THERMOREGULATION AND TEMPERATURE RELATIONS OF
ALLIGATORS AND OTHER LARGE ECTOTHERMS
INHABITING THERMALLY STRESSED
HABITATS

Summary Progress Report

For Period 1 October 1974-30 September 1977

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Abstract

Significant progress has been made in determining the mechanisms by which large ectotherms adjust to thermal stress in their natural environment. The effect of mouth gaping on head temperatures and the role of radiation, conduction and convection on body temperatures of alligators have been determined. The utility of energy budget modeling as a method for studying the thermoregulatory mechanisms of animals has been demonstrated. Steady state and time dependent models of body temperature have been tested.

Convection coefficients and evaporative water loss rates have been measured for the turtle, Chysemys scripta. Climate space diagrams have been formulated and are being tested. Behavioral thermoregulation of turtles has been studied in PAR pond on the Savannah River Plant, Aiken, S. C.

Steady state energy budget equations have been computed for largemouth bass. Experimental heat transfer coefficients indicate that most heat transfer is through the body wall and not via the gills. A time dependent model is being tested. It predicts the body temperature of a fish in a heterothermal environment.

Theoretical calculations have been made of the effects of body size, color and metabolism on the temperature regulation of ectotherms. CTM tests are useful indicators of stress in aquatic organisms.

Six articles have been published, 3 are in press, 2 in revision, 2 in review and 6 in preparation. Six masters theses have been completed. Nine papers have been delivered at national meetings and 5 more are scheduled for presentation this summer.

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Introduction

The overall purpose of this project has been to determine quantitatively some of the mechanisms by which large ectotherms adjust to thermal stress in their natural environment. During the 2½ years (October 1974-June 1977) that this project has been underway we have made significant progress in meeting this goal. We have accomplished most of our long term (3 year) objectives on schedule and milestones of progress have been met each year as projected in our annual proposals (see annual progress reports COO-2502-4, COO-2502-5, and COO-2502-13). We have reported the results of our research in eleven scientific articles in journals such as NATURE, PHYSIOLOGICAL ZOOLOGY, COMPARATIVE BIOCHEMISTRY AND PHYSIOLOGY, and COPEIA, in six masters theses, and in nine presentations at national scientific meetings. This summer (July 1977) I will present our findings on the thermoregulatory adaptations of the alligator at the XXVIIIth International Congress of Physiological Sciences in Paris, France.

Specific long term aims for this project as stated in the initial research proposal were to 1.) conduct laboratory studies on the physiological and behavioral bases for thermoregulation in alligators and large turtles 2.) carry out field studies on the body temperatures and thermoregulatory behavior of alligators, turtles, and bass in thermally loaded environments at the Savannah River Ecology Laboratory (SREL), 3.) construct energy budgets and climate space diagrams for all of the species being studied and 4.) begin measurements on the body temperatures of free swimming muskellunge in Lake Chautauqua, New York.

Details of our progress in meeting these objectives have been given in the annual progress reports cited above. The purpose of this summary report is to give an overall synopsis of this project to date (June 1977) and to indicate the degree to which specific and long term aims, have been met. This report and the annual progress report for 1976-1977 (COO-2502-13) provide the background for the renewal proposal for 1977-1978.

Progress Towards Specific Objectives

The first specific objective was to conduct laboratory experiments on the physiological and behavioral bases for thermoregulation in alligators and large turtles. Laboratory experiments on alligators will be essentially complete by the end of this contract year. We have measured the effect of mouth gaping on the head temperatures of alligators (Spotila et al. 1977), have determined the effect of radiation, conduction and convection on the body temperatures of these animals (Terpin and Spotila 1977) and have discovered an effect anesthetic for alligators (Terpin et al. 1977). We have completed half of the time dependent experiments in the Climate Space Simulation Chamber (C.S.S.C.) and will complete the remainder by October 1977. We plan to finish evaporative water loss measurement on alligators this summer. We have shown that the steady state energy budget model (Spotila et al. 1972) is correct and our results to date indicate that the transient model is also a good predictor (Spotila et al. 1973). We will complete all alligator experiments by October, 1977, and will need about six more months to prepare our results for publication.

