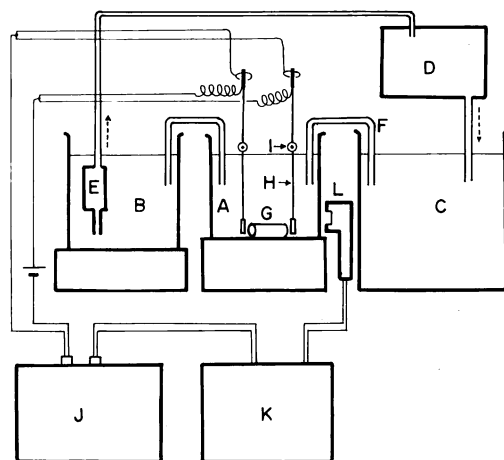


Fig. 1. Outline of the experimental apparatus. The symbols in the figure indicate the following: A, experimental glass aquarium; B and C, sub-aquaria; D, filter box; E, water pump; F, siphon; G, nest-hole fixed on the bottom of the aquarium; H and I, vertically suspended iron wire and fulcrum; J, dual channel recorder; K, microscopic exposure meter; L, photoreceptor. Arrows with dotted lines indicate a direction of water flow.

8.0 to 12.0 cm (the age estimated from the body length was 2 or 3 years) were used for the experiment from August, 1977 to May, 1978.

Fig. 1 shows an outline of the apparatus used

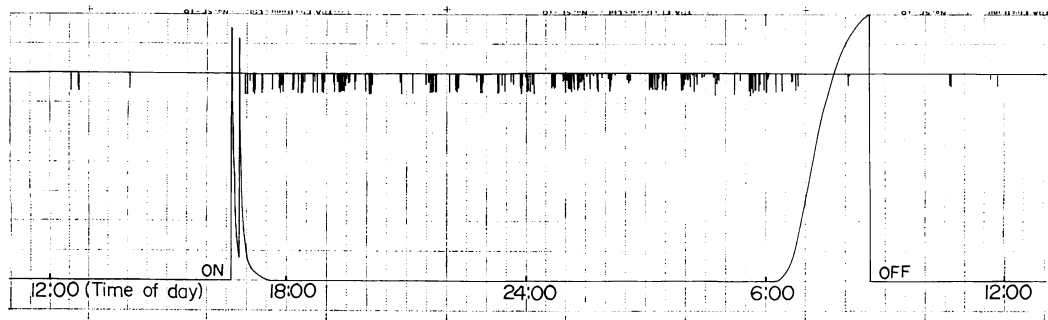


Fig. 2. An example of recording of spikes in a day, and change in light intensity under indirect natural light. The light intensity was recorded only from 16:38 hours till 8:38 hours the next day. The sensitivity of the photoreceptor was changed at 16:48 hours in the evening.

for the experiment. One individual was kept in an experimental glass aquarium (15l in volume), in which a pipe of polyvinyl chloride was fixed (the internal diameter and length were changed respectively from 2.2 to 2.5 cm, and from 10.0 to 15.0 cm according to the size of fish). The fish utilized the pipe for the nest-hole, and stayed in it in the daytime. At the positions of ca. 2 cm distance from both openings of the pipe, a linear iron wire (30 cm in length) coated with thin vinyl membrane was vertically suspended supported by a fulcrum at the point of a half length. Each of the iron wires was joined with a piece of glass tube (3 cm in length) at the lower end, and with a small piece of copper wire at the upper end. The piece of copper wire was connected with a copper filament, and encircled horizontally by a ring of another copper wire. Between the circulating and encircled copper wire, electric charges (D.C. 1.5 V) were given. Hence a fish's touching stimulus against the glass tube by a movement into and out of the nest-hole was changed to an electric signal through a pendulum-like movement of the iron wire suspended vertically. The electric signals were recorded as spikes with a dual channel recorder (EPR-3T, Toa-Electronics) through one input terminal. Light intensity was measured with a highly sensitive microscopic exposure meter (EMM-II, Olympus), and recorded with the aforesaid dual channel recorder through another input terminal parallel with recording of spikes by fish's movement. The photoreceptor of the exposure meter was slightly

