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HEAT TRANSFER AND THERMOREGULATION IN THE LARGEMOUTH BLACKBASS, *MICROPTERUS SALMOIDES*

Abstract of Thesis

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Arts at the
State University College at Buffalo

By

Dale J. Erskine
Buffalo, New York

Director: Dr. James R. Spotila, Assistant Professor of Biology
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Buffalo, New York

1976

DISCLAIMER

ABSTRACT OF THESIS

HEAT TRANSFER AND THERMOREGULATION IN THE LARGEMOUTH BLACKBASS, MICROPTERUS SALMOIDES

An energy budget equation, based on energy budget theory for terrestrial organisms, was developed to describe the heat energy exchange between a largemouth bass (Micropterus salmoides) and its aquatic environment. The energy budget equation indicated that convection and a combined conduction-convection process were major avenues of heat exchange for a fish.

Solid aluminum castings were used to experimentally determine heat transfer coefficients for the largemouth bass at water velocities covering the free and forced convection ranges. Heat energy budget theory was applied to the casting data and the derived coefficients were used to characterize heat exchange between the bass and its aquatic habitat.

The results indicate that direct transfer of heat from the body surface is the major mechanism of heat exchange for a fish.

Dale J. Erskine

Date

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INTRODUCTION

Water temperature plays a significant role in the life history and physiological processes of fish. As ectothermic organisms with low metabolic heat production and relatively poor insulation, fish are closely coupled to water temperature (Fry and Hochachka 1970, Fry 1971). Fish exhibit some physiological thermoregulation and have been found to maintain body temperatures slightly above ambient (Stevens and Fry 1970, 1974, Spigarelli, et al. 1974). However, except for fast swimming tuna and shark, this thermoregulatory ability is minimal (Carey and Teal 1969 a, b).

Research centered on the temperature relations of fish has resulted in an abundance of data which relate temperature changes and physiological effects in a stimulus - response format for specific species. Numerous studies on the relationship of temperature to metabolic rate, performance, growth rate, and reproduction have been conducted. Much of our present knowledge of the temperature relations of fish stems from the early studies of Fry, Hart, and Brett (see Brett 1956, Fry 1964, 1967, Fry and Hochachka 1970, Prosser 1973 and Coutant 1974 for a review of the literature). The effect of factors such as sex (Baker, Neill and Strawn 1970), season (Tyler 1966), and photoperiod (Terpin, Spotila, and Koons 1976) on thermal tolerance have also been examined. To date these studies have led to a partial understanding of the interactions between a fish and its aquatic environment.

Parallel research has investigated the influence of warm water discharges on the distribution of fish. Bennett (1971) discussed the distribution and body temperatures of largemouth bass inhabiting an artificially heated reservoir. Neill and Magnuson (1974) investigated the distributional ecology and behavioral thermoregulation of fish near a heated effluent. Using acoustic temperature telemetry Coutant (1974) traced the movement of fish near a thermal discharge.

The rapidity with which a fish may experience a harmful physiological effect as a result of a change in ambient temperature is directly related to its rate of energy exchange with the environment. Recent studies (Stevens and Fry 1970, 1974, Spigarelli, et al. 1974, McCauley and Huggins 1976) examined heating and cooling rates of fish in an attempt to develop the ability to predict the behavior of fish in response to thermal effluents. Half-times for equilibration of body temperature with ambient temperature have been determined, interspecific similarities in heat exchange rates have been examined, and short term residence times have been calculated. Despite these efforts we still lacked the ability to accurately predict the responses of fish to changing temperatures in their natural environment. This was due to the absence of a theoretical framework which can be used to analyze the abundance of empirical data that has accumulated on the effects of temperature on fish.

In this study I have approached the problem by examining temperature response from the viewpoint of the effects of the physical environment on the fish. Instead of focusing on the physiological processes within the organism, I began by considering the heat energy exchange between the fish and its environment. In this way I could outline the constraints placed on the internal processes of the fish by the characteristics of its physical environment.

The objectives of this study were to: 1) determine the mechanisms of heat exchange between a largemouth blackbass (<u>Micropterus salmoides</u>) and its environment; 2) derive a heat energy budget equation for use in thermoregulation studies; 3) examine the steady-state energy balance for a bass; and 4) make an initial examination of time dependent heat exchange between the bass and its environment.

THEORY

1. Heat Energy Exchange

The body temperature of ectothermic organisms is closely coupled to their heat energy exchange. Animal heat energy budget theory was developed by Gates (1962), Birkebak (1967), and Porter and Gates (1969). Their equations describe the energy balance of terrestrial organisms.

For any animal to survive it must be able to balance heat input and heat output so that its body temperature will remain within tolerable limits. In animals that have a minimum capability for physiological adjustment of internal temperature, behavioral thermoregulation is often employed to maintain a relatively constant body temperature. By alternately exposing itself to different climatic conditions (i.e., full sunlight/full shade) a terrestrial animal can exercise control over its internal temperature. This ability has been demonstrated for the marine iguana, *Amblyrhynchus cristatus*, (Bartholomew and Lasiewski 1965), plethodontid salamanders (Spotila 1972), the American alligator, *Alligator mississippiensis*, (Murphy and Brisbin 1974, Spotila, *et al*. 1972, Spotila 1974), tadpoles (Brattstrom 1962), small flies (Heinrich and Pantle 1975), tenebrionid beetles (Henwood 1975), desert millipedes, *Orthoporus ornatus*, (Wooten, *et al*. 1975) and several other organisms. Hammel (1968) discussed regulation of internal body temperature in vertebrates. Templeton (1970) reviewed behavioral thermoregulation in reptiles and Cloudsley-Thompson (1970) discussed thermoregulation in terrestrial invertebrates.

Large fish are able to move into thermally adverse areas for short periods of time as long as they return to their zone of tolerance before acquiring an excess heating or cooling debt. The duration of these excursions depends upon the ability of a particular fish to withstand the effects of an unfavorable thermal regime. Temperature selection and behavioral thermoregulation through the application of "shuttling behavior" are discussed by Bardach and Bjorklund (1957), Bennett (1971), Neill, et al. (1972), Crawshaw and Hammel (1974), Coutant (1974), Neill and Magnuson (1974), Reynolds and Thomson (1974), Romberg, et al. (1974), McCauley and Huggins (1976), Reynolds and Casterlin (1976) and several others.

The overall energy balance of an organism is contingent upon the available modes of heat transfer. Heat exchange mechanisms are imposed by environmental conditions and the rate of heat exchange is governed by physical laws (though the rate may be modified by physiological adjustment). For terrestrial organisms heat exchange with the physical environment is accomplished through the combined effects of radiation, convection, conduction, and evaporation. Heat production also results from the assimilation of foodstuffs and muscular activity.

