THE EFFECTS OF LIGHT ON CIRCADIAN OXYGEN CONSUMPTION IN TIGERFISH, *TERAPON JARBUA*

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Bao-Quey Huang and Tsuey-Rong Chang (1991) The effects of light on circadian oxygen consumption in tigerfish, *Terapon jarbua*. *Bull. Inst. Zool., Academia Sinica* 30(2): 107-116. This paper examines the influence of light on circadian oxygen consumption in the tigerfish (*Terapon jarbua*) measured and compared among three experimental photoperiods (natural, all-light and all-dark).

Three results were obtained: (1) Tigerfish showed a circadian rhythm of oxygen consumption with peaks at 6:00 and 18:00. (2) There was a significant difference in oxygen consumption ($p<0.005$) between daytime and nighttime periods under a natural photoperiod, while no significant differences occurred between them under all-light or all-dark conditions. (3) There were significantly different oxygen consumption levels during all-day, daytime and nighttime between all-light and all-dark conditions, and between natural and all-dark conditions.

It was discovered that the circadian rhythm of oxygen consumption in tigerfish may be regulated by endogenous mechanisms to become a twilight activity and it may also rely upon the mediation of exogenous light.

Key words: Circadian rhythm, Oxygen consumption, Tigerfish.

The ability of a teleost to integrate habitant information in adjusting its own metabolic rate would be advantageous for its adaptive abilities. It would allow the animal (the organism) to regulate a more flexible metabolism in order to successfully meet environmental oscillations (Delahunty and Vlaming, 1980). Therefore, metabolic rate is one of the identifiable rhythmic patterns in animals and is usually measured as a rate of oxygen consumption that arises from the total of the energy-demanding processes (Brady, 1982) Consequently, oxygen consumption rhythm can be considered as a significant result of the animal's physiological and behavioural activities.

Fish living in subtropic habitats where the aquatic environment is frequently oxygen-limited (Ross and Mc-Kinney, 1988), should evolve a significant adaptive oxygen consumption ability. Teleosts display various rates of respiratory changes with fluctuations in environmental conditions with circadian rhythm representing one of these peculiar adaptations (De Silva *et al.*, 1986; Ross and McKinney, 1988). Studies on oxygen consumption of tropical or subtropical species are rare and those in relation to changing environmental parameters are

even rarer (De Silva *et al.*, 1986).

Circadian rhythm in teleosts is affected by interactions between both the endogenous and exogenous rhythms and is a species-specific characteristic (Baba and Sano, 1987; Brodeur and Pearcy, 1987; Huang, 1989; Mashiko, 1979; Priede, 1978). The tigerfish (*Terapon jarbua*) is considered a potential species for mariculture in Taiwan and the Pescadores (Liao, 1988). If and when it becomes a popular species for intensive culture in the Taiwan area, circadian oxygen consumption should be a crucial factor in determining feeding strategies. However, little is known about the diurnal variations in respiratory metabolism of this species. The aim of this research is to develop a general understanding of the circadian rhythm of oxygen consumption in order to estimate the total energy requirements of the tigerfish throughout its daily activities. Oxygen consumption here is considered as an index of circadian rhythm integrated over both endogenous and exogenous conditions. The present study was also designed to assess the possible role of light, an exogenous factor,

in affecting daily oxygen consumption under all-light or all-dark conditions, in order to obtain a better understanding of basic respiratory physiology and to create better rearing conditions.

MATERIALS AND METHODS

Tigerfish (*Terapon jarbua*) obtained from off the east coast of Mid-Taiwan were brought to the dapartmental laboratory of the National Taiwan Ocean University. They were maintained in an aquarium (195×120×105 cm) containing recirculated and well-aerated sea water (salinity: 34‰) under a natural photoperiod at water temperatures of 18±1°C for more than two weeks prior to experimentation. During the acclimation period, food was presented daily at noon.