modified for this experiment, and fixed to be faced to the wall of the experimental aquarium. Measurable minimum range of light intensity by the exposure meter was 10^{-4} lux. The experiment was usually made under the condition of only indirect natural light which was introduced through windows with blinds. Furthermore especially strong light from a specific direction was avoided by vertically surrounding the whole experimental apparatus except the recorder with screens of veneer board. When artificial light and dark cycles were adopted for the light source, the experimental aquarium was lighted with three 20 W-fluorescent lamps from 30 cm above the water surface (1000 lux at the water surface), and the whole experimental apparatus except the recorder was covered with a black sheet in order to shut off the intrusion of external light. Water in the experimental aquarium was circulated through two sub-aquaria with siphons for the maintenance of placid water flow, and filtered through sand, active carbon and glass wool in a filter box. Water temperature was regulated constant with a fluctuation of $\pm 1^{\circ}\text{C}$ with a water cooler and heaters attached with a regulator.

Results

Fig. 2 shows an example of recording of spikes by the fish's movement in a day and the change in light intensity at dawn and dusk (Dec. 15, 1977). Usually dense trains of spikes appeared at dusk and continued till the next morning, though sporadic spikes were rarely recorded in the daytime. Ac-

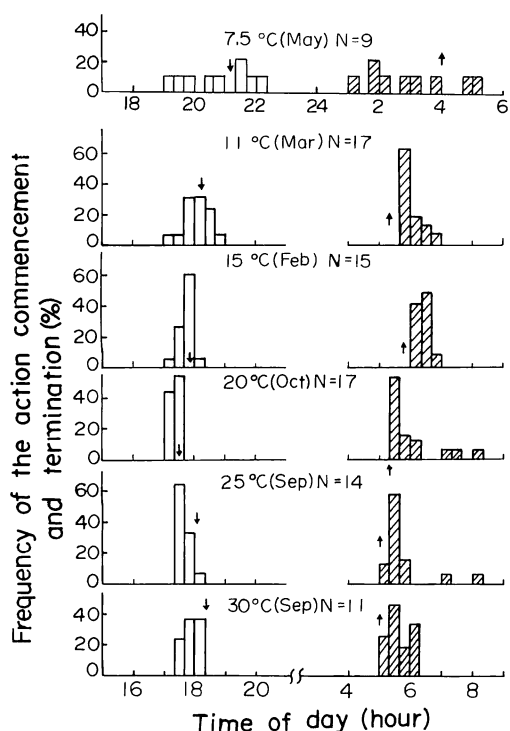


Fig. 3. The time when the fish's nocturnal action commenced (left) and terminated (right and obliquely lined) at the various water temperatures. The time is shown as a time band divided into 20 minute intervals. Observation frequencies (%) of the action commencement and termination are indicated by the ratio of number of days when the nocturnal action commenced and terminated respectively at each of the time bands against total number of days investigated. The symbols in the figure indicate the following: water temperature, month when the experiment was mainly carried out in parentheses, and total number of days investigated. Arrows ↓ and ↑ show the time of sunset and sunrise when each experiment was made. The time scale only at 7.5°C differs from the others.

According to direct observations on the movement of fish, the sporadic spikes in the daytime were ascertained to be made by touching of only fish's tail against the glass tube, regardless of fish's movement into and out of the nest-hole. The fish inside the nest-hole occasionally stirred forward and backward, and stretched out its tail from the openings

