THERMOREGULATION OF FISH AND TURTLES IN
THERMALLY STRESSED HABITATS

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ABSTRACT

Morphometric and heating and cooling studies on over 100 largemouth bass, Micropterus salmoides, have provided the data we needed to refine our time dependent body temperature model for fish. The model can now track the changes in body temperature of a bass if its weight and water temperature are known. The line generated with the model for predicted time constants vs body weight falls within the 95% confidence limits for the experimentally derived time constants vs body weight for 25 bass ranging in weight from 200 to 2700 g. The model is most sensitive to body diameter, body wall thickness and tissue conductivity. Doubling tissue conductivity is equivalent to decreasing body diameter by a factor of two.

Turtles, Chrysemys scripta, living in the heated portion of a cooling reservoir facultatively exploit the warmed water ($\Delta T = 4-10^{\circ}\text{C}$) as an auxiliary heat source for behavioral thermoregulation. Turtles in the heated arm of PAR pond have a smaller home range (200 m) than turtles in an ambient portion of the reservoir (507 m). The movement and home ranges of up to 30 turtles are being measured by telemetry. Basking behavior of turtles has been predicted from laboratory and field data.

The ability of animals to thermoregulate at a high constant body temperature depends upon the constraints imposed on them by their body size and physical characteristics and those of their environment. The net heat production required to maintain a specific body temperature changes as the size of an ectotherm increases.

Operative environmental temperature is an appropriate measure of environmental heat loading and can be used as a predictor of turtle behavior. This concept may become very valuable in quantifying the effect of thermal effluents on turtle and fish behavior.

Since June 1977 three articles have been published, five are in press, four are in review, and three are in preparation. Six papers have been presented at scientific meetings this year.

Introduction

The purpose of this research has been to determine quantitatively the mechanisms by which fish and turtles thermoregulate in response to thermal stress in their natural environment. During the last year significant progress has been made in laboratory and field studies of fish and turtles and in theoretical analysis of the mechanisms by which large ectotherms exchange heat with their environment and thermoregulate. In addition considerable effort has been expended in analyzing data and writing manuscripts based on our research of the previous two years.

Specific objectives to be accomplished in the last project year were to 1.) Complete laboratory testing of the climate space for the turtle, Chrysemys scripta, 2.) Begin formulation of a transient energy budget for this turtle, 3.) Test our first approximation model for time dependent heat flow in the largemouth bass, Micropterus salmoides, 4.) Continue field studies to quantify the extent to which turtles use thermal effluents in PAR pond as a heat source for thermoregulation, and 5.) Continue theoretical calculations on the effect of body size and physical characteristics on the thermoregulation of large ectotherms.

Significant progress has been made toward reaching all of these objectives. They are best discussed in order.

Turtle Studies - Laboratory

The first two objectives dealt with turtle thermoregulation. We completed experiments in the climate space simulation chamber that provided information required to test our steady state climate space for Chrysemys scripta. In addition we continued our analysis of evaporative water loss from turtles. We found that wind speed, air temperature, body size and vapor density

differences were the controlling variables in determining rates of water loss. We described the interaction of these variables using multiple regression equations (Fig. 1) and then made predictions of basking behavior based on those equations and field data from our PAR pond studies (Foley and Spotila 1978a).

At this time (June 1978) we continue our analysis in order to produce a transient energy budget model for C. scripta. During the past year Robert Foley completed another series of laboratory experiments to determine the convection coefficients of turtles in air and water. He used the technique of Erskine and Spotila (1977) to obtain convection coefficients in still and moving water and also completed wind tunnel tests for convection coefficients in air. Turtles act like spheres in air and have convection coefficients similar to those reported for spheres by Mitchell (1976). All laboratory experiments are now complete and we are conducting computer simulations to produce predictions of daily and seasonal behavior of these turtles in natural and thermally altered environments. We plan to complete a manuscript in the next few months that will include a cost benefit analysis of turtle thermoregulation similar to that of Huey and Slatkin (1976) for lizards.

