

RATES OF HEAT EXCHANGE IN LARGEMOUTH BASS: EXPERIMENT AND MODEL¹

DONALD E. WELLER,² DAVID J. ANDERSON,³ DONALD L. DEANGELIS,⁴
AND CHARLES C. COUTANT

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37830

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A mathematical model of body-core temperature change in fish was derived by modifying Newton's law of cooling to include an initial time lag in temperature adjustment. This model was tested with data from largemouth bass (*Micropterus salmoides*) subjected to step changes in ambient temperature and to more complex ambient regimes. Nonlinear least squares was used to fit model parameters k (min^{-1}) and L (initial lag time in minutes) to time series temperature data from step-change experiments. Temperature change halftimes ($t_{1/2}$, in minutes) were calculated from k and L . Significant differences ($P < .05$) were found in these parameters between warming and cooling conditions and between live and dead fish. Statistically significant regressions were developed relating k and $t_{1/2}$ to weight and L to length. Estimates of k and L from the step-change experiments were used with a computer solution of the model to stimulate body temperature response to continuously varying ambient regimes. These simulations explained between 52% and 99% of the variation in core temperature, with absolute errors in prediction ranging between 0 and 0.61 C when ambient temperature was varied over 4 C.

INTRODUCTION

The process of thermal exchange between fish and their environment is relevant to a number of questions in fish biology. For example, Neill, Chang, and Dizon (1976) postulated that the thermoregulatory responses of fish to spatial and temporal variations in temperature may depend on the perception of thermal gradients by sensory systems that constantly compare ambient temperature to body-core temperature. If this hypothesis is true, a thorough understanding of observed fish movements would require an accurate model of thermal exchange between the environment and the

body core. Predictions of fish movements in response to known gradients would also require such a model. Once validated by demonstrating that body temperatures predicted from ambient temperatures are acceptably close to measured body temperatures, the model could be used to predict core temperatures from field data on ambient temperatures. This would eliminate the behavioral disruption associated with the implantation of telemetric equipment (Fechhelm and Neill 1982).

Quantitative information on the rate of body temperature response to changes in water temperature is also valuable in assessing the ecological effects of thermal discharges on fish populations, since a description of individual response to a sharp thermal gradient can be used to understand the composite population distribution around a discharge. Fish attracted to a thermal plume for short periods of time may be subject only to temporarily unusual predator-prey relations and crowding effects. If they remain in the plume long enough for their body temperatures to rise significantly, physiological changes and alterations in reproductive potentials are possible. A predictive model based on observed rates of heat exchange and temperature change could be used to estimate residence times in a discharge from field data

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² Graduate Program in Ecology, University of Tennessee, Knoxville, Tennessee 37996.

³ Division of Biological Sciences, University of Michigan, Ann Arbor, Michigan 48109.

⁴ Author to whom reprint requests should be addressed.

on fish body temperature (Spigarelli et al. 1974).

Many studies (for references see Fechhelm and Neill [1982]) have described rates of temperature change in teleosts using Newton's law of excess temperature,

$$\frac{dT_b(t)}{dt} = k[T_a(t) - T_b(t)], \quad (1)$$

where T_b is the body-core temperature of the fish, T_a is the ambient temperature of the water, k is rate coefficient for temperature change (thermal conductance), and t is time. If the fish produces a significant amount of metabolic heat, T_a must be replaced by a temperature, T_e , which denotes an equilibrium temperature somewhat above the ambient. Unlike the equations of Fechhelm and Neill (1982), ours will ignore the effects of metabolic heat because both their experimental results and ours showed no significant excess temperature.

The solution of equation (1) can be written for any time-varying $T_a(t)$ as

$$T_b(t) = T_0 e^{-kt} + k \int_0^t e^{-k(t-s)} T_a(s) ds \quad (t \geq 0), \quad (2)$$

where T_0 is the initial core temperature at time $t = 0$.

This model assumes that the whole body instantaneously begins uniformly to exchange heat with the environment when the ambient temperature changes. This implicit assumption is approximately valid for small-bodied fish, but it is inappropriate for larger fish because a "lag" or "latency" period exists in which the body-core temperature does not change. This response has been observed by Crawshaw (1976), Neill et al. (1976), Reynolds (1977), and Spigarelli, Thommes, and Beiting (1977) and is found in our data on largemouth bass, *Micropterus salmoides* (fig. 1). As Fechhelm and Neill (1982) point out, Newton's law in this case can be rewritten in the form

$$\frac{dT_b(t)}{dt} = k[T_a(t - L) - T_b(t)], \quad (3)$$

where L is the length of the initial time lag.