If an animal is assumed to be in a steady-state energy balance with the environment its energy budget can be described as heat in = heat out. This relationship is expanded by combining the modes of heat transfer into a single equation:

$$\text{ABSORBED RADIATION} + \text{METABOLISM} = \text{RERADIATION} + \text{EVAPORATION} + \text{CONDUCTION} + \text{CONVECTION} \qquad (1)$$

A more precise form of Equation (1) incorporates physical constants and expressions that apply to environmental parameters:

$$Q_{abs} + M = \epsilon \sigma (T_r + 273)^4 + h_c (T_r - T_a) + E_t + C \qquad (2)$$

where, Q_{abs} = total absorbed radiation
M = metabolic heat production
ϵ = surface emissivity
σ = Stefan-Boltzman constant
T_r = radiant surface temperature
T_a = ambient temperature
h_c = convective heat transfer coefficient
E_t = total evaporative heat loss
C = heat loss through conduction

Equation (2) is a generalized form of the heat energy budget equation described by Gates (1962), Birkebak (1967), and Porter and Gates (1969) for terrestrial organisms. Energy budget theory provides a means for quantifying both the physical and physiological mechanisms of heat exchange available to an animal. Using energy budget analysis it is possible to predict the microclimatic requirements of an animal. In order to apply this type of analysis to a fish the initial task was to modify the existing equations to conform to an aquatic habitat.

2. Heat Exchange in an Aquatic Environment

Heat exchange is defined as the transmission of energy between two regions as the result of a temperature differential. Modes of heat transfer are distinguished by means of transmission and properties of the medium through which heat is transmitted. Complete discussions of the individual modes can be found in an appropriate text (e.g., Kreith 1973). When considering the environment occupied by a freshwater fish, I determined that the available modes of heat transfer are restricted. Limitations imposed by the habitat and the morphology of the fish require that modifications be made to equation (2).

a. Absorbed Radiation and Reradiation

Incident solar radiation at the earth's surface is largely in the visible range with most thermal radiation being absorbed, scattered, or reflected in the atmosphere. The remainder warms surface water and is rapidly attenuated (Odum 1971, Eskinazi 1975). Further transmission of thermal radiation in water is negligible (Gates 1972). Therefore, direct warming by longwave radiation is not possible.

The absorbed radiation term, Q_{abs}, now limited to shortwave and visible, may prove to be a negligible quantity when considering an aquatic environment. Water transparency data indicate severe attenuation of solar energy within a meter of the surface for many inland lakes. If a highly productive body of water is considered, the extinction of light is even more marked. Ganf

(1974) noted that the relative spectral energy of incident radiation in Lake George, Uganda, approached zero within the upper fifty centimeters. Furthermore, any turbulence due to wave action increases the scattering of light and thereby decreases direct radiation.

Brattstrom (1962) demonstrated that toad tadpoles congregated in shallow waters exposing maximum dorsal surface areas to solar radiation. As a result, radiant energy was absorbed and the immediate environment was warmed. Brattstrom concluded that the effect of this behavior was to increase body temperature. Thus, it is possible that fish which periodically inhabit shallow waters or swim near the surface can gain heat through solar radiation. However, for a first approximation of the energy budget let us consider the fish to be occupying a depth where absorbed radiation is negligible.

Radiant cooling follows the blackbody law of radiation; that is, an object will radiate energy at a rate proportional to the fourth power of its absolute temperature. Emitted radiation at biological temperatures is longwave (Gates 1962, Kerslake 1972). Transmission coefficients for longwave radiation in water indicate that such transmission does not occur.

Eliminating solar radiation as a heat input and reradiation as a means of cooling, equation (2) is rewritten as:

$$M = h_c \ (T_r - T_w) + E_t + C \qquad (3)$$

where T_w is water temperature and replaces T_a in equation (2).

b. Evaporative Cooling

Evaporation involves a change from liquid to gas or vapor states. Evaporative cooling occurs when water moves outward through the skin of a terrestrial animal and changes to the gaseous state. Freshwater fish occupy an osmotically stressful environment and the osmotic gradient creates a driving force that tends to move water inward through the integument. This is counteracted by the impermeable nature of the integument (Evans 1969, Motais, et al. 1969, see also Bentley 1971). Even if water was transported through the skin or gills of a fish, evaporation could not occur because the water would not change in state. Thus, the expression for evaporation can be eliminated from equation (3) yielding:

$$M = h_c (T_r - T_w) + C \tag{4}$$

c. The Conduction - Convection Effect

Kreith (1973) defines conduction as a process by which heat is transmitted between two regions of different temperature within a medium or between different media in direct physical contact. Energy transfer through conduction is by direct molecular communication. In water, heat exchange by conduction is possible in the absence of appreciable fluid motion. In this situation heat is conducted from the fish across some distance in the water before density currents are set in motion by the temperature differential. Therefore, under conditions of still water, heat exchange will be by a combined conduction - convection process. This relationship is defined by equation (4).

d. The Convective Effect

Conductive heat transfer between the surface of an animal and a fluid becomes a complex process when the fluid is in motion. As Kerslake (1972) notes, "under conditions of interest in physiology the fluid near the skin is exchanged rapidly, and so far as the fluid is concerned the process can be regarded as in the steady state." Therefore, in the instance when a fish is exposed to fluid flow the major portion of energy exchange at the surface is primarily the result of the fluid movement. Water movement should affect the heat energy exchange of a fish in the same way that wind affects the energy balance of terrestrial organisms. Porter and Gates (1969), Heller and Gates (1971), and Spotila, et al. (1972) have demonstrated that, in terrestrial environments, body temperatures of animals become more closely coupled to air temperature as wind velocity increases. A similar convective effect should occur as a result of currents in an aquatic environment. This relationship is expressed as:

$$M = h_c (T_r - T_w) \tag{5}$$

Equation (5) implies that the primary mode of heat transfer available to a swimming fish is convection and that convective heat transfer is the most important mechanism for controlling the body temperature of a fish subjected to fluid flow.

3. Convection Theory

In the absence of radiation, convection or a combined conduction - convection process is considered the primary mode of heat transfer between a surface and a surrounding fluid medium. Heat transfer laws governing convection are derived from Newton's law of cooling. The rate at which heat is convected to or from an object is proportional to the surface area available for heat exchange and the temperature differential. Convection is the result of the combined action of conduction and fluid mixing motion. When heat is transported by the fluid, it is necessary to examine conduction, fluid dynamics, and boundary layer theory. Newton's law combines these parameters into a single equation:

$$\frac{dq}{dt} = h_c A(T_r - T_w) \tag{6}$$

where A is surface area, $(T_r - T_w)$ is the temperature differential, and the proportionality factor, h_c, is the convective heat transfer coefficient. Because surface geometry and fluid properties are not necessarily constant over the entire surface of the fish, equation (6) will yield an average convection coefficient.

Natural or free convection is a consequence of fluid motion generated by density differences. The "convection currents" are set up by the temperature differential. If an external force is the causative agent for the mixing motion, the convection is termed forced. Conduction may be neglected in the presence of forced convection.

The convection coefficient in equation (6) is an indicator of the rate of heat transfer. The coefficient is not a property of the material but is dependent on the properties of the fluid and the nature of the flow. The value of h_c is affected by the shape and configuration of the surface, orientation with respect to flow, physical properties of the fluid, velocity of flow, and temperature differential. For any object in a fluid medium, the coefficient will not be a constant but will vary with velocity, orientation, and nature of flow.

Convection coefficients have been derived for inanimate objects of various geometric shapes. Convective heat transfer laws generated by these studies have been used to evaluate the extent of convective heat transfer in conifers (Tibbals, et al. 1964), broad leaves of plants (Parkhurst, et al. 1968 a, b), several small animals (Porter and Gates 1969), small mammals (Heller 1972), tenebrionid beetles (Henwood 1975), jackrabbit ears (Wathen, et al. 1971), and the desert iguana (Porter, et al. 1973).