Robert Foley has measured convection coefficients and rates of evaporative

water loss for the turtle Chrysemys scripta in air. He has also formulated a steady state climate space for this animal (Foley and Spotila 1977a, b). At this time he is measuring the body temperatures of turtles exposed to various microclimates in the C.S.S.C. in order to test the accuracy of the climate space model. Later this summer he will determine the convection coefficients of turtles in still and moving water. The object of these measurements will be to determine the limiting factor(s) in the transfer of heat between a turtle and the water. That is, the relative importance of the shell, physiological changes such as blood flow, and water movement in the heat exchange process. Completion of these experiments will help us to develop an equation to predict heating and cooling rates of turtles exposed to thermal effluents. These experiments (in C.S.S.C. and in water) will continue into the next project year. Plans to develop a time dependent energy budget model for the turtle were deemphasized in order to concentrate on the transient energy budget for the fish and on analysis of field data on the thermoregulation of turtles in PAR pond at SREL. Next year we will resume efforts at time dependent modeling in conjunction with the experiments discussed above.

The second specific objective was to conduct field studies on alligators, turtles and largemouth bass. We conducted some observational studies of alligators and one intense field experiment at PAR pond as part of our study on mouth gaping (Spotila et al. 1977). We curtailed all other field studies on alligators at SREL in deference to the research being conducted there by Dr. I. Lehr Brisbin and Mr. Edward Standora. We have cooperated in their study by lending our expertise and time and have cooperated with Dr. J. W. Gibbons in collecting alligators along the coast of South Carolina. We used these animals in our laboratory experiments.

We have conducted extensive and intensive field studies on turtles in PAR pond at SREL. Progress has been reported in the third annual report COO-2502-13. To summarize, we have conducted experiments and made observations during all seasons of the year. We have spent two summers studying turtles in thermally affected and control sites. At this time we are analysing data and preparing manuscripts for presentation at the ecosystem stress symposium to be hosted in November, 1977, by SREL; and for publication. In addition, Joseph Schubauer, a graduate student, is now conducting an intensive field study of turtles at PAR pond. He is jointly supervised by Dr. Gibbons and myself. He is supported by SREL, by this ERDA contract, and by a small grant from the faculty of Natural Sciences of this college.

Preliminary observations have been made on largemouth bass in PAR pond. Additional experiments are planned for this summer. These are detailed in the annual progress report (COO-2502-13). They are designed to test the transient energy budget model that we are developing for fish. More extensive use of PAR pond bass is planned for the future. We have held off on large scale field studies to date in order to emphasize development of mathematical models and laboratory tests of model parameters. After an acceptable time dependent model has been formulated and tested we will conduct further field experiments to validate the predictive capability of the model.

Our third objective has been to construct energy budgets and climate space diagrams for all of the species being tested. We have validated the steady state energy budget and climate space for the alligator (Terpin 1976, Terpin and Spotila 1977) and are presently testing the time dependent energy budget model. Foley (1976) produced a steady state energy budget and climate space for the turtle Chrysemys scripta. He also determined convection

coefficients for this animal. These results are summarized in an article in preparation (Foley and Spotila 1977a).

We have made very important progress towards formulating steady state and time dependent energy budgets for fish using largemouth bass (Micropterus salmoides) as a model animal. Originally we planned to conduct field studies on the response of bass to thermal effluents in PAR pond on the Savannah River Plant, Aiken S. C. We also planned to construct a climate space for this fish. Taking advantage of our initial success in theoretical analysis of heat exchange between a fish and its environment we have shifted our goals and made much more progress towards a predictive, time dependent, mathematical model that we originally planned for the first three years of this project.

Dale Erskine provided a great impetus to this part of our project by formulating a steady state energy budget model for the bass and demonstrating that most heat transfer occurred directly through the body wall and not via the gills (Erskine 1976, Erskine and Spotila 1977). These findings provided a basis for time dependent modeling. Rather than tracking bass in thermal effluents, research already being done by Charles Coutant at Oak Ridge National Laboratory (Coutant 1975), we decided to hold off on field studies and concentrate instead on development of a time dependent model. Richard Kubb has formulated a transient model to predict time dependent temperature change of a fish in a heterothermal environment. We plan to test this model this summer in the laboratory and in the field in PAR pond. By October, 1977, we will have sufficient data to evaluate it. Next project year we will concentrate on data analysis and systems identification to determine the accuracy and precision of this model. Eventually we plan to be able to predict the temperature of a fish as it swims in and out of a thermal effluent and ultimately we hope

to couple behavioral parameters to this model in order to predict the behavior of a fish in response to such an effluent. See the annual progress report for 1976-1977 (COO-2502-13) for a further discussion of this topic.