The general solution to equation (3) is

$$T_b(t) = \begin{cases} T_0 & (0 < t < L) \\ T_0 e^{-k(t-L)} + k \int_L^t e^{-k(t-s)} \times T_a(s - L) ds & (t > L). \end{cases} \quad (4)$$

Except for the fact that we use the ambient temperature, T_a , as the equilibrium temperature of the fish, rather than T_e , this solution is more general than that of Fechhelm and Neill (1982). If our continuous-time expression is replaced by a discrete-time formulation, and if $T_a(t)$ is replaced over short intervals by linear approximation with respect to time, then our equation (4) reduces to their equation (4) (except for our use of T_a rather than T_e).

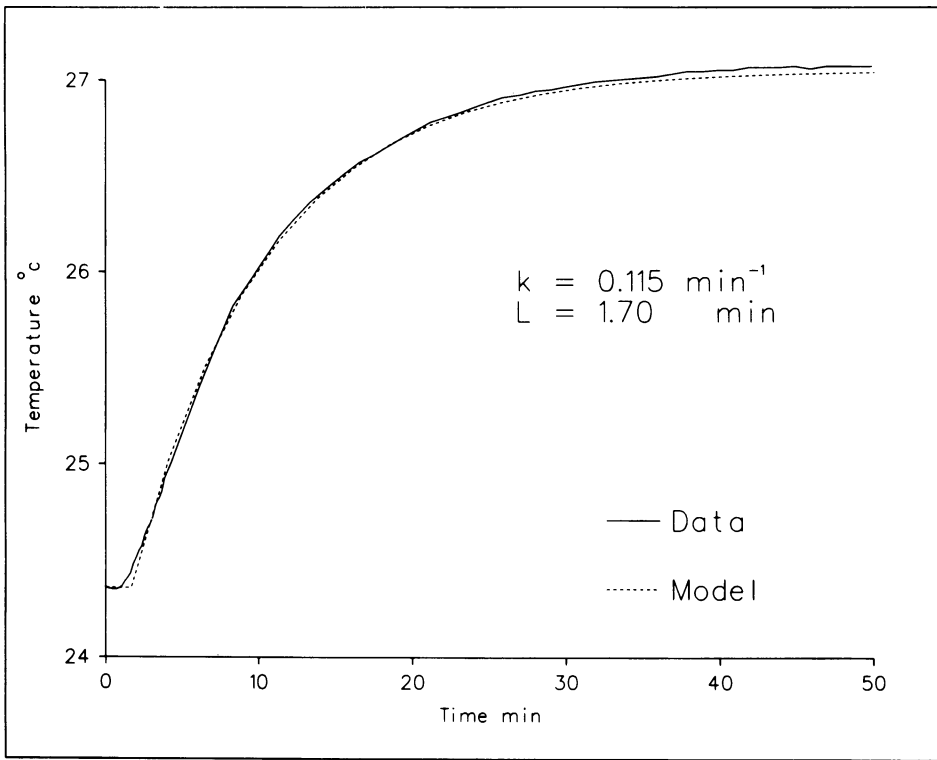
In the particular case where the fish is subjected to a step-function temperature change at time $t = 0$, say from $T_a = T_0$ to $T_a = T_1$, equation (4) simplifies to