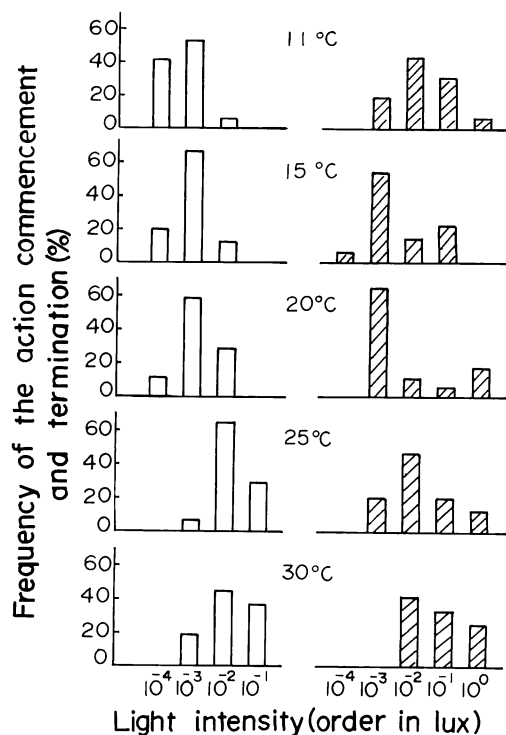


Fig. 4. Relationship between the light intensity (represented only by the order of exponent of 10 in lux) and observation frequency (%) of the action commencement and termination (the definition and representation are the same as in Fig. 3) at the various water temperatures indicated in the figure.

of the nest-hole. Therefore the fish's actual movement into and out of the nest-hole is indicated by the frequent spikes in the evening which can be readily discriminated from the sporadic spikes in the daytime. In this report the commencement and termination of nocturnal action are defined respectively as the first appearance of the frequent spikes and their disappearance. The maximum light intensity in indirect natural light during the day was about 100 lux, and the minimum was 10^{-4} lux throughout the periods of the experiment.

Fig. 3 shows the time of day (represented as the time bands divided into 20 minutes each) when the commencement and termination of nocturnal action were observed in one individual at various water temperatures (11°, 15°, 20°, 25° and 30°C). Also the result at

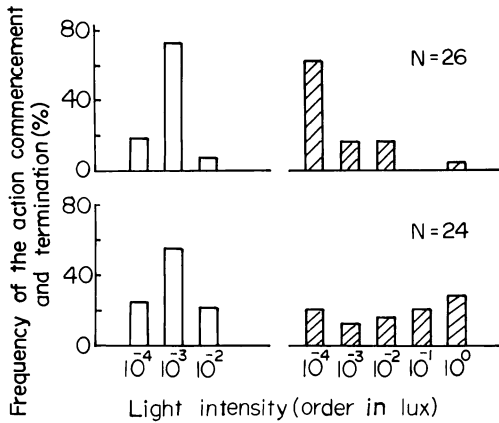


Fig. 5. Relationship between the light intensity (represented only by the order of exponent of 10 in lux) and the observation frequency (%) of the action commencement and termination (the definition and representation are the same as in Fig. 3) in two other individuals at water temperature 20°C. N indicates total number of days investigated.

7.5°C obtained from another individual is added in this figure. The action commencement tended to concentrate to small time bands as compared with the action termination at above 20°C. The action commencement climaxed at about sunset at 15°~20°C, and a half or more hour before sunset at 25°~30°C. At lower water temperature such as 7.5°C, both the action commencement and termination became irregular, and distributed over a wide range of the time bands.

The above results are rearranged in Fig. 4 from the view point of the relationship between the light intensity (represented only by the order of exponent of 10 in lux; for instance 10^{-1} lux includes the values between 0.10 and 0.99 lux) and the observation frequency (%) of the action commencement and termination at various water temperatures (11°, 15°, 20°, 25° and 30°C). The light intensity when the nocturnal action commenced was significantly fixed, and the frequency peak was 10^{-3} order in lux at water temperatures from 11° to 20°C, and 10^{-2} order in lux at 25°~30°C. According to the increase of water temperature, the light intensity at this frequency peak increases, and the increasing rate is near to 10 times in lux every 10°C increment between 15° and 30°C. This