It is beyond the scope of this study to attempt to partition the conductive and convective components of heat transfer in still water. Therefore, an average heat transfer coefficient that encompasses both convection and conduction will be derived.

METHODS AND MATERIALS

1. Modeling

a. Aluminum Casting Construction

Five aluminum castings of _M_. _salmoides_ were constructed for experimental determination of the heat transfer coefficient. Preserved fish were imbedded in dental investment compound (Caulk Jeltrate or Bosworth Supergel) and then covered with a second layer of compound. This procedure yielded a nearly exact flexible mold of each fish. A positive wax cast of each fish was then made from the mold. Solid aluminum fish were then cast commercially by using the wax molds as models. This procedure is similar to that described by Porter, _et_ _al_. (1973) and Bakken and Gates (1975). The castings ranged from 19 to 42.5 cm in total length and 244 to 2938 g in mass. An initial test casting was sectioned to examine the uniformity and porosity of the aluminum. No flaws in the cast aluminum were detected.

The center of mass was estimated for each casting and 38 gauge copper-constantan thermocouples were inserted through 0.838 mm drilled holes and secured with epoxy. To facilitate suspension in water a supporting rod was attached to each fish by means of a tapped hole on the ventral surface. Non-conductive plastic rods were used for smaller fish and aluminum rods for larger casts. Heat loss through the plastic or aluminum rods was considered negligible because of differences in thermal conductivity and available surface area for heat loss.

Surface area of each casting was determined using a method described by W. P. Porter (personal communication). Briefly, each cast was covered with a layer of cellophane tape which was subsequently removed and spray painted. The tape mold was then placed flat on a sheet of paper and photocopied. The surface area was then evaluated using a Charvoz planimeter. Each surface area was checked by a second individual and all determinations were in close agreement.

The aluminum castings provided extremely accurate representations of size, shape, and body surface characteristics for each bass. I would like to note two shortcomings of the sand casting technique. It was necessary to construct the fins and tail in thicker proportions, to allow for free flow of the molten aluminum, and subsequently sand them to an appropriate thickness. The result was a loss of much of the fin and tail surface detail. However, the percent surface area for the fins and tail was consistent (21 - 24% of the total surface area) for each casting. Secondly, a loss of approximately 1 - 2% of the total length was noted for each casting. This reduction in length was consistent and was assumed to have a non-significant effect on the results.

b. Experimental Procedure

This phase of the research was conducted at the Environmental Physiology Laboratory, State University of New York at Buffalo, in a circular, ring-shaped pool. This laboratory is described by Morin and Lanphier (1972). The test section was 244 x 244 cm.

Each casting was heated in an oven to approximately 50°C above water temperature, submerged in the center of the test section, and allowed to equilibrate with water temperature. Transfer of the casting from oven to water was accomplished in less than two minutes. The rate of temperature change of the casting and water temperature were monitored continuously with a Kaye multichannel temperature recorder (Model 6000).

Cooling experiments were conducted in still water and at three water velocities. Water speed was monitored with a Meade flow probe and read from a voltmeter that was calibrated in centimeters per second. Flow was previously determined to be laminar (D. Pendergast, unpublished data). Cooling rates were determined for parallel flow at three velocities.

c. Determination of the Heat Transfer Coefficient

The method of Wathen, et al. (1971) was used to evaluate the heat transfer coefficient. The casting was assumed to have negligible internal resistance to heat flow; therefore, the change in internal energy of the casting during some time, t, must equal the net heat flow from the casting to the water. This relationship can be summarized as:

$$mc\,\frac{dT}{dt} = h_t A(T - T_w) \tag{7}$$

where,

m = mass of casting (g)

c = specific heat of casting (cal g^{-1} $^{o}C^{-1}$)

A = casting surface area (cm^2)

h_t = heat transfer coefficient (cal $cm^{-2} min^{-1}\ {}^oC^{-1}$)

$T-t_w$ = temperature differential (${}^oC$)

$\frac{dT}{dt}$ = instantaneous rate of change in casting temperature (${}^oC\ min^{-1}$)

Equation (7) is then rearranged to isolate h_t and the integral is evaluated from the initial time and temperature to a temperature, T, at some time, t:

$$h_t \int_{t_i}^{t} dt = (mc/A) \int_{T_i}^{T} dT(T - T_w) \qquad (8)$$

Equation (8) is rewritten as:

$$h_t = (mc/A)\ \ln[(T - T_w)/(T_i - T_w)]\ (t - t_i)^{-1} \qquad (9)$$

Equation (9) will yield a total (convection + conduction) heat transfer coefficient in still or moving water. The time - temperature response for each casting was recorded and then analyzed by a least square regression method. Corresponding times and temperatures were then entered in equation (9) to solve for the heat transfer coefficient.

2. Heat Exchange Rate Experiments

Largemouth blackbass (<u>Micropterus</u> <u>salmoides</u>) were obtained from Chautauqua Lake, New York, in May, 1975. The bass ranged in weight from 129 to 1346 grams and were 20 to 44 cm in total length. Prior to testing, the bass were maintained in laboratory aquaria at $24^{o} \pm 1^{o}C$ for up to 12 hours. Test fish were not fed during this holding period.

Experiments were conducted in two separate holding tanks. The cooling tank measured 91 x 91 x 122 cm and the warming tank was 105 x 55 x 75 cm. Tank temperatures were maintained using a refrigeration unit ($\pm$ 0.2°C) or heating element controlled by a Bromwill thermoregulator ($\pm$ 1°C). Water temperatures and deep body temperatures of experimental fish were continuously monitored with 24 ga. copper-constantan thermocouples linked to a Kaye multichannel temperature recorder (Model 6000). Water temperature was monitored within 5 cm of each fish.

Thermocouples were introduced into the cloaca and secured with sutures inserted immediately posterior to the cloacal opening. This procedure took approximately 5 minutes to complete and was performed in a water filled operating tray. The fish were then placed in a wide mesh wire cage and submerged in the cooling or warming tank to simulate a sudden change in ambient temperature. Test fish were allowed to warm and cool and the time - temperature response was continuously monitored. The bass were then sacrificed by severing the spinal cord and the procedure was repeated. In this way heat exchange rates were examined for both live and dead fish.

Following the heat exchange experiments the bass were preserved by freezing for use in model construction.

RESULTS

Heat Transfer Coefficients

Heat transfer coefficients, h_t, for the five aluminum castings are plotted in Figure 1. The effect of surface area, water velocity, and temperature differential between casting and water on h_t were assessed by analysis of variance (ANOVA) using a 4 x 4 x 5 factorial design. (The statistical procedures employed in this study are described by Sokal and Rohlf, 1969.) Results of this analysis are summarized in Table I. Velocity, temperature differential, and their interaction had a significant effect on h_t. Size alone (surface area) did not have a significant effect on h_t although the interaction of size and velocity was significant. The significance of the interaction is probably the result of the highly significant effect ($P > 0.01$) of water velocity. Since the variation in h_t could not be uniformly correlated with casting size, the values of h_t for all sizes were pooled for all combinations of water velocity and temperature differences.