$$T_b(t) = T_1 - (T_1 - T_0)e^{-k(t-L)} \quad (t > L). \quad (5)$$

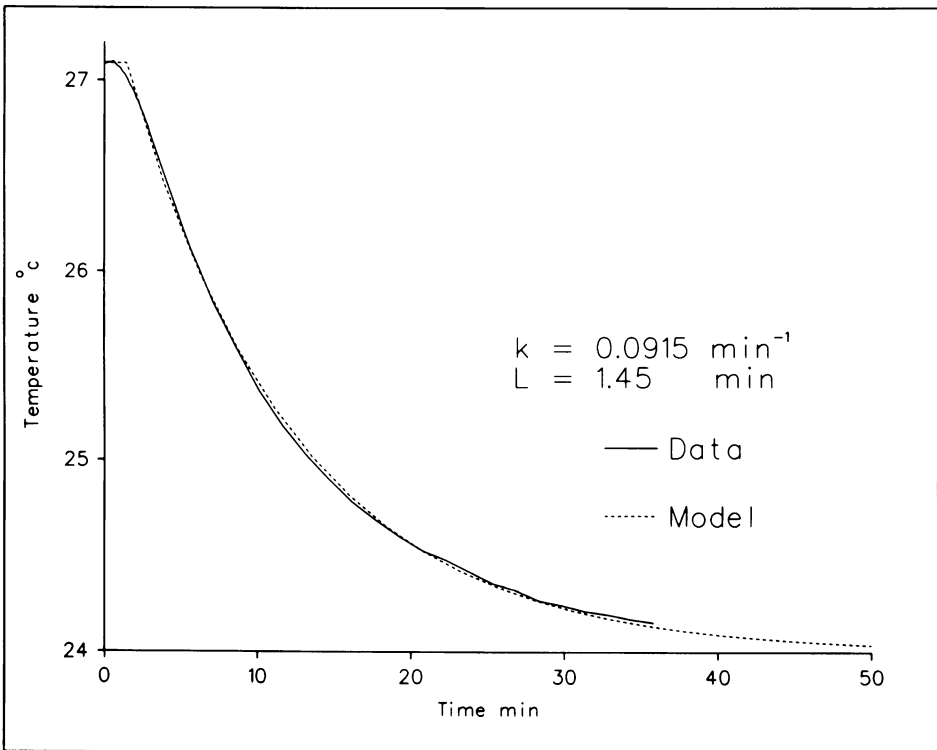
In the present study, experiments were done to assess the accuracy of equation (5) in predicting the response of body-core temperature to a step change in ambient temperature. Replicate experiments were used to estimate the variabilities in the coefficient of heat exchange, k , and in the initial lag time, L , for individual fish. The estimates of k and L measured under warming and cooling conditions were compared, and the parameter estimates of live and dead fish were compared to assess the importance of physiological processes in heat exchange. Finally, experiments were done on one bass to examine the accuracy of equation (4) in predicting the response of body-core temperature to a complexly varying ambient temperature. This required the development of a computer simulation model to solve the differential equation (3).

MATERIAL AND METHODS

Eight adult largemouth bass (*Micropterus salmoides*) ranging in weight from 515 to 2,710 g (see table 1) were used in this study. The fish were captured during fall 1978



a



b

FIG. 1.—Typical fits of eq. (5) to body temperature data from step-change trials under warming (a) and cooling (b) conditions. Parameters k and L for each fitted curve are shown.

TABLE 1
SIZE MEASUREMENTS OF THE EIGHT LARGEMOUTH
BASS USED IN THIS STUDY

Fish No.	Weight (g)	Length (cm)
1	1,620	50.4
6	1,824	49.0
7	1,239	45.5
13	1,623 ^a	47.2
101	515	33.5
102	1,772	52.8
103	2,710	54.5
104	841	41.5
Average (<i>N</i> = 8)	1,518	46.8

^a Fish 13 was weighed 36 h after death and had absorbed an unknown amount of water.

and summer 1979 by electroshocking in Fort Loudon, Melton Hill, and Watts Bar reservoirs (all near Oak Ridge, Tenn.) and by angling in a small pond on the grounds of the Oak Ridge National Laboratory. The fish were maintained without food in well-aerated 800-liter tanks at 27 C for at least 2 days prior to testing. The laboratory lighting was turned on at sunrise and switched off at sunset by an outdoor photocell control system.

Internal body temperatures were measured by ultrasonic telemetry as described by Coutant (1975). A temperature-sensitive transmitter was either inserted through the gullet into the stomach or surgically implanted in the coelomic cavity with the thermistor 2 cm posterior to the pericardial cavity. X-ray photography showed that the thermistors of stomach-tagged fish were centrally located in the viscera from both dorsoventral and lateral perspectives. Similar body temperature data were obtained from the stomach-tagged fish and the single surgically tagged fish (fish 1).