fact of increase of light intensity of the frequency peak according to increase of water temperature was supported by experiments on other individuals. On the other hand, the action termination is not so intimately correlated with light intensity as is the action commencement, though the light intensity when the nocturnal action terminated was limited to the range between 10^{-4} and 10^0 order in lux. This relationship in two other individuals in 20°C is shown in Fig. 5. The light intensity of the frequency peak of action commencement was at 10^{-3} order in lux in both individuals, and these results correspond well with results at the same water temperature in Fig. 3. The individual difference in the critical light intensity when the catfish begins the first nocturnal movement appears to be very little. However, light intensity at the action termination ranged to a comparatively large extent (10^0 ~ 10^{-4} order in lux) also in these two individuals. In these three individuals including one shown in Fig. 4, the light intensity of the frequency peak of the action termination at 20°C was varied. But the clear correspondence in the critical point of light intensity, at least at the action commencement in the three individuals, suggests that the catfish's nocturnal action directly depends on the fall of external light intensity. To investigate this correlation further, the fish's movements into and out of the nest-hole were analysed under the artificial light-dark (LD) cycles.

Fig. 6 shows diel change of spike frequency at one hour intervals on 19 continuous days in one individual under the various series of LD cycles, i.e. LD: L (1000 lux) for 10 hours and D (lower than 2×10^{-4} lux) for 14 hours during the period of the first 5 days and the intermediate 4 days, DD: continuous dark lower than 2×10^{-4} lux during the second 5 days, and LL: continuous light of 1000 lux during the last 5 days. The test fish was acclimatized for a week to the first LD cycles beforehand. Water temperature was maintained at 20°C, and food was given at 12:00 a.m. except during the period of DD cycles. At the period of DD cycles, fresh food of an amount sufficient for these 5 days was given once at 12:00 a.m. on the first day

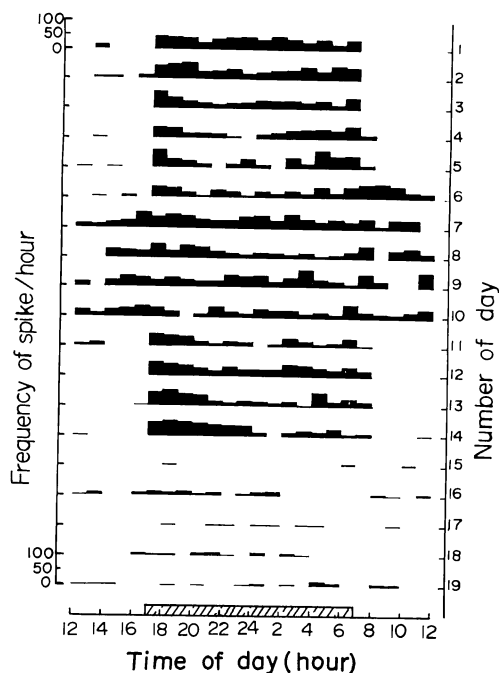


Fig. 6. Diel changes in spike frequency every one hour in one individual (11.1 cm in BL) for 19 continuous day under the various series of artificial LD cycles. One compartment of spike frequency on the longitudinal axis shows 100 times per hour. Light conditions during the experiment were as follows: LD from the first day to the 5th day, DD from the 6th day (at 17:00 hours) to the 10th day (at 12:00 hours), the original LD from the 11th day to the 14th day, and LL after that. A shaded block by oblique lines on the abscissa indicates the dark period when LD cycles were made.

of the DD cycles (the 6th day after the start of experiment), and no more food was given in order to shut off the intrusion of external light accompanied with the introduction of food. The fish's movement was nearly restricted to the dark period under the LD cycles. However, immediately after the establishment of DD cycles, the catfish became active even during the time corresponding to the initial light period (from 7:00 to 17:00 hours) as well as the initial dark period (from 17:00 to the next 7:00). This active movement during the time corresponding to the initial light period, under the DD cycles, disappeared immediately after the establishment of the