A three dimensional coordinate system was used to visualize the relationship between h_t, water velocity, and temperature difference (Fig. 1). From this plot it was apparent that water velocity exerted a strong influence on h_t, resulting in a marked increase in the value of h_t at velocities exceeding 23.1 cm sec^{-1}. A Student - Newman - Keuls (SNK) test with equal sample sizes indicated that no significant differences existed between water velocities of 0 and 23.1 cm sec^{-1} (Table II). With only one exception, significant differences existed between all other velocities.

The influence of the temperature differential was not as self-evident. A one-way analysis of variance (ANOVA) was performed on the coefficients at each velocity using temperature differences as treatment effects (Table III a-d). No significant differences due to temperature differential occurred in the data for 0 and 23.1 cm $\sec^{-1}$. Thus, I computed an average (n=40) heat transfer coefficient for still water (1.567 ± 0.30 cal $\mathrm{cm}^{-2}\mathrm{min}^{-1}\ {}^{o}\mathrm{C}^{-1}$) and for 23.1 cm $\sec^{-1}$ (1.612 ± 0.27 cal $\mathrm{cm}^{-2}\mathrm{min}^{-1}\ {}^{o}\mathrm{C}^{-1}$). Statistically significant differences due to temperature differential that occurred at 55.4 and 67.1 cm $\sec^{-1}$ were probably not true differences. The possibility that these variations may have been due to experimental error is discussed below.

Using the method of least squares, heat transfer coefficients were plotted as a function of water velocity for each temperature difference (Fig. 2). Due to overlaps in the 95% confidence intervals of each best fit line, the variation in the coefficients could not be uniformly correlated with temperature differences. Because of this overlap the variation in h_t presumably reflected experimental error. Therefore, I averaged the data for all temperature differences and computed a least squares fit of all the coefficients (Fig. 3). The empirical equation describing h_t as a function of velocity ($h_t = 0.03\ v + 0.9$) may be useful in predicting h_t for other fish species of similar size and shape under comparable conditions.

Non-dimensional Analysis

A routine method for expressing the heat transfer coefficient is through non-dimensional analysis. This method facilitates a comparison of the behavior of objects having similar shape and orientation, regardless of size. The physical properties of the fluid are incorporated as parameters in the dimensionless groups. In order to present the results depicted in Figure 3 in dimensionless form, it is necessary to introduce three dimensionless variables:

1. The Nusselt number, $Nu = h_t L/k$ where L is a characteristic dimension in the direction of flow (length, cm), k is thermal conductivity of the fluid (cal cm^{-1} min^{-1} $^oC^{-1}$), and h_t is the heat transfer coefficient.

2. The Reynolds number, $Re = v L/n$ where v is water velocity (cm sec^{-1}) and n is the kinematic viscosity (cm^2 sec^{-1}).

3 The Prandtl number, $Pr = c_p u/k$ where c_p is the specific heat of water (cal gm^{-1} $^oC^{-1}$) and u is the viscosity (g sec^{-1} cm^{-1}).

Under conditions of forced fluid flow the Nusselt number is a function of the Prandtl and Reynolds numbers,

$$Nu = f(Pr, Re)$$

However, the Prandtl number is a function of fluid properties and, if the water temperature is maintained constant, the above relationship becomes,

$$Nu = f(Re)$$

This functional relationship, for parallel orientation, is expressed graphically in Figure 4. It should be noted that orientation is not accounted for in the plot and any comparisons must be made with similar shaped objects in parallel flow. For a more complete discussion of dimensional analysis, including the advantages and disadvantages of this technique, the reader should refer to an appropriate text (e.g., Kreith 1973).

Steady-State Energy Budget

Using energy budget theory and the coefficients determined in this study, it was possible to make a preliminary prediction of the body temperature of a fish in a steady-state energy balance with its surroundings.

The surface temperature, T_r, of a fish is related to its body temperature and is a function of the insulation, I, and internal heat production, M,

$$T_b - T_r = I(M) \tag{10}$$

The insulating layer of the fish is primarily fat and muscle of thickness, d_s, and conductivity, k_s. The insulation can be described mathematically as (Spotila, et al. 1972):

$$I = d_s/k_s \tag{11}$$

Substitution into Equation (5) yielded:

$$M = h_t A[(T_b - M\frac{d_s}{k_s}) - T_w] \qquad (12)$$

Equation (12) was then rearranged to predict T_b at a given T_w,

$$T_b = (M/h_t A) + (T_w) + (M\ d_s/k_s) \qquad (13)$$

where,

$T_w, T_b = {}^{o}C$

$h_t = \text{cal cm}^{-2}\text{min}^{-1}\ {}^{o}C^{-1}$

$A = \text{cm}^2$

$M = \text{cal cm}^{-2}\text{min}^{-1}$

$d_s = \text{cm}$

$k_s = \text{cal cm}^{-1}\text{min}^{-1}\ {}^{o}C^{-1}$

Conductivity values were obtained from Bowman, <u>et</u> <u>al</u>. (1975), skin thickness was measured to the nearest millimeter, and metabolic rate data was taken from Glass (1968, 1971). Predicted body temperatures are presented in Table IV. It is important to note that these values are estimates based on metabolic rate determinations from other sources. Metabolic rate determinations are normally conducted after some fixed period of fasting (Beamish 1970, Glass 1971). In the natural environment the fish cannot be assumed to fast for a period of time which would allow for the normal decay in metabolic rate (Glass 1971). Thus, food assimilation, specific dynamic action of food, and lipogenesis are not accounted for in the calculations. Therefore, if metabolic heat production in the equation were to double, a concomitant doubling in excess internal body temperature would result.

The Time - Temperature Response

An attempt was made to predict the temperature response of a fish exposed to a sudden change in ambient temperature. Figures 5 and 6 compare predicted and observed warming and cooling curves for a 146g bass. The predicted curves showed an exponential warming or cooling response for the body surface while the observed values were cloacal temperatures. The predicted curves show a surface response that is far more rapid than the observed internal response. This discrepancy is most probably due to the rate limiting nature of the insulating skin layer and not to an error in the model. A more exact formulation, based on heat transfer coefficients and skin thermal conductivity, should yield a predicted response that more closely parallels the measured response.

DISCUSSION

Experimental determinations of heat transfer coefficients, h_t, have provided fundamental insights into the conduction - convection of energy between a fish-shaped object (casting) and water. Increases in the value of h_t coincide with increases in water velocity even though the temperature differential between casting and water and size of the casting appear to have no effect within the range of sizes tested.

These findings provide basic information concerning the physical mechanisms of heat transfer and energy exchange between a largemouth bass, or similarly shaped fish, and its environment. Heat transfer coefficients (Figs. 1-3) are approximately two orders of magnitude greater than similar coefficients determined for terrestrial organisms (see Wathen, _et al_. 1971, Heller 1972, Porter, _et al_. 1973, Henwood, 1975). The values of h_t are due to the physical properties of water and demonstrate the capacity of this medium to rapidly absorb any heat available at the surface of an organism. The thermal boundary layer surrounding the fish is proportional to the viscosity and density of the fluid. Although both the viscosity and density are greater in water than in air, the true determinant of boundary layer thickness, the kinematic viscosity, is less in water. Kinematic viscosity is the ratio of viscosity to density. The reduced boundary layer thickness coupled with the high heat capacity of water allows for rapid transfer of energy. The specific heat of water, about 1.0 cal $g^{-1}\ {}^{o}C^{-1}$, is approximately four times that of air and the density of water, about 1.0 g cm^{-3}, is nearly 800 times that of air. Thus, the heat capacity of water is about 3,000 times greater than that of air (List 1971). Since the potential for heat transfer is so great, even in still water, heat will be transported away by the fluid as rapidly as it reaches the surface from the body core.