Ten healthy fishes of 10.0–11.3 cm in length were chosen for this study. Each fish was placed in a one-litre bottle plugged with inlet and outlet tubes (Fig. 1). All bottles were immersed in a 140-L plastic opaque tank filled with water. To ensure that well-filtered, air-saturated water was supplied to the test bottle,
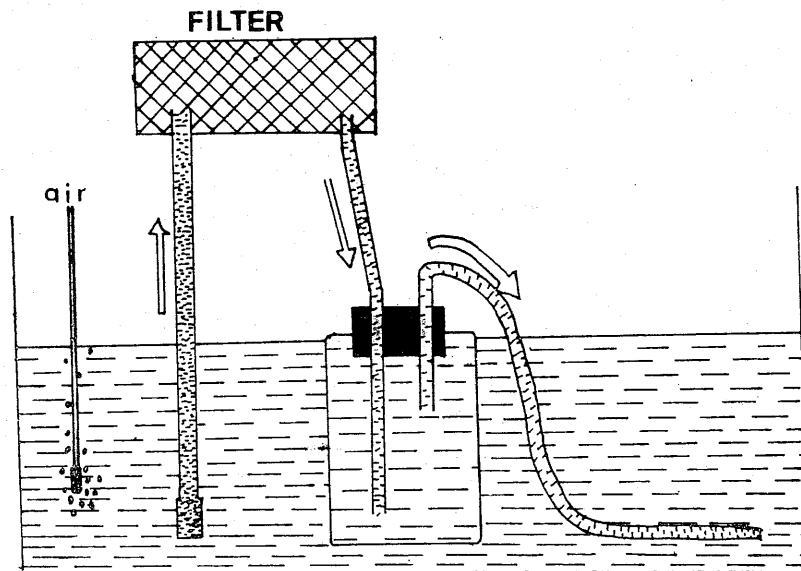

Fig. 1. Schematic diagram of the experimental arrangement used to measure the oxygen consumption rate of tigerfish. Arrowheads point in the direction of the circulated water.

one tube connected with the filtering apparatus was used for delivering water. The other tube served as the outlet. To minimize external stimuli, water-samplings were carefully performed from the extended portion of the exit tube, and all experimental tanks were set in isolated places away from the sounds of people walking and traffic. It is well recognized that oxygen consumption rates may vary greatly at different levels of extraneous activity, a "still", closed and recirculated test chamber was designed to minimize the variance and to assume the effects of daily timing.

Measurements of oxygen concentration were made using a dissolved-oxygen probe (Delta, Model 4010). Samples of 100 ml test water were collected at the beginning and completion of each 30-min experimental period. Although the test bottles apparently were unstirred, the swimming of the experimental fish served as a stirring function to ensure proper mixing of the contents. The inlet tube for delivering water was shut during the experimental period to keep the water in the test bottle still and to deliver oxygen to the test bottle. Because oxygen uptake is dependent on ambient O_2 concentration, the water in the respiration bottles was circulated with the air-saturated water in the experimental tank. Rates of oxygen consumption were calculated from the differences between these two readings, and was expressed in mg/g/hr (mg oxygen per gram body weight per hour). However, the extent of oxygen consumed was small and the efficiency was identical at the same 30-min experimental periods. Rates were measured over a 72-hour period at four-hour intervals. The fishes were not fed during this period to minimize the effects from feeding activity.

Fishes placed in the test bottles were allowed to settle and acclimate overnight. The data were not collected until the next afternoon. ANOVA (Analysis of Variance) tests analyzed the differences between daytime, nighttime and twilight periods among 6 measured daily records of data.

To assess the potential role of light in regulating circadian rhythm, oxygen consumption was measured over a 120-hour period at two-hour intervals under three light conditions (i.e. natural, all-light and all-dark). Nine fishes were used under three light regimens. There were three experimental animals for each condition (one died during the continuous darkness experimental period). The Student's t-test was also applied in comparing the variation of daily oxygen consumption.