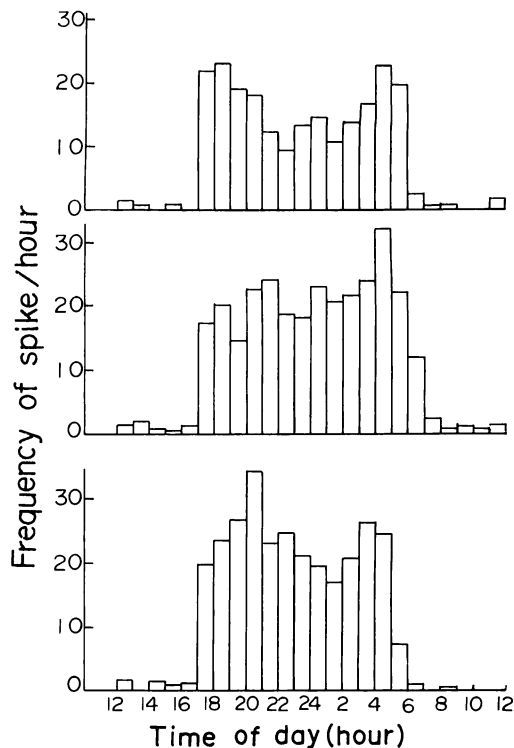


Fig. 7. Diel changes in spike frequency every one hour in the three individuals under indirect natural light. The frequencies are indicated by the mean values obtained by seven day experiments respectively.

next LD cycles. The fish became nearly inactive for a whole day after the establishment of LL cycles. According to a correlogram analysis (Itô and Murai, 1977) a significant rhythmicity with a period of 24 hours was detected statistically at 5% significant level in the change in spike frequency under the LD cycles. However, such significant rhythmicity was not detected in the changes in spike frequency under both the DD and LL cycles. These results indicate that the action of the catfish is not directly controlled by endogenous factors, but by exogenous ones, especially by external light intensity.

The correlation with the change of external light intensity was strict at the action commencement as compared with the action termination, however the significance of this difference is obscure. Fig. 7 shows the diel change in the spike frequency every one hour in three individuals under indirect natural

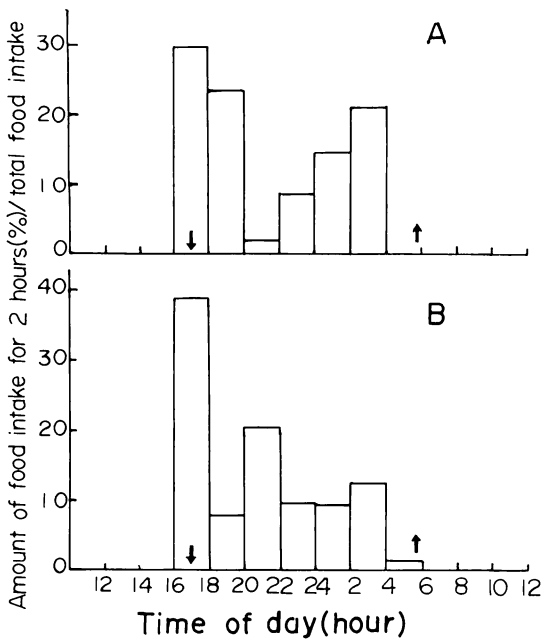


Fig. 8. Diel change in the amount of food intake every two hours in two individuals. Food amount eaten for each two hours is shown by the percentage against the total amount of food intake in a day. Arrows ↓ and ↑ in the figure indicate the time of sunset and sunrise.

light at a water temperature of 20°C. The frequencies of spikes at each time are represented by the mean value of seven day experiments. Although a bimodal change is clearly recognized in one individual (the upper) and slightly in another (the lower), in either case the catfish is active throughout the night. The sporadic spikes during the daytime are also represented in Fig. 7. But those frequencies are small enough to be negligible, and they do not indicate actual fish movement into and out of the nest-hole as previously mentioned.