Our time dependent modeling of fish body temperatures is complementary to the research of Spigarelli and his colleagues at Argonne National Laboratory (Spigarelli et al. 1977, Spigarelli 1975, Spigarelli et al. 1974, Romberg et al. 1974, and Beitingner et al. 1977). They have tracked salmonids in thermal effluent plumes, have studied heating and cooling rates and reported on heat transfer between gizzard shad, Dorosoma cepedianum, and water. Our study is also complementary to some of the research being conducted at Oak Ridge National Laboratory by Coutant and his colleagues. They are studying the effects of water temperature, velocity and turbulence on the behavior of fish (Griffith 1977, Bowles 1976), temperature selection by fishes in the field (Coutant 1975) and the effects of cold shock on susceptibility of fish to predation (Coutant et al. 1976, Wolters and Coutant 1976). We have been approaching fish-temperature questions from a theoretical viewpoint while these researchers have been more field or directly problem oriented. Our plan is to develop a time dependent model of fish body temperature that will be useful in predicting the response of a fish to a heterothermal environment. This will provide a theoretical basis for field studies such as those of Coutant and Spigarelli and should provide insight into the mechanisms by which fish respond to thermal effluents in their natural environment.

The fourth objective of this project as stated in the original proposal was to begin measurements on the body temperatures of free swimming muskellunge in Lake Chautauqua, New York. The rationale for this was that this fish, being very large, might show specific adaptations in its response to water temperature

that were not evident in smaller freshwater fish. This objective was not pursued during this project for the following reasons: First, it was not directly related to the problem of a fish in a thermal effluent--muskellunge are not normally found in such situations. Second, the rapid development of the modeling effort on largemouth bass promised more substantial results and in turn required a much greater input of time and effort. We deemphasized the muskellunge research in order to concentrate on the bass model. Third, the field study of turtle behavioral thermoregulation in PAR pond has developed into a major effort and has dominated our field time. Again, this forced us to curtail field studies of the muskellunge. In the future we may return to the muskellunge as an example of a large freshwater ectotherm if our analytical efforts suggest that such a study would be worthwhile.

Additional Research

In addition to the studies discussed above, we have become involved in two other research areas during the course of this project. The first is a mathematical analysis of the effect of body size and physical characteristics on temperature regulation of ectotherms and the second is the development of model systems for the study of stress in aquatic organisms. Mathematical analysis of heat energy transfer (Spotila et al. 1972, 1973) provided a framework for the studies on thermoregulation that we have conducted during this project. During this project we have continued our efforts in this area, and have examined theoretically the role of body size, color, and metabolism in the temperature regulation of ectotherms. The validity of this approach has been demonstrated by our experimental findings of the past 2½ years (see annual

progress report COO-2502-13). During the past year we have used our time dependent mathematical model for the body temperatures of large reptiles to compute the effect of color, size and metabolism on the body temperature of ectotherms. These projections provide a framework for the design of future experimental studies.

Our efforts towards the development of model systems for the study of stress arose from studies on the effects of temperature and arsenic on larval fish and minnows. As a result of these studies we have found that the Critical Thermal Maximum (CTM) test for temperature tolerance is a useful indicator of stress. The application of a stress, such as a toxic material, the presence of a disease, or a developmental change in the life history of a fish will be indicated by a sharp decrease in its CTM. This will occur before any outward manifestation of other symptoms. Thus the CTM might be useful as a real time test for the screening of toxicants or as an indicator of stress in a natural population of aquatic organisms. For additional comments see annual report COO-2502-13.

Major Accomplishments

We have clarified the effect of mouth gaping on head temperature and the roles of radiation, convection and conduction in heat exchange between an alligator and its environment. We have demonstrated the utility of energy budget modeling as a method for studying the thermoregulatory mechanisms of animals. We have tested the steady state heat exchange models for the alligator in the laboratory and are now documenting the time dependent model.

Convection coefficients and climate space diagrams have been determined

for the turtle, Chrysemys scripta. We have also ascertained the roles of body size, wind speed, and air temperature in controlling evaporative water loss from this animal. Our field studies in PAR pond, on the Savannah River Plant, are clarifying the behavioral mechanisms employed by this turtle in adapting to thermal stress in its natural habitat.

We have delineated the mechanisms of heat transfer between a fish and its aquatic environment and have formulated steady state energy budgets to describe them. Most heat transfer occurs through the body wall, not through the gills. Water velocity does not appear to affect the rate of heat transfer.

During the course of this project we have published 6 articles and have 3 more in press. Two articles are in revision, 2 are in review and 6 are in preparation. Six masters theses have been completed. My students and I have presented 9 papers at national scientific meetings. We will deliver 5 more this summer including one at the XXVIIth International Congress of the Physiological Sciences in Paris, France, in July. We plan to deliver 4 papers at the symposium entitled, "Energy and Environmental Stress in Aquatic Systems," to be held in Augusta, Georgia in November, 1977. A list of Scientific Publications generated during this project is given in Appendix I.

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APPENDIX I

Scientific Presentations

Articles

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