Largemouth Bass Studies

Two series of heating and cooling experiments and a morphometric study have been completed on largemouth bass, Micropterus salmoides, during the past 1 1/2 years. Initial laboratory experiments carried out at the environmental physiology laboratory at the State University of New York at Buffalo were important in developing a time dependent model for heat flow in the bass. After initial simulations with the model we designed two new studies. In the first we completed a detailed morphometric analysis of over 100 bass from PAR pond. Measurements included length, weight, diameter, body wall thickness, skull

thickness and heart body wall thickness. This provided information needed to generate a more accurate body temperature model. Typical results are given in figures 2, 3 and 4. In the second study Richard Kubb conducted a series of heating and cooling tests on bass from PAR pond at the Savannah River Ecology Laboratory (SREL). He measured heart, brain, and core (gut) temperatures of 25 bass ranging in size from 200 to 2700 g. while they were heated and cooled, alive and dead, in still and then moving water. There was no difference in the time constant for the heart with change in body size. Changes in body core temperature lagged behind heart temperature, especially in larger fish (Figure 5).

The time dependent model was accurate in tracking the body temperature of an individual fish (Fig. 6). The line generated with the model for predicted time constants vs body weight fell within the 95% confidence limits for the experimental time constants vs body weight from the SREL experiments (Fig. 7). A small change in tissue conductivity could put the predicted line right on top of the experimental line. Since tissue conductivity was not measured but was taken from the literature for dead fish muscle we feel that these results are quite promising. Measurement of tissue conductivity for live fish will be an important experiment for the next project year.

Sensitivity analysis of the model has indicated the components of the fish that are primarily responsible for changes in heating and cooling rates. Body diameter and body wall thickness act independently in governing the rate of temperature change of a fish (Fig. 8). For all fish sizes a change in body diameter has a slightly greater effect on time constant than a similar change in body wall thickness. Changes in tissue conductivity are also very important (Fig. 9). The effect of doubling the tissue conductivity is equivalent to decreasing the body diameter by a factor of two.

By October 1978 Richard Kubb should complete and defend his thesis. Then we will prepare a manuscript for publication based on the data discussed above. In the next project year we will begin field experiments to record the behavior of bass in Pond C on the Savannah River Plant. These experiments will concentrate on the thermoregulatory behavior of bass that live in a cool sanctuary cove of Pond C and are exposed to heated effluents along the edge of their home range. A graduate student will observe these bass while recording body core, heart and deep muscle temperatures of one or more fish on a minute by minute basis using radio telemetry.

These experiments will be needed to further test the model and to begin to enlarge it to include behavioral components. More details of this field study are provided in the renewal proposal.

PAR Pond Field Studies

Turtles, Chrysemys scripta, living in the heated portion of a cooling reservoir facultatively exploit the warmed water ($\Delta T = 4-10^{\circ}\text{C}$) as an auxiliary heat source for behavioral thermoregulation. During 2,300 people hours of intensive observation on PAR pond since 1975 we have not seen any turtles basking in the Hot Arm (Fig. 10) although they bask in all ambient portions of the reservoir. Turtles in the heated areas often had body temperatures (measured by telemetry) within their preferred limits ($26-34^{\circ}\text{C}$). These conclusions became clear as we analyzed our 1974-1977 PAR pond field data over the course of the last year. They are summarized in Spotila et al. (1978). Our microclimate studies on PAR pond have been reported in Foley and Spotila (1978b).

During this project year Joseph Schubauer has been measuring the home ranges and movement patterns of C. scripta in thermally altered and ambient regions of PAR pond. He has been supported by a student fellowship from

SREL and by this contract. He studied turtles in the Hot Arm and West Arm of the reservoir by trapping and radio telemetry. Turtles in the West Arm had a larger home range (507.5 m, N = 6) than turtles in the Hot Arm (200.0 m, N = 7) as measured by telemetry. These differences were not apparent from the trapping data (Fig. 11).

Examining these results, we conclude that (1) our present trapping records underestimate the home range of C. scripta in Par Pond, (2) turtles can be very mobile and are not as sedentary as suggested by previous authors, and (3) thermal effluents introduced in the Hot Arm of Par Pond have influenced the behavior of the turtles, C. scripta, as measured by home range differences. The difference in home range size exhibited by turtles in the Hot Arm compared to those in the West Arm could be translated as either a direct thermal effect on C. scripta (i.e., physiological) or an indirect thermal effect acting on the habitat or resources of C. scripta. The introduction of thermal effluents in the Hot Arm possibly creates a patchy habitat, which might act to restrict the movement of C. scripta to smaller areas or "sanctuaries."