Fig. 8 shows the diel change in amount of food intake for every 2 hours in two individuals. Food amount eaten was represented by the percentage against total amount of food intake a day, and indicated by the mean values obtained during a three-day experiment (Dec. 9, Dec. 13 and Dec. 21, 1977). Both test fish (BL, A: 10.5 cm, B: 6.2 cm) were acclimatized for a week in advance to the

experiment in glass aquaria (10l in volume) into which a nest-hole of polyvinyl chloride was introduced. Water in the aquaria was circulated and filtered by nearly the same method as previously mentioned. Water temperature was maintained at 20°C. Constant numbers (40 individuals in many cases; nearly twice amount of food taken usually in a day) of individually weighed *Chironomus* larvae (20 ± 3 mg per larva) were given at 12:00 a.m. into the aquaria. The amount of larvae eaten after that was calculated by counting the number of larvae remaining at intervals of 2 hours till 12:00 a.m. of the next day. A weak spotlight was directed into the aquaria for a short time for the count at night, but the spotlight was ascertained previously hardly to influence the feeding of the fish. The mean value of total amount of food intake a day was 413 mg in individual A, and 399 mg in individual B. Nearly half the amount of food taken in a day was eaten within 4 hours from 16:00 till 20:00 hours in the two individuals. When this feeding experiment was made, however, the nocturnal action of the used catfish was considered to begin at about 17:00 hours because the sunset was at that time (see Fig. 3). Therefore half of the total amount of food intake in a day was eaten substantially within three hours after the commencement of nocturnal action in the both individuals.

Discussion

Periodic changes in some kinds of biological activity are known to continue even after removal of periodic stimulus from the surroundings in not a few organisms, and the connection with endogenous rhythmicity, or "physiological (biological) clock," has been studied (Bünning, 1973; Chiba, 1975). The catfish *P. aurantiacus* becomes active for nearly a whole day in DD cycles without a 24 hour-periodicity, and becomes inactive in LL cycles. Therefore, the mechanism of endogenous rhythmicity is considered not to play an important role in timing of the commencement and termination of the nocturnal action. These behavioral switchings seem to directly depend on the change of light intensity of the surroundings. For instance, the critical point

of light intensity at the climax of nocturnal action commencement at the water temperature of 20°C is 10^{-3} order in lux. This mechanism of the behavioral switching reasonably explains the observational fact of this catfish's movement in muddy water in the daytime, as reported by Miyadi et al. (1976). Even in the daytime *P. aurantiacus* was surely supposed to go to action when the light intensity at their habitat dropped down to the levels between 10^{-1} and 10^{-3} order in lux at usual water temperatures.

However, the above results, i.e. no connection of the movemental activity of *P. aurantiacus* with endogenous rhythmicity, does not deny the existence itself of this mechanism in this catfish. According to Welsh and Osborn (1937), daily change of the position of retinal pigment of the catfish, *Ameiurus nebulosus*, continued in constant darkness. Endogenous rhythmic change in the body color of the killifish *Fundulus heteroclitus* was reported by Kavaliers and Abbott (1977). On the other hand, also arrhythmical reactions under constant condition have been frequently reported in fishes (Eriksson, 1975, cited in Van Veen et al., 1976). We should discriminate between the existence of mechanisms of endogenous rhythmicity and the actual appearance connected with some kinds of biological activity.

The considerably fixed values of light intensity at the action commencement of *P. aurantiacus* may be understood as a result of two antagonistic demands in its life. One is the native demand for darkness to guard themselves from enemies including predators. The other is the necessity of action for foraging, etc. The earlier a catfish begins its foraging, the more its catch may become in interspecific and intraspecific competition for food. As shown in Fig. 8, nearly half the food taken in a day was eaten during the comparatively short time immediately after the commencement of nocturnal action. Because this result was obtained under experimental conditions in which the fish could easily catch food supplied with movements of short distance, it may not directly reflect feeding in their natural habitat. However, it may be safely said that the large amount of food

intake immediately after the nocturnal action commencement indicates high degree of feeding intensity at that time, which should be related to lack of daytime feeding. Contrasting to nocturnal action commencement, however, the relationship with the light intensity becomes loose at action termination. This difference may come from inequalities in the feeding intensity in the evening (probably in hunger) and in the morning (after feeding at night). At least worth of these times is not equivalent for the survivalship in these nocturnal fishes.