RESULTS

Fig. 2 shows diel changes of oxygen consumption for three days among five individuals. Fig. 2A demonstrates three-day means of oxygen consumption in each individual and Fig. 2B presents the fluctuation rates over three-day experimental periods in each individual. Under a natural photoperiod, oxygen consumption of individual fish revealed considerable variation, while the diel oxygen consumption more or less demonstrated a cyclic trend (Fig. 2B). The peaks of the daily uptake cycles from five replicated individuals coincided with periods between twilight and darkness. Table 1 shows the statistical differences of averaged oxygen consumption among daytime (10:00 to 14:00), twilight (6:00 and 18:00) and nighttime (22:00 to 2:00) by the Student's t-test. The results showed that there was no difference in rates of oxygen consumption between twilight and nighttime, but significant differences occurred between daytime and
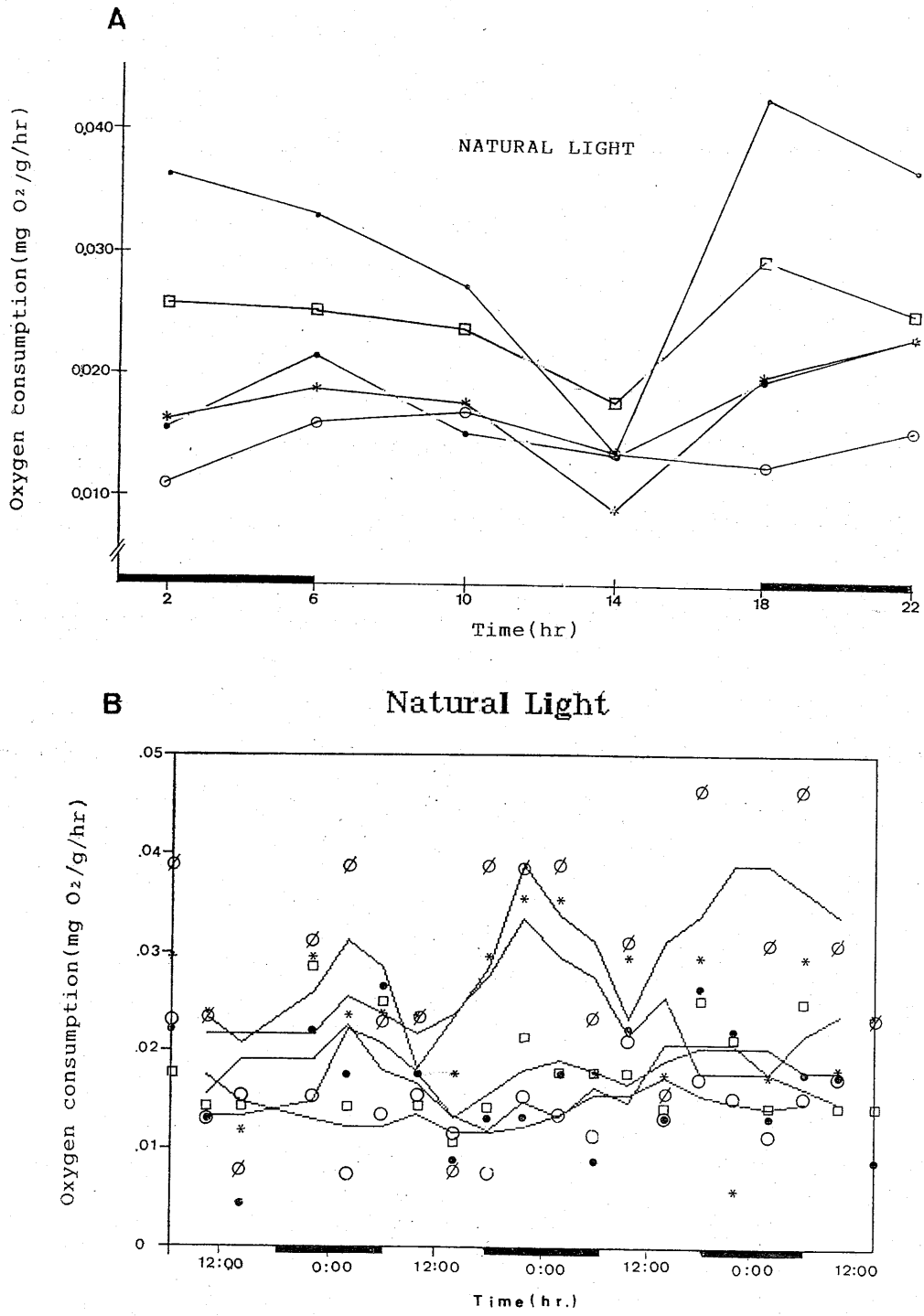
Fig. 2. Diel changes of oxygen consumption rate (mg O_2/g/hr) with time of day (mean of three days). The black segment on the abscissa shows night periods (18:00-6:00). A: Each value of measured interval derived from the means of three-day measurements. B: Curves derived from three-point moving averages.

