EFFECTS OF TEMPERATURE AND LIGHT ON AERIAL BREATHING BEHAVIOR OF THE SPOTTED GAR, LEPISOSTEUS OCULATUS¹

GERARDUS C. DE ROTH

Department of Natural Systems, The Defiance College, Defiance, Ohio 43512

ABSTRACT

The affects of temperature and of light on air-breathing activities of five spotted gar (*Lepisosteus oculatus*) were studied in the laboratory during the summer of 1965. A total of 4320 "fish-hours" of surface breathing activities were recorded using "ripple detectors" and a six-channel physiograph.

Numbers of aerial breaths per hour increased as temperature increased from 55° to 80°F. Rates of breathing were consistently higher during hours of darkness than during light hours. Significantly higher rates of breathing during the hour following light changes were attributed to a "shock effect", from the unnatural instantaneous change of lighting. Highest rates of aerial breathing were recorded during the post-offset hour. Evidence is presented suggesting 65–75°F as the "thermal preferendum" for this particular group of spotted gar.

It was concluded that the rate of aerial breathing is a valid index of total respiratory oxygen-demand which may be influenced by, but not necessarily determined by, gross variations in dissolved-oxygen content of the water. No significant correlation between average rates of aerial breathing and dissolved-oxygen content of the water was detected within the range of concentration (1-4.5 ppm) existing during this study.

INTRODUCTION

Many of the early studies of air breathing in fishes placed most emphasis on structural adaptations of accessory breathing organs such as the air bladder. More recently, studies emphasizing the physiological and behavioral aspects of air breathing in fishes have appeared in the literature (Dehadrai, 1962; Grigg, 1965; Todd and Ebeling, 1966; Johansen, Lenfant, and Grigg, 1966/67; Johansen and Lenfant, 1967 and 1968; Johansen, Lenfant, and Grigg, 1967; Lenfant and Johansen, 1968; and Johansen, Lenfant, and Hanson, 1968). All of these studies, however, have concentrated upon exotic species such as the lungfishes and other tropical fishes.

The air-breathing habit in North American fishes such as the bowfin (Amia calva) and the gars (Lepisosteus) has received somewhat less attention than the aerial breathing habits of exotic fishes. Among the early papers, Potter (1927) made a very detailed study of air breathing in gars. More recently, Saksena (1963) and Winston (1967) contributed reports on the effects of light and temperature on air-breathing behavior of gars. Excellent studies of both the physiological and behavioral aspects of aerial and aquatic respiration among the gars have been contributed by McCormack (1967, 1970) and by Rahn, et al. (1971). Horn (1965) and Johansen, Hanson, and Lenfant (1970) have contributed to the knowledge of the air-breathing habit of the bowfin from both the physiological and behavioral points of view.

The present study examines certain aspects of the relationships among light, temperature, and the air-breathing behavior of the spotted gar.

PROCEDURE

The effects of temperature and of artificial light periods on the aerial breathing behavior of the spotted gar (*Lepisosteus oculatus*) were studied during the period 6 June 1965 to 13 August 1965 at the University of Oklahoma Biological Station at Lake Texoma.

Fish were collected after dark using an electric shocker along the shoreline of

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the Buncomb Creek arm of Lake Texoma. Five individuals from 38 to 51 centimeters in total length were selected for the study. One fish was placed in each of five 50-gallon aquaria. Water temperatures in the aquaria were controlled thermostatically to within 1.5°F (0.83°C) at each of six temperatures, starting at 55°F (12.8°C) and progressing upwards in increments of five degrees F (3.2°C) to 80°F (26.6°C) in all the aquaria.

Lighting, which consisted of five 400-watt cool white fluorescent tubes, installed on the ceiling of the room, was controlled by a time switch. Lights were turned on (onset) at 0630 hours and off (offset) at 1830 hours. Dissolved oxygen ranging between 1.0 and 4.5 ppm was monitored daily, using the standard Winkler procedure. During three-day intervals between experimental runs, the fish were

fed live minnows and acclimated to the next higher temperature.

Aerial breathing activities, as indicated by disturbances of the water surface, were recorded by a ripple detector (Saksena, 1963). The ripple detector, as developed at the University of Oklahoma by Dr. Carl Riggs and his students, consists of a ping pong ball suspended by a taut thread from a myograph transducer connected to an E and M physiograph. The apparatus was adjusted so that the slightest disturbance of the water surface would be recorded. The physiograph recordings provided a permanent chronologic record of surface-breathing activities of each gar.