During experiments, ultrasonic pulses from the implanted transmitters were received by a submerged hydrophone connected to a Smith-Root Sonic Receiver Type TA60. Pulse frequency was determined by a Hewlett-Packard Electronic Counter Model 5221 B and recorded by a paper tape punch. Ambient water temperature was monitored with a Yellow Springs Instruments telethermometer and recorded by a YSI paper tape recorder. The trans-

mitter pulse data and the telethermometer were calibrated to the same mercury thermometer. Body temperature and water temperature measurements had accuracies of ± 0.02 and ± 0.05 C, respectively.

TEMPERATURE STEP-CHANGE TRIALS

Sixty-six sudden temperature change tests on single fish were conducted by maintaining two adjacent tanks at constant temperatures (± 0.05 C) and transferring the fish from one tank to the other in dip nets. Ambient and body temperature data were recorded at 10–60-s intervals for 30–90 min after the transfer. The actual numbers of tests done on each fish are shown in table 2.

Marquardt's method of nonlinear least squares (Helwig and Council 1979) was used to fit model (5) to the data, yielding estimates of the two model parameters *k* and *L* for each of the 66 experiments. The quality of each fit was evaluated by calculating percentage of variance explained = $100 \times \text{SSR}/\text{SST}$, where SST is the total sum of squares in observed body temperature (corrected for the mean) and SSR is the mean sum of squares accounted for by the model. This quantity is analogous to the coefficient of determination, r^2 , used in linear regression.

To facilitate comparison with previous studies, a heat exchange half-time, $t_{1/2}$, defined as the time required for body temperature to reach the halfway point between the new and old environmental temperatures, was calculated. Because the original formula for $t_{1/2}$ developed by Spigarelli et al. (1974), $t_{1/2} = -\ln(0.5)/k = 0.693/k$, does not allow for initial lag period in thermal response, a new formula incorporating this effect was developed and used in this study:

$$t_{1/2} = L - \ln(0.5)/k = L + 0.693/k. \quad (6)$$

Analysis of variance (Helwig and Council 1979) was used to check for differences in *k*, *L*, and $t_{1/2}$ under warming and cooling conditions. Linear and nonlinear regressions were also performed to relate *k*, *L*, and $t_{1/2}$ to the two fish size measurements, length and weight.

Three fish were sacrificed and used immediately in sudden temperature-change

TABLE 2

THERMAL EXCHANGE PARAMETERS OF EIGHT LIVE BASS AS MEASURED IN THE TEMPERATURE STEP-CHANGE EXPERIMENTS

FISH NO. AND DIRECTION	n	k (min ⁻¹)			L (min)			t _{1/2} (min)		
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
1: C	3	.0931	.0062	.0879-.0999	1.15	.55	.52-1.49	8.62	1.02	7.45-9.37
H	3	.1119	.0078	.1030-.1176	1.60	.07	1.54-1.68	7.81	.41	7.47-8.27
6: C	2	.0538	.0037	.0512-.0565	1.86	.05	1.82-1.89	14.76	.84	14.16-15.36
H	2	.0790	.0151	.0682-.0897	2.28	.35	2.03-2.53	11.22	1.37	10.25-12.19
7: C	2	.1001	.0052	.0964-.1039	.080	.113	.0-.160	7.01	.25	6.83-7.19
H	2	.1577	.0038	.1551-.1604	.363	.269	.173-.553	4.76	.37	4.49-5.02
13: C	6	.0835	.0058	.0768-.0927	.839	.239	.440-1.15	9.17	.74	7.91-10.00
H	6	.0930	.0038	.0853-.0950	.767	.543	.244-1.76	8.23	.64	7.54-9.08
101: C	5	.1639	.0340	.1351-.2198	.268	.266	.010-.690	4.63	1.01	3.25-5.82
H	5	.1856	.0331	.1505-.2274	.337	.316	.0-.678	4.17	.71	3.25-5.10
102: C	5	.0734	.0054	.0654-.0789	2.66	.59	1.78-3.28	12.14	.96	10.56-13.13
H	5	.1057	.0086	.0932-.1148	3.85	.10	3.73-3.95	10.45	.57	9.77-11.32
103: C	5	.0559	.0103	.0465-.0704	2.67	1.33	1.39-4.75	15.39	3.38	11.23-19.24
H	5	.0760	.0095	.0657-.0863	2.88	1.35	1.27-4.44	12.12	2.41	9.30-14.99
104: C	5	.1107	.0103	.0992-.1230	1.24	.46	.54-1.64	7.55	.49	7.06-8.13
H	5	.1301	.0120	.1150-.1429	1.52	.45	.82-2.01	6.89	.80	6.24-8.04
All fish: C	33	.0942	.0375	.0465-.2198	1.41	1.10	.0-4.75	9.79	3.85	3.25-19.24
H	33	.1168	.0392	.0657-.2274	1.75	1.36	.0-4.43	8.27	2.89	3.25-14.99
All fish: H & C	66	.1055	.0397	.0465-.2274	1.58	1.24	.0-4.75	9.03	3.46	3.25-19.24