Historically, two major pathways for heat loss from a fish have been recognized; heat exchange at gill surfaces and diffusion of heat through the body tissues. It has been commonly assumed that fish cannot maintain a significant excess internal body temperature due to the loss of internal heat through the gills (Fry and Hochachka 1970, Stevens and Fry, 1970, Fry 1971, Gordon 1972). Exceptions are the large, fast-swimming fishes which incorporate a form of countercurrent heat exchange in parallel blood vessels prior to the passage of blood through the gills (Carey and Teal 1969 a, b, Carey, et al. 1971). Based on the findings of Steen and Kruysse (1964), Stevens and Fry (1970) hypothesized that blood temperature must nearly equilibrate with water temperature with each complete circuit of blood through the gills.

The respiratory surfaces of fish are structurally efficient heat exchangers. However, fish may exercise some selectivity in the route of blood flow through the gills and Fry and Hochachka (1970) speculated on the possibility that some fish might alter their rate of temperature change upon entering water of a different temperature by partially restricting blood flow to the gills. The converse, engorging the gills with blood, would have the effect of accelerating the rate of temperature change. Nevertheless, heat exchange at the gills cannot preclude the transfer of heat directly through the body.

Stevens and Sutterlin (1975) presented a technique for measuring heat exchange across the gills of a teleost and provided an indirect approximation of heat loss through the body wall. They reported that approximately 80 - 90% of the heat contained in venous blood of the sea raven, Hemitripterus americanus, was lost as it passed through the gills (at 5 - 7°C).

Heat lost via the gills involves primarily that fraction of the total heat content of the body that is produced through metabolic activity. In the case where a fish is confronted with a sudden change in ambient temperature, most of the heat transfer probably occurs through the body wall (Stevens and Fry 1970). Stevens and Sutterlin (1975) suggested that between 80 and 95% of total body heat must be dissipated through the body wall. Heat transfer coefficients derived in this study support their contention. Further, a simultaneous increase in the value of h_t with an increase in water velocity indicates a closer coupling to the environment as swimming speeds increase. This coupling may be somewhat counterbalanced by a parallel increase in metabolic heat production. However, since the heat transfer coefficient is so great it probably overwhelms any effect resulting from increased metabolism (in all but the largest of fish).

In cases of thermal stress, "excitement metabolism" will account for an increase in internal heat production. Excitement metabolism involves heat production in excess of that expected from normal physical activity (Fry 1971). The increase in metabolic rate will cause an increase in the transfer factor at the gills (Randall, Holeton, and Stevens 1967) and a subsequent increase in heat exchange. However, even under circumstances of thermal stress, heat exchange at the gills will fall far short of that required to account for the rate of change in the body temperature of a fish exposed to a sudden change in ambient temperature. Therefore, restriction of blood flow to respiratory surfaces would not appreciably alter the fish's rate of thermal exchange with its fluid environment.

Since the physical properties of water insure that the transport of heat away from the body surface will be extremely rapid, an alteration in the heating or cooling response of a fish would most likely be a consequence of a change in the fish's insulating layer. Thus, the rate limiting factor for heat transfer is the thickness and thermal conductivity of the insulation and not external heat transfer or thermal exchange at respiratory surfaces.

Vasoconstriction or vasodilation of the vascularized periphery has the effect of increasing or decreasing the conductivity of the insulating layer (Kleiber 1961, 1972) and can alter the time course for heat flow through the layer. Vasoconstriction would have the same effect as a thickening of the insulating layer. Therefore, the effective distance across which heat must be transmitted would be increased and the rate of heat exchange reduced. The immediate outcome of a physiological adjustment such as vasoconstriction is demonstrated by its effect on excess internal body temperature (Table III). Calculated excess internal body temperatures for a hypothetical 150 gram largemouth bass (under steady-state energy balance conditions) are elevated by an increase in skin thickness.

Previous studies have been of restricted usefulness because point measurements of temperature and temperature change within the body of a fish are of limited value for extrapolation to the total organism (Stevens and Fry 1974). A thermal model has now been developed employing heat exchange parameters that apply to a largemouth bass (or similarly shaped fish) in water. The magnitude of the derived heat transfer coefficient (h_t) shows that some degree of behavioral and/or physiological adjustment, beyond restriction of blood flow to the gills, must occur when the fish enters a thermally adverse environment. The thermal model should enable us to assess the efficacy of such thermal strategies. We are able to discern that portion of internal heat transferred at the gills and are left with quantifying that portion exchanged through the insulating layers. Since the heat transfer coefficient is derived for a unit of body surface, the exchange of heat at the surface of the entire organism can now be evaluated.

SUMMARY

1. An energy budget equation, based on energy budget theory for terrestrial organisms, was developed to describe the heat energy exchange between a fish and its aquatic environment.

2. The mathematical model indicated that convection and a combined conduction - convection process were the major avenues of heat exchange for a fish.

3. Solid aluminum castings of largemouth blackbass (Micropterus salmoides) were constructed and used to experimentally determine heat transfer coefficients at water velocities covering the free and forced convection ranges. The derived coefficients were used to characterize heat exchange between the bass and its aquatic habitat.

4. The derived heat transfer coefficients (h_t) are approximately two orders of magnitude greater than similar coefficients determined for terrestrial organisms. The magnitude of the coefficients is due to the physical properties of the medium.

5. Increases in the value of h_t coincided with increases in water velocity. Temperature differential between casting (fish) and water and size of the casting had no significant effect on the value of h_t within the range of sizes tested.

6. The magnitude of h_t indicates that the greatest portion of

heat exchange is through the body wall with heat exchange at respiratory surfaces being of minimal importance.

7. The rate limiting factor for heat transfer in the largemouth bass (and structurally similar fish) appears to be the thickness and thermal conductivity of the insulating layer and not external heat exchange between the fish and water.

Table I. Results of ANOVA using a 4 x 4 x 5 factorial design. This procedure evaluates the individual effects of water velocity, v (4), temperature difference between casting and water, ΔT (4), casting size (5), and their interactions.

SOURCE	d.f.	S.S.	m.s.	F
v	3	15660	5220	215.7 **
ΔT	3	1107	369	15.2 **
Size	4	207	52	2.1
v x ΔT	9	711	79	3.3 **
v x Size	12	2019	168	7.0 **
ΔT x Size	12	178	15	0.6
v x ΔT Size	36	178	4.9	0.2
error	80	1935	24.2	
total	159			

* P = 0.05, ** P = 0.01

Table II. Results of the Student - Newman - Keuls (SNK) test comparing the velocity component at each temperature difference, ΔT. The range is used as the statistic to measure differences between means. The K value is the difference between the mean h_t values at the two velocities. K values for each comparison are tested against a least significant range (LSR) for the appropriate degrees of freedom. A significant difference exists between means if the K value exceeds the LSR.