During 1977 Schubauer tracked the movements of 17 adult C. scripta using locational radio transmitters. He now is monitoring 29 turtles, 17 in the Hot Arm and 12 in the West Arm. He should complete his data gathering by this winter and will complete his thesis by June 1979. At this time he is preparing a manuscript for publication based on the basking behavior study conducted on PAR pond during the summer of 1976.

Theoretical Analysis

Some of our most exciting progress has been in the area of theoretical calculations on the effect of body size and physical characteristics on the thermoregulation of large ectotherms. Results of these calculations have been

detailed in a paper in press (Spotila 1978) in a AAAS symposium volume on dinosaur temperature regulation.

I found that the ability of animals to thermoregulate at a high constant body temperature depends upon the constraints imposed on them by their body size and physical characteristics and those of their environment. Thus there may be more similarities between the thermoregulatory capacities of large reptiles and mammals than between large and small members of either class alone. The net heat production required to maintain a specific body temperature changes as the size of an ectotherm increases (Fig. 12). Metabolic requirements are reduced for all large animals and we expect to see a convergence of heat production and insulative capacities as the size of animals increase.

As a result of this analysis it is apparent that we should pay more attention to the mechanisms by which large ectotherms maintain their heat balance with their environment. One of the best model systems for such studies is the American alligator, Alligator mississippiensis. While we completed our investigations of alligator thermoregulation in 1977 we now plan to conduct a new series of investigations. These experiments will be designed to answer a number of questions that have arisen as a result of our theoretical studies.

We already know that there are quantitative and qualitative differences in the manner by which large and small alligators exchange heat with their environment, (Terpin et al. 1978) Small alligators (total length < 100 cm) are much more affected by convection and conduction than larger animals. Physiological thermoregulation has its primary importance in altering internal heat flow within the animal thus enhancing the physical heat transfer properties already present in large alligators due to their increased body size. Numerous investigators have studied the thermoregulation of alligators, (e.g., Grigg and Alchin 1976, Smith 1975, 1976a, b, c, Smith and Adams 1978, Standora 1977, as well as ourselves). Despite these studies a number of important questions remain unanswered.

These center around the role of the circulatory system in the internal heat distribution of large ectotherms such as alligators and the role of tissue conductivity in heat flow through the skin and body wall of these animals.

During the next project year we will study the heat distribution inside alligators and will obtain accurate values for tissue conductivity of the skin and body wall musculature. An attempt will be made to measure blood flow at the skin and regionally in the body during heating and cooling in a cooperative study with Dr. David Pendergast of the SUNYAB Physiology Department. Details of these experiments are given in the renewal proposal.

Operative Environmental Temperature

Another major area of theoretical concern has been an evaluation of George Bakken's concept of operative environmental temperature as an effective means of describing the complex microclimate of an animal in its natural habitat. Bakken and Gates (1975) and Bakken (1976) have defined operative environmental temperature as the environmental temperature seen by the animal and stated that it was equivalent to the temperature of a blackbody cavity producing the same thermal load on the animal as the actual non-blackbody microclimate.

During the past year we have analyzed this concept and have had George Bakken, C. Richard Tracy and Warren Porter visit Buffalo for discussions on this topic. We have now concluded that operative environmental temperature is a most appropriate measure of environmental heat loading and have already applied it as a predictor of turtle behavior (Foley and Spotila 1978a).

Beginning in the next project year we will conduct experiments to determine the operative environmental temperatures of turtles in ambient temperature and thermally affected areas of PAR pond and Pond C. These experiments

are detailed in the renewal proposal. We will also analyze our 1974-1977 field data in an attempt to relate behavior of turtles to their operative environmental temperature. This concept may become very valuable in quantifying the effect of thermal effluents on turtle and fish behavior.

Concluding Comments

During the past year three articles have been published (Erskine and Spotila 1977, Bonin and Spotila 1978 and Terpin et al. 1978), five articles are in press (Foley and Spotila 1978a, Paladino and Spotila 1978, Foley et al. 1978, Kowalski et al. 1978), four are in review, and three articles are in preparation. We presented four papers at the Stress Symposium at SRL-SREL in November 1977, one at the American Society of Zoologists meeting in December 1977 and one at the Association of Southern Biologists meeting in Spring 1978. Two masters theses should be completed by December 1978.