Table 1

Mean, standard deviation and Student's t-test for the means of oxygen consumption (mg O_2/g/hr.) obtained from daytime, nighttime and twilight under natural photoperiod

Means and Standard deviation

		Means	Standard deviation
daily		0.021176	0.008239
daytime	(10:00, 14:00)	0.016782	0.005325
nighttime	(22:00, 2:00)	0.022859	0.008737
twilight	(6:00, 18:00)	0.023886	0.009016

Student's t-test

	t-value
twilight/nighttime	0.258832
twilight/daytime	2.145437**
nighttime/daytime	1.878068*

* mean significant at $p<0.1$ (two tails)
** mean significant at $p<0.05$ (two tails)

twilight ($p<0.05$), and between daytime and nighttime ($p<0.1$).

To investigate the potential role of light on the circadian rhythm of oxygen consumption, three experiments were done simultaneously under three light regimens (natural photoperiod, continuous light and continuous darkness) (Fig. 3). The rates of oxygen consumption of fish at each light regimen were compared using the Student's t-test (Table 2). Means and standard deviations of oxygen

Table 2

Mean, standard deviation and t-test for the means of oxygen consumption (mg O_2/g/hr.) in different dailytime and under different photoperiods (NL: natural, LL: all light, DD: all dark)

A. Mean and standard deviation of oxygen consumption during daily, daytime and nighttime trials

	Daily		Daytime		Nighttime	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
NL	0.016108	0.002503	0.014703	0.001520	0.018216	0.002208
LL	0.016059	0.001513	0.016060	0.001494	0.016057	0.001609
DD	0.012634	0.000962	0.012399	0.000744	0.012986	0.001186

B. t-test for daytime and nighttime under three photoperiods

t-value	Daytime v.s. Nighttime
NL	5.173841**
LL	0.004785
DD	1.365517

C. t-test for different pairs of photoperiods

t-value	Daily	Daytime	Nighttime
NL/LL	0.092343	2.700731*	2.737019*
NL/DD	6.876127**	5.512635**	6.472121**
LL/DD	9.390560**	8.874366**	4.610556**

* Mean significant at $p<0.025$ (one tail)
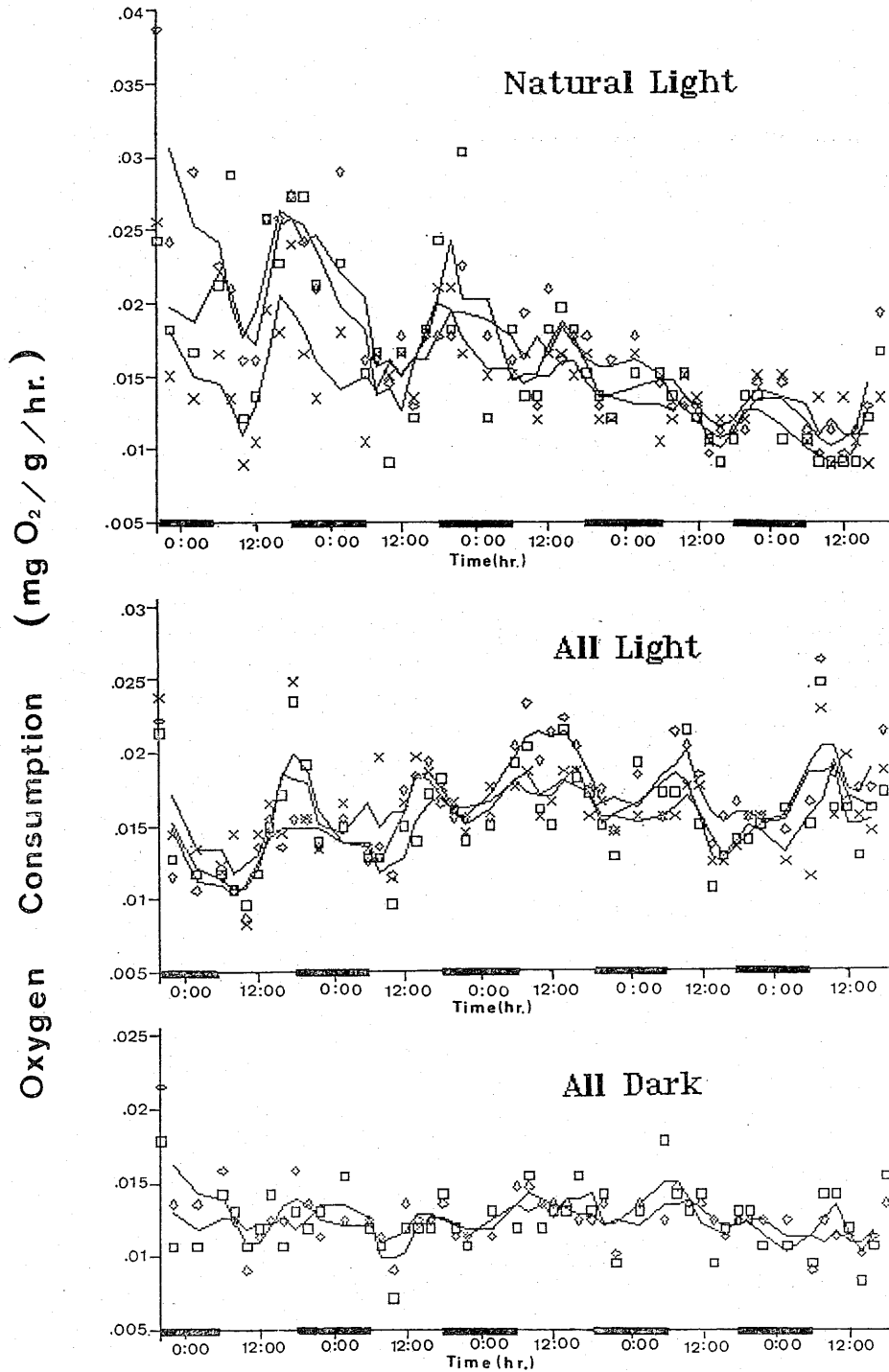** Mean significant at $p<0.005$ (one tail)