	K			
VELOCITIES (cm/sec)	5^{o}C ΔT	10^{o}C ΔT	15^{o}C ΔT	20^{o}C ΔT
0 vs 23.1	1.75	1.00	0.62	1.40
0 vs 55.4	22.32*	18.35*	15.95*	13.55*
0 vs 67.1	27.91*	24.20*	22.98*	14.56*
23.1 vs 55.4	20.57*	17.35*	15.33*	14.95*
23.1 vs 67.1	26.16*	23.20*	22.36*	15.96*
55.4 vs 67.1	5.59*	5.85*	7.03*	1.01

* P = 0.05

Table III. Results of ANOVA used to evaluate the effect of temperature difference on the values of h_t at each velocity. Still water, a, and velocities of 23.1 cm sec^{-1}, b, 55.4 cm sec^{-1}, c, and 67.1 cm sec^{-1}, d, are examined using temperature differential between casting and water as the treatment effect.

(a)

SOURCE	d.f.	S.S.	m.s.	F
between	3	69.0	23.0	0.79
within	36	1053.4	29.3	
total	39	1122.4		

(b)

SOURCE	d.f.	S.S.	m.s.	F
between	3	93.2	31.1	1.70
within	36	659.8	18.3	
total	39	753.1		

(c)

SOURCE	d.f.	S.S.	m.s.	F
between	3	60.7	20.2	7.60 **
within	36	95.9	2.7	
total	39	156.6		

(d)

SOURCE	d.f.	S.S.	m.s.	F
between	3	91.0	30.3	7.10 **
within	36	153.9	4.3	
total	39	244.9		

* P = 0.05

** P = 0.01

Table IV. Calculated excess internal body temperature as a function of water temperature from the steady-state energy budget (Equation 13). The hypothetical fish is a 150g largemouth bass in still water with routine metabolism, M (cal $cm^{-2}min^{-1}$), and skin thickness, ds(cm).

	EXCESS INTERNAL TEMPERATURE (°C)			
water temperature (°C)	routine M ds = 0.7	routine M ds = 1.0	2x routine M ds = 0.7	2x routine M ds = 1.0
5	0.037	0.05	0.07	0.10
10	0.065	0.09	0.13	0.18
15	0.097	0.14	0.19	0.28
20	0.130	0.19	0.26	0.38

Figure 1. A three dimensional coordinate system relating the heat transfer coefficient, h_t, to temperature differential, ΔT, and water velocity, v. Solid vertical lines indicate the range of the pooled data (n = 10), solid horizontal lines the mean, and open rectangles one standard deviation to each side of the mean. A least squares fit of all data (n = 160) has been included. Axes representing the heat transfer coefficient and temperature differential are in the plane of the page; the velocity axis is into the plane of the page.

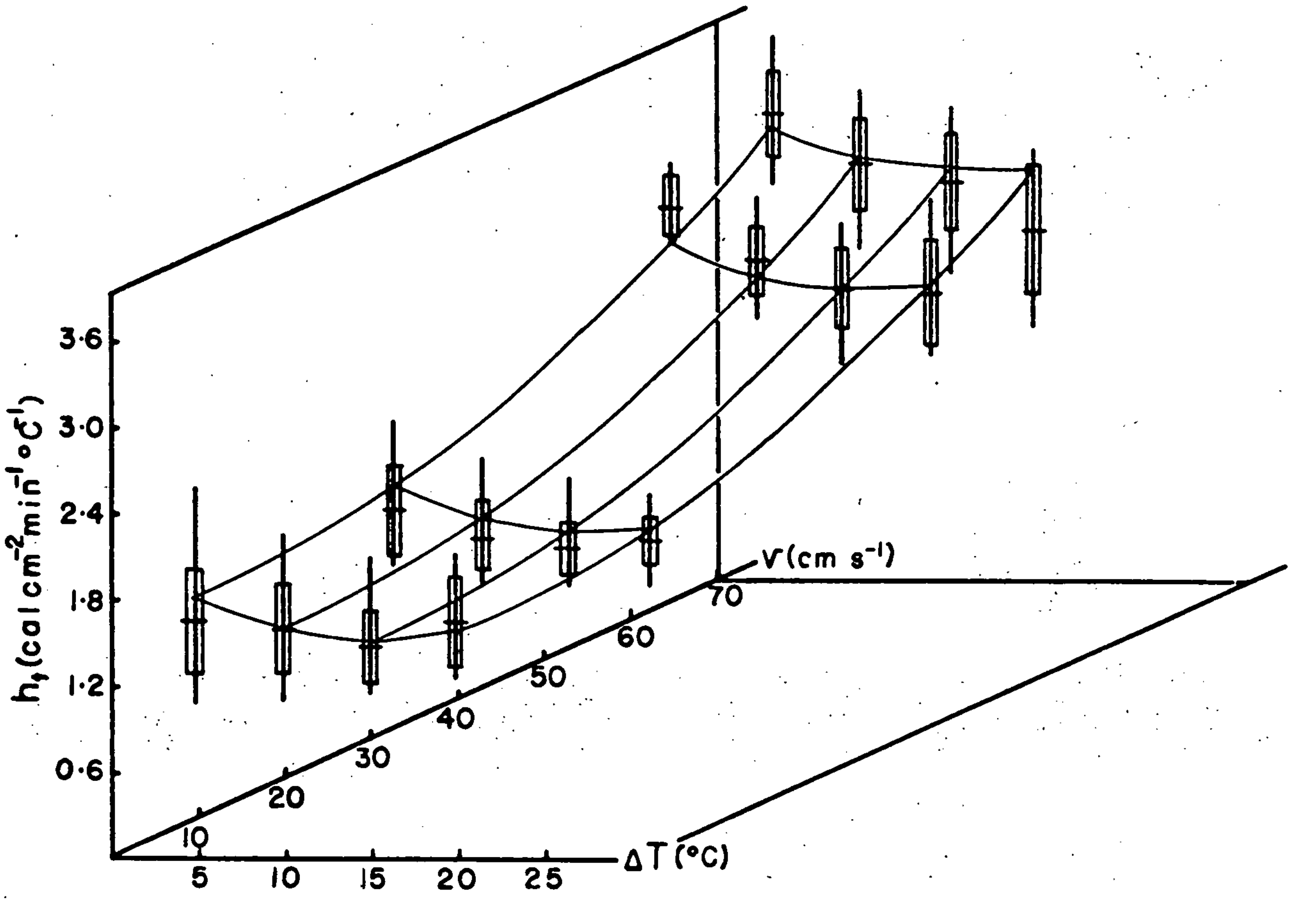

h_t (cal cm^{-2} min^{-1} °C^{-1})
3·6
3·0
2·4
1·8
1·2
0·6
ΔT (°C)
5
10
15
20
25
V (cm s^{-1})
10
20
30
40
50
60
70

Figure 2. Least squares plots of h_t as a function of velocity for each temperature difference between casting and water. Slopes and intercepts of each line are: (ΔT 5°C) 0.036v + 0.93, (ΔT 10°C) 0.032v + 0.84, (ΔT 15°C) 0.030v + 0.80, (ΔT 20°C) 0.023v + 1.0. Each line is the best fit of 30 data points and the 95% confidence intervals of all lines overlap. For reasons of clarity, only the regression line is presented for each temperature difference.