NOTE.—Direction is the direction of ambient temperature change (H = heating = 27–29 C, C = cooling = 29–27 C, k = heat exchange coefficient, L = initial lag time, and t_{1/2} = temperature change halftime.

tests as described above to provide data for comparison of the temperature-change dynamics of live and dead fish. Data from two fish had to be discarded because the stomach tag apparently came into contact with water circulating through the relaxed gullet. The gullet of the third fish (fish 13) was sutured shut to prevent such seepage. The data from this fish were used to examine the relative importance of the two primary mechanisms of heat exchange in fish, conduction through body tissues and convection mediated by the bloodstream. The convection index developed by Beiting, Thommes, and Spigarelli (1977) was calculated by dividing the mean $t_{1/2}$ value for the dead fish by the mean $t_{1/2}$ value for the living fish. The reciprocal of this ratio is the relative percentage importance of conduction in the heat exchange of the live fish.

CONTINUOUS TEMPERATURE-CHANGE SIMULATION MODEL

To measure the response of central body temperature to a continuously varying ambient temperature, three experiments were performed on fish 104. In each experiment, the fish was initially equilibrated to a constant water temperature (± 0.05 C) between 27 and 29 C, then the ambient temperature was varied over 3–5 C for 10–15 min by introducing relatively warmer or cooler water with rapid mixing. After this period, water inflow was stopped, allowing both the ambient and fish core temperatures to approach a new constant level. Ambient and core temperatures were recorded as described previously every 10 s for a period of 20–30 min starting just before the initiation of water temperature variation.

For each of these three experiments, equation (3) was used to predict body temperature from the ambient temperature data and estimated values of the model parameters k and L . The solution to (3) was obtained by numerical integration using a fourth-order Runge-Kutta algorithm (Westley and Watts 1970). Cubic spline interpolation (Westley and Watts 1970) was used to estimate the ambient temperature function $T_a(t)$ between recorded data points.

Because the value of the parameter k was found to be significantly greater in warming

fish than in cooling fish, the solution algorithm for core temperature used two estimates of k , k_h and k_c . In the course of the numerical solution, k_h was used whenever ambient temperature was greater than central body temperature, while k_c was used when the reverse was true. A single value of L was used for both warming and cooling since differences in this parameter under the two exchange regimes were much less pronounced.

Model performance was evaluated by calculating the percentage of variance explained and by recording the mean, minimum, maximum, and ninetieth percentile values for the absolute error in predicted body temperature in each simulation.

RESULTS

TEMPERATURE STEP-CHANGE TRIALS

In some of the step-change experiments, final body-core temperature was slightly above ambient; however, in others the final body temperature was below ambient. These deviations from ambient were within the experimental precision of the measuring instruments. The absence of significant core temperature elevation indicates that metabolic activity does not maintain an excess temperature above ambient in largemouth bass of the sizes studied here.

Model (5) gave good fits to the data from the sudden temperature-change tests, explaining at least 97% of the variance in body temperature in each test. The model more closely fitted the temperature response than did Newton's law without the time lag, particularly in the pre-exponential portion; however, the model still tended to enter the exponential phase of temperature change slightly after the observed data (fig. 1).

Values of the heat exchange coefficient, k , and initial time lag, L , resulting from fitting model (2) to the sudden temperature-change data are shown in table 2, along with temperature change halftimes, $t_{1/2}$, calculated from equation (6). A two-way analysis of variance of the effects of fish used, direction of temperature change (warming or cooling), and the interaction of fish and direction was performed. All three measurements, k , L , and $t_{1/2}$, differed very significantly ($P < .0001$) among the tested fish. The effect of the direction of temperature change was highly significant

($P < .0001$) for the two measurements, k and $t_{1/2}$, and significant for L at $P = .046$. There were no significant interaction terms between the temperature direction and fish effects.