Fig. 3. The effect of photoperiods on daily oxygen consumption rate (mg O₂/g/hr). Three repli-
cated individuals (one died during continuous darkness experimental period) used for five
continuous days. Curves derived from three-point moving averages.

consumption during all-day, daytime and nighttime under three photoperiods are shown in Table 2A. There were significant differences between mean rates of oxygen consumption for daytime (6:00–16:00) and nighttime (18:00–2:00) during the five-day test period under natural photoperiods (Table 2B, $t=5.174$, $p<0.005$), while no significant differences occurred under either all-light or all-dark conditions (Table 2B, $t=0.005$ and $t=1.366$, respectively). It was also demonstrated that the oxygen consumption rate decreases through the daily cycle under all-dark (from natural 0.0161 to 0.0126 mg/g/hr), while oxygen consumption did not differ greatly between natural and all-light groups (from 0.0161 to 0.0160 mg/g/hr). Mean oxygen consumption during daytime changed from 0.0147 to 0.0124 mg/g/hr under all-dark and from 0.0147 to 0.0161 mg/g/hr under all-light conditions (Table 2A). Table 2C uses the Student's t-test to compare the means of oxygen consumption among all-day, daytime and nighttime under three different light conditions. The results indicate that the oxygen consumption of both daytime and nighttime were significantly different ($p<0.025$) between groups under natural photoperiod and those under all light conditions. When comparisons were made of oxygen consumption of all-day, daytime or nighttime between all-dark and natural photoperiod and between all-dark and all-light the results showed that all were significantly different ($p<0.005$) as shown in Table 2C.

In summary, the tigerfish is a twilight-active teleost with a higher oxygen consumption at dawn (6:00) and at dusk (18:00). Light can enhance oxygen consumption, while darkness can inhibit oxygen consumption. Light, an exogenous factor, probably functions as an enhancer in oxygen consumption.

DISCUSSION

It is evident that performance capacity of a teleost in integrating environmental fluctuations such as the influence of photoperiod in regulating its own activities is a crucial adaptation. Of these fluctuation factors, photoperiod often interacts with other factors but also acts independently of rhythm caused by some physiological activities (Delahunty et al., 1978; Delahunty and Vlaming, 1980). Blaxter (1980) has stated that vision is a crucial sense for many near-surface teleosts and that many fishes exhibit their diel rhythms of feeding by intensive feeding at dawn after a period of nocturnal non-availability of food, followed by daytime satiation and then a second feeding at dusk. Therefore, switching the light on and off would gradually influence the animal's activities by endogenous mediation. Animals should sooner or later adapt to such changes in their rhythm cycle. In addition, it is likely that predation pressure is decreased during low-light hours (Townsend and Winfield, 1985). Thus, fish with dim-light vision could solve the conflict between searching for prey and being hunted by predators at the same time. Under any circumstances it seems reasonable to state that maximum feeding activity coincides with a balance between prey and predator feeding. The tigerfish, a twilight-active species, has probably evolved in this way in order to gain from this advantageous adaptation.