The time of nocturnal action commencement and termination became irregular, and ranged over a large extent on the time bands, at low water temperatures such as 7.5°C (Fig. 3). Under such low water temperatures, this catfish became inactive for a whole day (for instance, the mean value of spike frequency during the night was 3.5 times per hour at 7.5°C), and both the nocturnal action commencement and termination occurred independent of changes of light intensity. This may be concerned with hibernation in this species, though their winter life in a natural habitat is not well known.

Literature cited

- Bünning, E. 1973. The physiological clock. Circadian rhythm and biological chronometry. 3rd ed. After the Japanese translation by Furuya, M. and T. Furuya (1977), University of Tokyo Press, Tokyo, 290 pp., 134 figs.
- Chiba, Y. 1975. The biological clock. Mechanism of circadian rhythm. Iwanami Shoten, Tokyo, 244 pp., 77 figs. (In Japanese).
- Darnell, R. M. and R. R. Meierotto. 1965. Diurnal periodicity in the black bullhead, *Ictalurus melas* (Rafinesque). Trans. Amer. Fish. Soc., 94: 1~8, figs. 1~4.
- Itô, Y. and M. Murai. 1977. Study methods in animal ecology. Kokin Shoin, Tokyo, 558 pp., 190 figs. (In Japanese).
- Kavaliers, M. and F. S. Abott. 1977. Rhythmic colour change of the killifish, *Fundulus heteroclitus*. Can. J. Zool., 55: 553~561, figs. 1~10.
- Miyadi, D., H. Kawanabe and N. Mizuno. 1976. Coloured illustrations of the freshwater fishes of Japan. New ed. Hoikusha, Osaka, 462 pp., 56 pls.
- Moyle, P. B. 1976. Inland fishes of California. University of California Press, 405 pp., 134 figs.

- Okada, Y. 1960. Studies of the freshwater fishes of Japan. Prefectural University of Mie, Tsu, 860 pp., 133 figs., 61 pls.
- Okada, Y. and R. Shiishi. 1937. Morphological and ecological studies of the larvae and young of freshwater fishes in Japan. (4) *Pseudobagrus aurantiacus* (T. and S.). Suisan Kenkyūshi, 32: 620~623, figs. 1~7. (In Japanese).
- Scott, W. B. and E. J. Crossman. 1973. Freshwater fishes of Canada. Fish. Res. Board. Can., Ottawa, 966 pp.
- Van Veen, Th., H. G. Hartwig and K. Müller. 1976. Light-dependent motor activity and photo-negative behavior in the eel (*Anguilla anguilla* L.). Evidence for extraretinal and extrapineal photoreception. J. Com. Physiol., 111: 209~219, figs. 1~5.
- Welsh, J. H. and C. M. Osborn. 1937. Diurnal changes in the retina of the catfish, *Ameiurus nebulosus*. J. Comp. Neurol., 66: 349~359, figs. 1~4.

(Department of Zoology, Faculty of Medicine, Teikyo University, Hachioji, Tokyo 192-03, Japan)

ギバチの日周活動における光要因の役割

益子 計夫

夜行性を示すギバチの日周活動について、アクトグラフを用いて種々の水温のもとでの夜間活動の開始と終了時刻、および照度との関係を実験的に調べた。ギバチは日没時前後から活動を開始し、活動開始がピークとなる照度は、水温 11°~20°C で 10^{-3} lux 台、水温 25°~30°C で 10^{-2} lux 台とほぼ一定しており、外界の照度と深い相関を示した。一方、活動開始後 3 時間以内で、1 日の全摂餌量の約半分が摂食され、外界の照度低下に依存する活動開始の規則性は、この時刻における高い摂食強度に裏うちされたものではないかと推測された。ギバチは恒暗条件では終日活動を続行し、また恒明条件では終日活動が抑制され、いずれの場合でも明暗周期下で認められた活動の周期性は失なわれる。これらの事実から、ギバチの活動は外界の光の強度低下に一義的に規定されているものと思われる。

(192-03 八王子市大塚 359 帝京大学医学部動物学教室)