The project director, James R. Spotila, spent 100% of his time on this investigation in June 1978. He spent 50% of his time on this project during the 1977-78 academic year.

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Figure 1. Three dimensional plot of evaporative water loss of Chrysemys scripta as a function of body weight, vapor density difference (VDD) and wind speed (V). Plane outlined with dotted lines is water loss in still air (10 cm s⁻¹), plane outlined with dashed lines is water loss at 100 cm s⁻¹, and plane outlined with solid lines is water loss at 400 cm s⁻¹. This function is described by the equation:

$$\log \text{EWL} = -0.249 + 0.172 \log V + 0.472 \log \text{VDD} - 0.420 \log W$$

Figure 2. Regression of total length vs body weight for largemouth bass, Micropterus salmoides, collected from PAR pond, on the Savannah River Plant. Regression line was computed by the method of least squares.

Figure 3. Body diameter at mid point of gut vs body weight for largemouth bass collected from PAR pond on the Savannah River Plant. Regression line was computed by the method of least squares.

Figure 4. Body wall thickness vs body weight for largemouth bass collected from PAR pond on the Savannah River Plant. Solid line with circles is for the gut, dashed line with triangles is for the brain, and dotted line with squares is for the heart. Regression lines were computed by the method of least squares.

Figure 5. Time constants vs body weight for body core (thermocouple inserted through body wall) - solid line with circles, cloaca - dashed line with triangles, and heart - dotted line with squares. Experiment was on live largemouth bass heated in still water. Regression lines were computed by the method of least squares.

Fig. 6 - Comparison of predicted and experimental heating curves and time constants for two fish tested under laboratory conditions at the environmental physiology laboratory, S.U.N.Y. at Buffalo.

A. Fish total length (28 cm.) and body diameter (3 cm.).

B. Fish total length (35 cm.) and body diameter (4 cm.).

In both A and B solid lines indicate predicted cloacal and muscle temperatures. Solid circles and solid triangles represent experimental cloacal and muscle temperatures.

Figure 7. Predicted and experimental time constants vs body weight for the body core of largemouth bass heated alive in still water. Solid line is regression line for actual data. Dashed line is predicted line from mathematical model.

Fig. 8 - Combined effect of body diameter and body wall thickness on predicted time constants. Body diameters range from 2.0 cm to 20.0 cm. Body wall thicknesses range from 0.2 cm to 1.0 cm.

Fig. 9 - Effect of tissue conductivity on predicted time constants over a range of body diameters for two different body wall thicknesses (1.0 - 0.2 cm). Tissue conductivities range from 0.038 cal cm⁻¹ min⁻¹ °C⁻¹, to 0.152 cal cm⁻¹ min⁻¹ °C⁻¹. The value 0.076 cal cm⁻¹ min⁻¹ °C⁻¹ represents a normal tissue conductivity for fish flesh taken from Bowman et al. (1975).

Par Pond

Figure 10. Map of PAR Pond on the Savannah River Plant. Cooling water flows from Pond C into PAR Pond at point H. Most of Beyers Bay and all of the reservoir outside the Hot Arm remained at ambient water temperature throughout this study. The Hot Arm has a $+\Delta T = 4-10^{\circ}\text{C}$ throughout the year. Points A, B and C were our main observation sites in 1975-77. We have not observed turtles basking in the heated portion (stippled area) of the Hot Arm.

Figure 11. Straight-line distance of individuals telemetered and trapped in the Hot Arm (HA) and the West Arm (WA). Means are represented by the largest vertical lines and ranges are depicted by horizontal lines bounded by two smaller vertical lines (sample size is given to the right of the $\bar{x}$ for each group). Rectangles illustrate estimates of μ at the 95% C.I. Where the rectangles do not overlap, a significant difference exists ($P \leq 0.05$) between groups.

Figure 12. Net heat production (M-E) required of ectotherms as a function of body size, body temperature and climate. Insulation (fat) thickness was a constant 10% of body diameter. Temperatures are in °C, wind speed is 100 cm s⁻¹ and radiation absorbed is in cal cm⁻² min⁻¹.