Handling in experimental facilities is one of the stress mechanisms that affects fishes' metabolic rhythm (Donaldson, 1981; Schreck, 1981). To a twilight-feeding teleost, all-day lighting could be another stress factor that might produce a variety of physiological responses and/or behavioural changes. The oxygen consumption rate could then become non-cyclic. However, these results can be

attributed to the influence of light which causes the stress and causes the oxygen consumption rate to fluctuate, probably *via* some endogenous control system (Donaldson, 1981; Knight, 1985), while the evidence of the endogenous origin is very clearly influenced by exogenous light.

Delahunty and Vlaming (1980) stated that the length of the day is involved in regulating diurnal metabolic rhythms. Teleost diurnal activities affected by the photoperiod as well as by the time of day are probably responsive to endogenous changes in either the endocrine or the neural control system, which have the ability to alter the circadian rhythm of the hormonal or alert mechanism (Ross and Mckinney, 1988). Thus, elevation or depression of oxygen consumption is certainly influenced by environmental, experimental and fish internal conditions (Mitz and Newman, 1989). The circadian activity of tigerfish was maintained in the twilight pattern under a natural photoperiod, while in the present study it was shifted to an arythmic pattern under continuous darkness or lightness. Ross and Mckinney (1988) found that both constant light or constant darkness did not affect the cyclic respiratory rhythm of Tilapia (*Oreochromis niloticus*) over a 7-day period. They also stated that endogenous control plays a potential role in respiratory cycles. During periods of constant darkness or constant light, the circadian pattern of oxygen consumption in the present investigation revealed inconsistent results and therefore might be mediated by an inconsistent mechanism. It is readily apparent that the circadian rhythm of oxygen consumption in tigerfish is influenced exogenously. Thus, it is difficult in this study to specify the relative importance of endogenous and exogenous factors because many interacting and influencing factors have yet to be understood.

Furthermore, Mashiko (1981) stated that actual nocturnal action of catfish (*Silurus asotus*) in the field may be mediated by both endogenous rhythmical system and exogenous environmental factors. In addition, the free-running circadian rhythm in total light and in complete darkness may be initiated by an intrinsic timing system. The periodic nocturnal action of another catfish species, *Pseudobagrus aurantiacus*, was stimulated into activity without periodicity with continuous illumination (100 lux). The light intensity was considered a key factor in the switching of their activity (Mashiko, 1979). It is well recognized that circadian rhythms could be important in defining better aquacultue strategies, therefore major food acceptance by tigerfish seems to occur at twilight, prior to dawn and at dusk in each 24-hour cycle. However, it is clear that the regulation of circadian rhythm is a remarkable species-specific mechanism and further studies are indeed required to determine how light plays its role in modulating circadian rhythm in tigerfish.

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光照對花身鷄魚 (*Terapon jarbua*) 耗氧之
日夜周期性之影響

黃　寶　貴　　　張　翠　容

爲瞭解光照對花身鷄魚（*Terapon jarbua*）耗氧之日夜周期性之影響，本實驗利用三組不同光照周期（自然光照，全光照及全黑暗）以比較其影響。

實驗結果顯示：(1)花身鷄魚之日夜周期性中，每日之耗氧在 6:00 和 18:00 爲高峰。(2)在自然光照組，其日、夜之耗氧量呈顯著差異 ($p<0.005$)，而全光照及全黑暗組兩者之日夜間之耗氧量，則無顯著差異。(3)全黑暗組與全光照組間，及其與自然光照組間，比較兩者間之全天，日間及夜間各別之耗氧量，均顯著差異。

因此，花身鷄魚之日夜耗氧量之周期性受本身內在機制 (endogenous mechanism) 之調節，而呈現「微暗」(twilight) 之活動周期，且外在光照確實對該魚種之日夜耗氧量造成影響。