Surface-breathing activities of the five fish were recorded continuously for six days and nights at each of the six experimental temperatures, providing a total of 4320 fish-hours of recordings for interpretation. The data for each of the six-day recording periods were partitioned to provide average numbers of breaths per hour during the hours of light and of darkness, and for the hour before and the hour after each light change. For purposes of this discussion, time periods are designated as follows: day or daylight, 0730–1730; night, 0930–0530; pre-onset, 0530–0630; post-onset, 0630–0730; pre-offset, 1730–1830; post-offset, 1830–1930 hours.

RESULTS

Effects of Temperature and Light on Aerial Breathing

Average hourly rates of aerial breathing increased as the temperature of the water was raised from 55° to 80°F (Table 1, fig. 1). The rate of increase was greatest between 55° and 70°F. From 70° through 80°F, the number of breaths per hour continued to increase, but at a somewhat reduced rate.

Average numbers of breaths per hour were significantly greater at all temperatures during the hours of darkness than during the daylight hours. Maximum differences between rates of breathing during light and dark were reached from 65° to 75°F.

Aerial-breathing activities during post-onset and post-offset were significantly greater than were average rates of breathing during the remainder of the corresponding day and night photoperiods, with the greatest numbers of breaths per hour occurring during post-offset (fig. 1). Higher rates of aerial breathing during post-offset occurred at all temperatures, but were greatest at 65° and 70°F. At temperatures above 70 F, changes in lighting elicited lesser responses than they did at lower temperatures.

Aerial breathing activities during post-offset and post-onset were consistently greater in the 55° to 70° range, when compared to averages for the preceding days and nights. Greatest increases in surface-breathing rates occurred at 65°F during post-offset. Somewhat smaller increases in aerial breathing rates were characteristic of the post-onset hours, with a maximum at 70°F. Above 70°F, increases in rates of aerial breathing during post-offset where less than at 70°, but remained greater than the average rates for the preceding daylight hours. At the two higher temperatures, however, the change from night to day seemed to have had a depressant effect on post-onset breathing activity. Resulting average

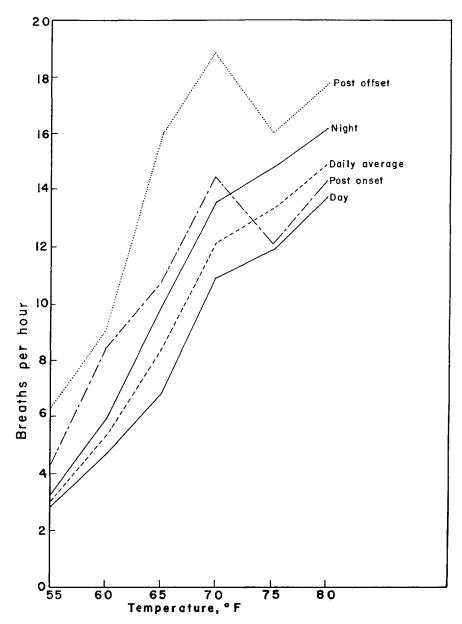


FIGURE 1. Mean number of breaths per hour at six different temperatures.

rates of aerial breathing for the post-onset period were actually lower than average rates for the preceding night hours (fig. 2).

Daily Rhythm in Aerial-Breathing Activities of the Spotted Gar

Daily rhythms of aerial breathing were examined by plotting averages of numbers of breaths per hour for each hour of the day versus time of day at each

Table 1
Average daily rates of aerial breathing of spotted gar at six different water temperatures

Average numbers of breaths per hour							
Temperature		0.41		10.1		10 1	
°F	°C	period	S.E.*	12-hour night	S.E.	12-hour day	S.E
55	12.8	2.83 ± 0.121		3.03 ± 0.167		2.63 ± 0.357	
60	15.5	5.37 ± 0.147		5.97 ± 0.187		4.78 ± 0.209	
65	18.4	8.23 ± 0.226		9.98 ± 0.318		6.88 ± 0.144	
70	21.1	12.10 ± 0.288		13.56 ± 0.395		10.89 ± 0.761	
75	23.9	13.39 ± 0.229		14.84 ± 0.308		11.94 ± 0.239	
80	26.6	14 79:	± 0.234	16.22 ± 0.182		13.84 ± 0.368	

^{*}S.E.—standard error.