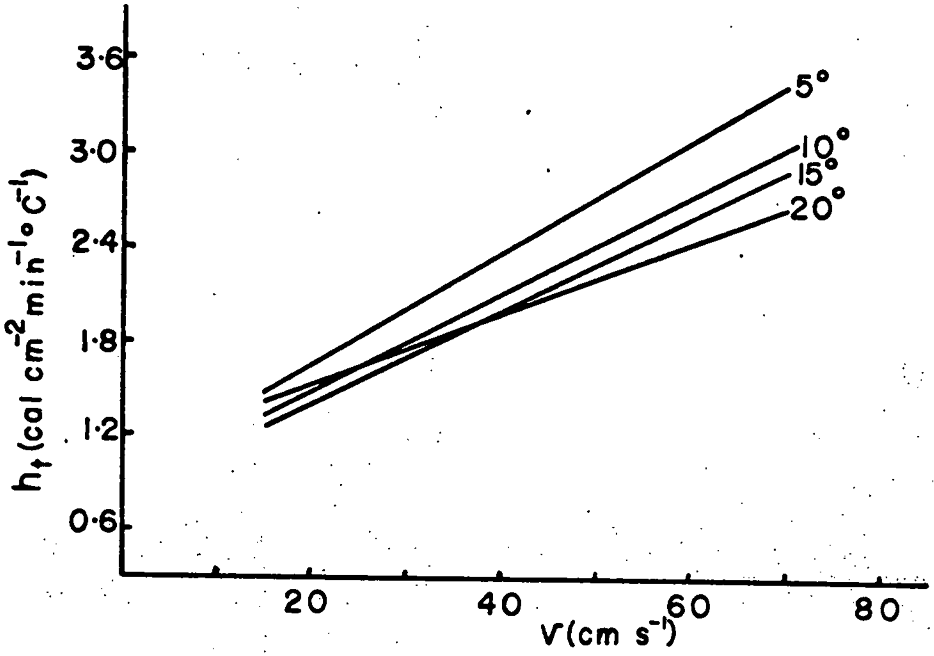

h_t (cal cm^-2 min^-1 °C^-1)
3·6
3·0
2·4
1·8
1·2
0·6
20
40
60
80
V (cm s^-1)
5°
10°
15°
20°

Figure 3. A least squares fit of all heat transfer coefficients, h_t, as a function of water velocity (n = 120).

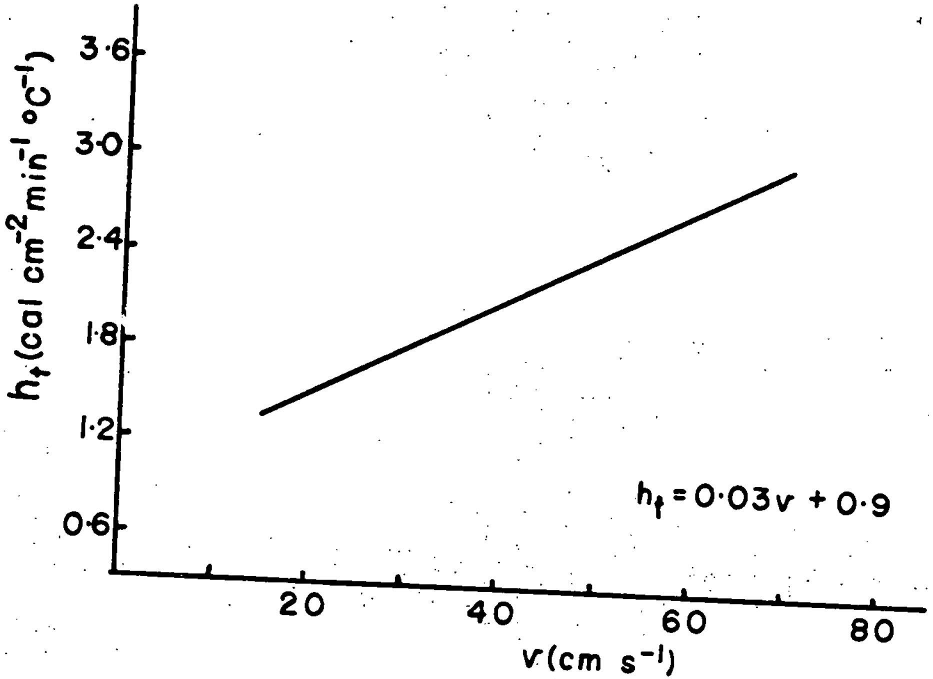

h_t (cal cm^{-2} min^{-1} °C^{-1})
3·6
3·0
2·4
1·8
1·2
0·6
20
40
60
80
v (cm s^{-1})
$h_t = 0{\cdot}03v + 0{\cdot}9$

Figure 4. Dimensionless plot of Nusselt number versus Reynolds number in forced convection (n = 30). The plot is for a temperature difference of 15°C and the solid line is a least squares fit of the data. h_t is the heat transfer coefficient (cal $\text{cm}^{-2}\text{min}^{-1}\ {}^{o}\text{C}^{-1}$), L is length of casting (cm), k is thermal conductivity of the fluid (cal $\text{cm}^{-1}\text{min}^{-1}\ {}^{o}\text{C}^{-1}$), v is water velocity (cm sec^{-1}), and ν is kinematic viscosity of the fluid (cm^2 sec^{-1}).

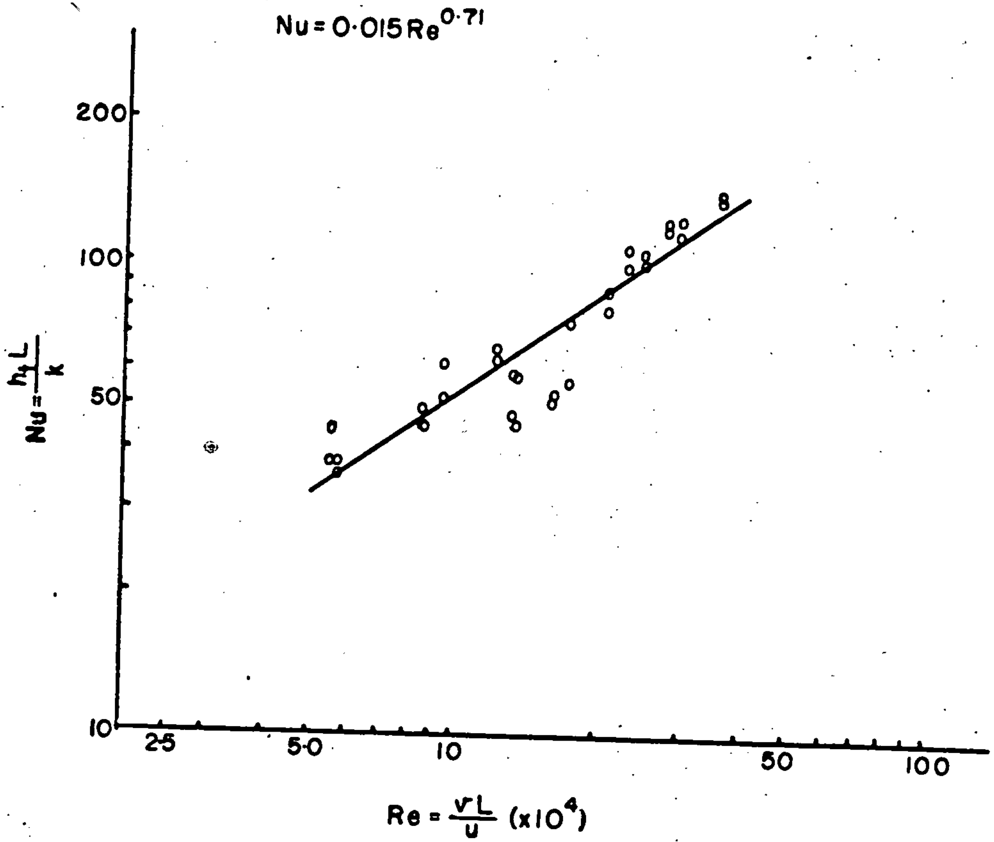
Nu = 0·015 Re^0·71
200
100
50
10
Nu = h₁L/k
2·5
5·0
10
50
100
Re = vL/u (x10⁴)