These results indicate that the bass exchanged heat faster during warming than during cooling ($k_h > k_c$); however, the initial time delay period was longer under warming conditions than under cooling conditions ($L_h > L_c$). These two effects seem to conflict in that the faster heat exchange rate contributes to more rapid temperature equilibration in warming fish relative to cooling fish, whereas the longer time lag tends to delay temperature adjustment of warming fish relative to cooling fish. However, when the two effects are combined in calculating temperature change halftimes, the differences in heat exchange rate predominate so that warming fish complete one-half of their adjustment to a new temperature significantly sooner than do cooling fish ($t_{1/2h} > t_{1/2c}$).

The heat exchange coefficient k was closely related to bass weight by a power relationship which explained 77% of the variation in heating k and 83% of the variation in cooling k (see fig. 2). The initial time lag L was more closely related to body length than to mass; however, only 57% of the variation each in both heating and cooling L was explained by the exponential relationships shown in figure 3. Seventy-four percent of the variation in temperature change halftime, $t_{1/2}$, in heating fish and 75% of that variation in cooling fish was explained by the linear model relating $t_{1/2}$ to weight (illustrated in fig. 4).

A comparison of the heat exchange characteristics of live and dead fish is presented in table 3, which gives values of the measurements k , L , and $t_{1/2}$ for fish 13 subjected to temperature step changes when alive and when dead. The dead fish exchanged heat more slowly than the live fish. The initial time lag L was approximately 10 times longer in the dead fish, whereas

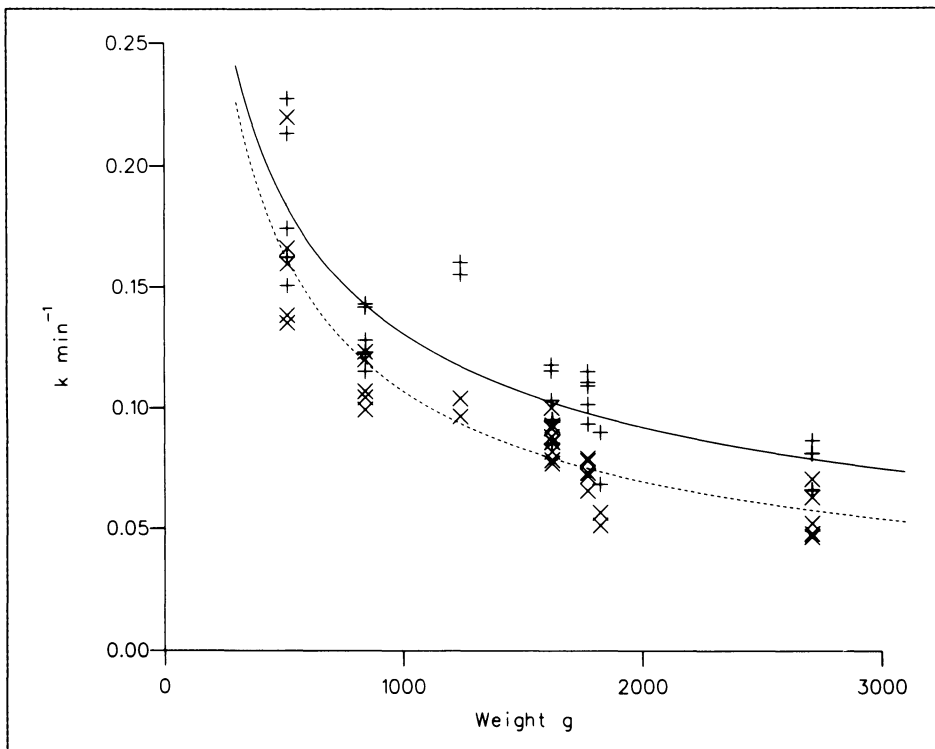


FIG. 2.—Power equation fits of the step-change thermal exchange rates (k) to fish weight. Points from 33 warming trials are indicated by the symbol +. The solid line shows the curve, $k_h = 7.89W^{-0.623}$, fitted to these points ($r^2 = .83$, $P < .0001$). The symbol \times indicates k values from 33 cooling trials. The fitted curve (dashed line) is $k_c = 4.38W^{-0.509}$ ($r^2 = .77$, $P < .001$).

the heat exchange coefficient k was less than one-half as fast as that of the live fish. These two differences combined to give the dead fish a thermal exchange haltime approximately four times longer than that of the live fish. Analysis of variance showed that these differences in k , L , and $t_{1/2}$ between the living and dead fish were all statistically very significant ($P < .0001$). This indicates that all three parameters are significantly dependent on the convection processes occurring in live fish.