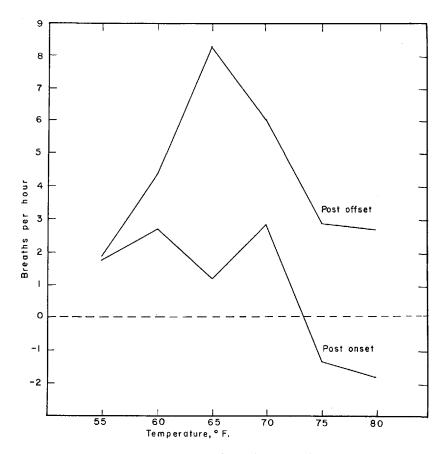


FIGURE 2. Differences between average numbers of breaths during the hour following light changes and average numbers of breaths per hour for the preceding day and night.

of the six experimental temperatures (fig. 3). Maxima of breathing activities during post-onset and post-offset are conspicuous features of the 24-hour cycle. Slight increases in breathing rates during pre-onset and pre-offset at all temperatures except at 75° are also detectable. Although the pre-onset and pre-offset increases are not statistically significant, when compared to averages for corresponding days and nights, they are, nevertheless, reasonably consistent features of the daily cycle.

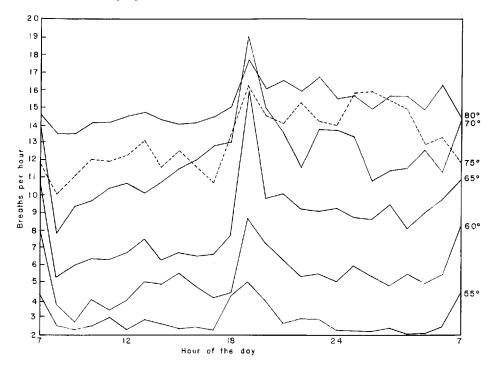


FIGURE 3. Average numbers of breaths per hour for each hour of the 24-hour day at six different temperatures.

Two gradual trends in rates of aerial breathing are discernible within the daily cycles at the five higher temperatures. Hourly rates for the 24-hour period generally are lowest during the first daylight hour (hour following post-onset), and thereafter increase gradually to pre-offset. Similarly, there is a slight declining trend in numbers of breaths per hour from the earlier to the later hours of night, although the decreases are neither as regular nor as conspicuous as the daytime upward trend.

DISCUSSION AND CONCLUSIONS

Freshwater gars generally are considered to be facultative rather than obligatory air breathers. However, if free to surface, gars do not necessarily conform to true facultative status. They continue rising to the surface to gulp air even at the highest levels of dissolved oxygen. Whether this behavior reflects an inability to satisfy respiratory needs by use of the gills alone or serves some additional function such as hydrostasis is not completely clear, but some direct relationship between total metabolic needs and rate of aerial breathing seems evident.

Others have reported on studies of aerial breathing. Saksena (1963) has reported increased aerial-breathing activity following feeding, presumably the

direct result of increased metabolic activity associated with the digestive processes. Grigg (1965) feels that activity is more important than deoxygenation of the water in determining air-breathing activity in the Queensland lungfish (Neoceratodus forsteri) within a dissolved-oxygen range of from 7.0 to 12.0 ppm. In contrast, Johansen, Hanson, and Lenfant (1970) state that ". . . oxygen deficiency in the water is considered the most important single factor favoring selection of air breathing in fishes." Observations by Rahn, et al. (1971), however, suggest that there is little or no correlation between oxygen tension of the water and rate of aerial breathing in the Longnose gar (L. osseus). In still another study, McCormack (1970) found that gar (L. platyrhincus) were obligate air breathers at levels of oxygen lower than 4.5 ppm and that active gar were obligatory air breathers even at higher oxygen concentrations.

In the present study, the gar were probably behaving as obligatory air breathers, in view of the low concentrations of dissolved oxygen (1.0–4.5 ppm) to which the fish were exposed, and the absence of any correlation between oxygen tension and aerial breathing rates. If gar are obligatory air breathers at low concentrations of dissolved oxygen, as some evidence suggests, then any extrinsic or intrinsic factor affecting metabolism should be reflected in rates of aerial breathing. That such a relationship exists seems to be confirmed by the aerial-breathing response of the spotted gar to an increase in temperature (Table 1, fig. 1), since it is generally conceded that metabolic rates of poikilotherms are related directly to environmental temperature.