Figure 5. Comparison of predicted and observed warming curves for a 146 gram largemouth bass. The temperature difference between fish and water (ΔT) is plotted as a function of time (t). The predicted surface response (open circles) is far more rapid than the measured internal response (closed circles).

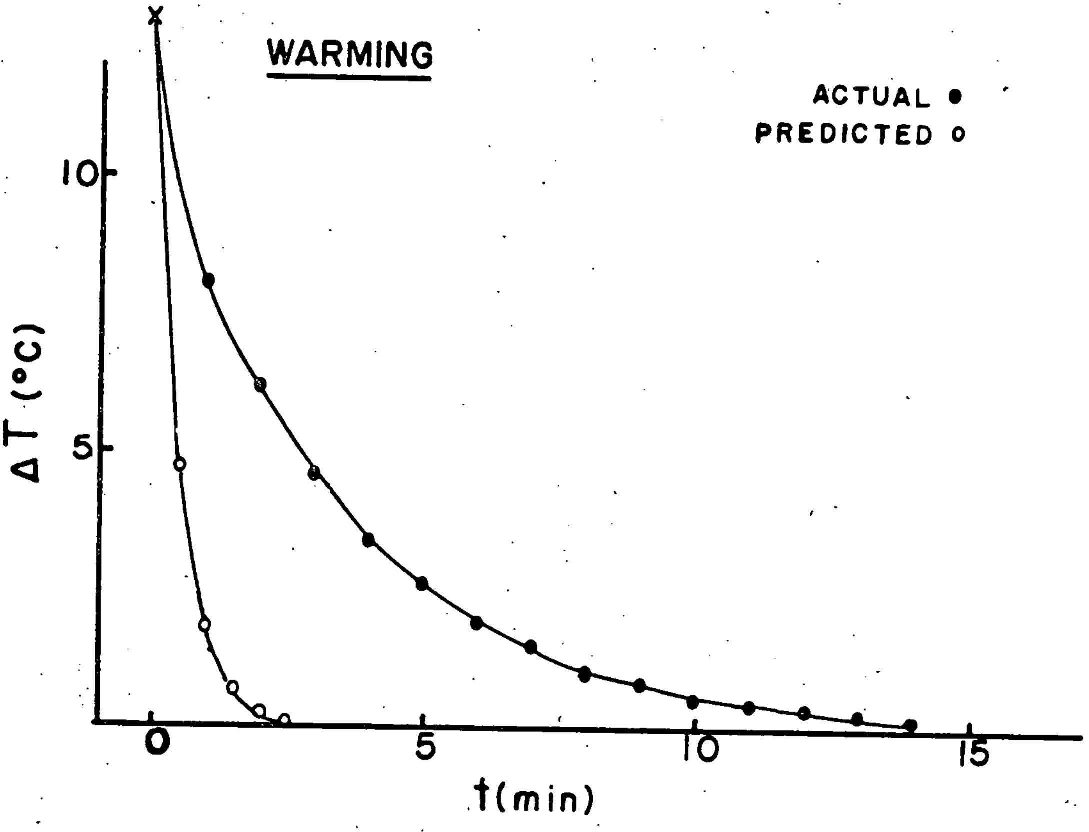
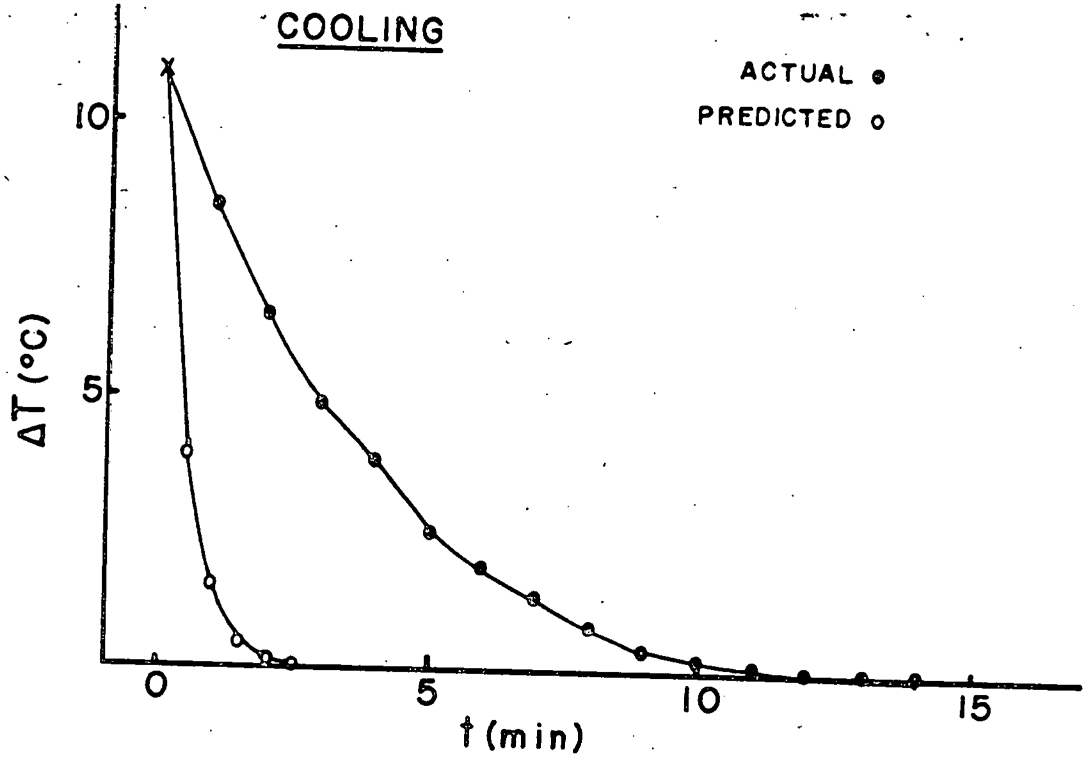

WARMING
ACTUAL ●
PREDICTED ○
ΔT (°C)
10
5
X
0
5
10
15
t(min)

Figure 6. Comparison of predicted and observed cooling curves for a 146 gram largemouth bass. The temperature difference between fish and water (ΔT) is plotted as a function of time (t). The predicted surface response (open circles) is far more rapid than the measured internal response (closed circles).


COOLING
ACTUAL ●
PREDICTED ○
ΔT (°C)
10
5
0
5
10
15
t (min)

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