Diurnal-nocturnal differences in activity rates and metabolic rates have been widely accepted as indicative of the daily activity patterns of animals in their natural habitats. Such a conclusion was reached by Grigg (1965), who correlated greater frequency of air breathing with increased nocturnal activity of Neoceratodus forsteri under field conditions. Similar results have been reported by Saksena (1965), by Winston (1967), and by Horn (1965), working with spotted gar, alligator gar (Lepisosteus spatula), and Amia calva, respectively. An increase in nocturnal-feeding activity in the Florida gar (L. platyrhincus), has been observed by Hunt (1960). The significantly higher nocturnal rates of air breathing among spotted gar probably also reflect a natural pattern of increased activity during the hours of darkness.

The significant increase in breathing rates associated with changes in light intensity seems to be a phenomenon independent of average diurnal-nocturnal differences in air-breathing behavior. Under natural conditions, changes from light to dark and from dark to light are gradual phenomena, whereas the change in lighting in the experimental setup used in this study was instantaneous. The increases in breathing activities of the spotted gar during post-offset and post-onset were almost certainly responses to changes in light intensity and may have been associated with a "shock" effect, or with a circadian rhythmic increase in activity during crepuscular periods.

The former interpretation, involving "shock" effect, seems more acceptable when the artificial conditions imposed upon the fish are taken into consideration. The shock effect can be explained by means of the stimulus-response theory, which states that any change in an external condition imposed upon an organism is generally regarded as a stimulus resulting in an attempt by that organism to adapt (react) to that change. Furthermore, the degree of response to any change in condition is frequently related to the rate of that change. In addition, it has been found that some fishes seem to have a circadian rhythm of sensitivity to external stimuli, and that periods of greatest sensitivity correspond to dawn and dusk (Zusser and Chestnol, 1963). Perhaps the combination of a sudden change in light intensity at times of greatest sensitivity to external stimuli explains the increased rates of breathing during post-onset and post-offset.

Not explained, however, is why the average number of breaths per hour for

the first hour following light changes decreases so unexpectedly in the 75°F and 80°F ranges (figs. 1 and 2). A similar phenomenon is mentioned in a discussion of aquatic respiration in fishes by Fry (1957). Active metabolic rates of some fishes breathing by means of gills alone show a pattern of oxygen consumption in relation to temperature that is similar to the air-breathing response of spotted gar during post-offset and post-onset. Since increases in rates of air breathing during these periods appear to be in response to the external stimulus of light change, it seems reasonable to assume that the gar are metabolically more "active" than during the intervening days and nights, thus corresponding to an active metabolic condition in aquatic breathers. Average breathing rates during day and night, the periods during which the stimulus of a sudden light change is lacking, then could be comparable to a condition of standard metabolism in gill-breathing The difference between active metabolism and standard metabolism has been interpreted as the scope for activity, and the temperature at which the greatest scope for activity occurs has been interpreted as the optimum temperature for activity of the fish (Fry, 1957). The maximum differences between active and standard metabolism, or scope for activity, among the spotted gar used in this study, occurred at 65° and 70°F. The further increase in rate of aerial breathing at 80°F following a decrease at 75°F may be an indication of additional spontaneous activity associated with temperatures approaching the lethal limit for spotted

Similar results have been reported by Sullivan and Fisher (1947), who found that spontaneous movements and oxygen consumption of brook trout (Salvelinus fontinalis) increased directly with temperature, reaching a maximum at the thermal preferendum for the species. As the temperature was gradually increased above the thermal preferendum, spontaneous activity first decreased and then increased

again, until the lethal temperature was reached.

One further feature of the daily cycle of breathing activities (fig. 3) is the slight increase in rate of aerial breathing during the hour preceding the light change. Although most evident during the pre-offset hour (1730–1830), there is some indication of a similar increase during the pre-onset hour (0530–0630). Davis (1964) has shown that bluegills and largemouth bass, under conditions very similar to those used in this study, exhibited what he called a "predawn peak" of activity. He attributed this to an ability of the fish to predict the change by means of an inherent rhythm, which controlled the daily-activity cycle. Apparently the spotted gar also is capable of predicting a change of condition before the change occurs, providing the fish has become accustomed to a daily rhythm over a long enough period of time.

Much work remains to be done in investigating the behavioral and physiological aspects of air breathing in gars and in other fishes of similar habit. Data presented here are certainly not conclusive and the author admits to a certain amount of speculation concerning the results of this study in the hope that such speculation may serve to stimulate further experimental work on the subject of air breathing

in fishes.

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