A further difference between the live and dead fish can also be seen in table 3. Although the cooling and warming properties of living fish were statistically different, the dead fish exhibited no significant differences in the measurements k , L , or $t_{1/2}$ when tests conducted under warming and cooling conditions were compared.

The convection index for fish 13 was calculated as (dead $t_{1/2}$)/(live $t_{1/2}$) = 31.24/8.67 = 3.60. The reciprocal of this value is 0.278, indicating that conduction through

body tissues accounts for about 28% of the heat exchange of the living fish, whereas convection mediated by the circulatory system accounts for the remaining 72%.

CONTINUOUS TEMPERATURE-CHANGE SIMULATIONS

The actual responses of fish core temperature in the three experiments involving continuously varying ambient temperatures are shown in figures 5 and 6, along with core temperatures predicted by model equation (3). General qualitative agreement of the model with measured core temperature is evident in both figures, as seen in the similarities in direction and timing of predicted and actual body temperature changes.

In figure 5, the values of k_h , k_c , and L used with equation (3) to model fish core temperature were the average values determined from 10 sudden temperature-change experiments (see table 1). For experiments 1, 2, and 3, the model with these parameters explained 73%, 89%, and 52%,

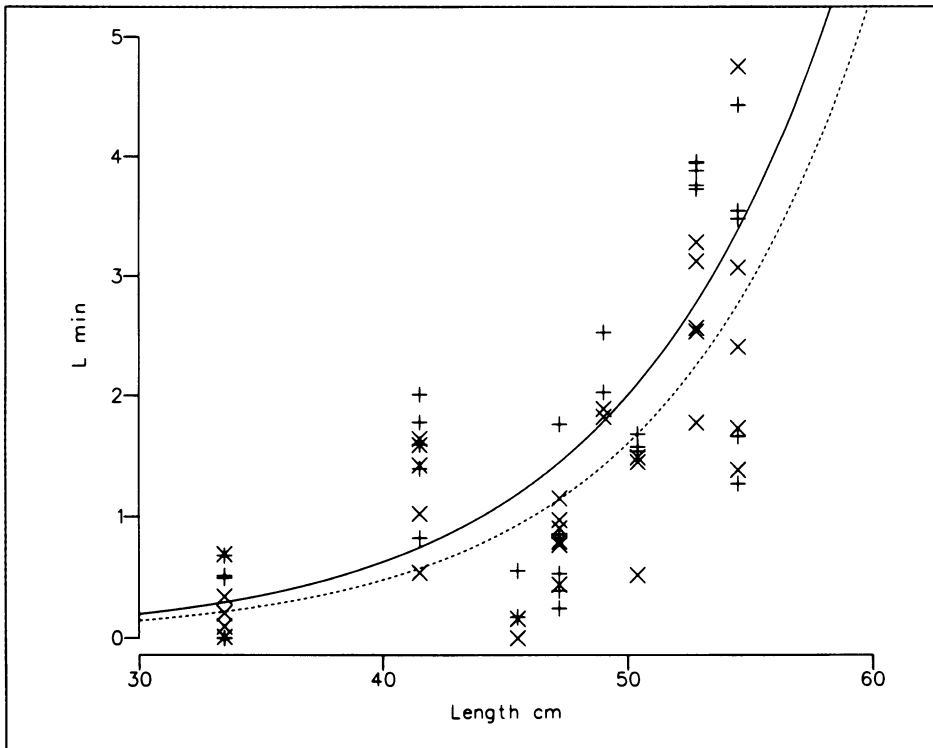


FIG. 3.—Exponential equation fits of the step-change time lag, L , to fish length, l . Sample sizes, symbols, and line types are as in fig. 2. The fitted equations are $L_h = 0.00598e^{0.116l}$ ($r^2 = .57$, $P < .0001$) and $L_c = .00379e^{0.121l}$ ($r^2 = .57$, $P < .0001$).

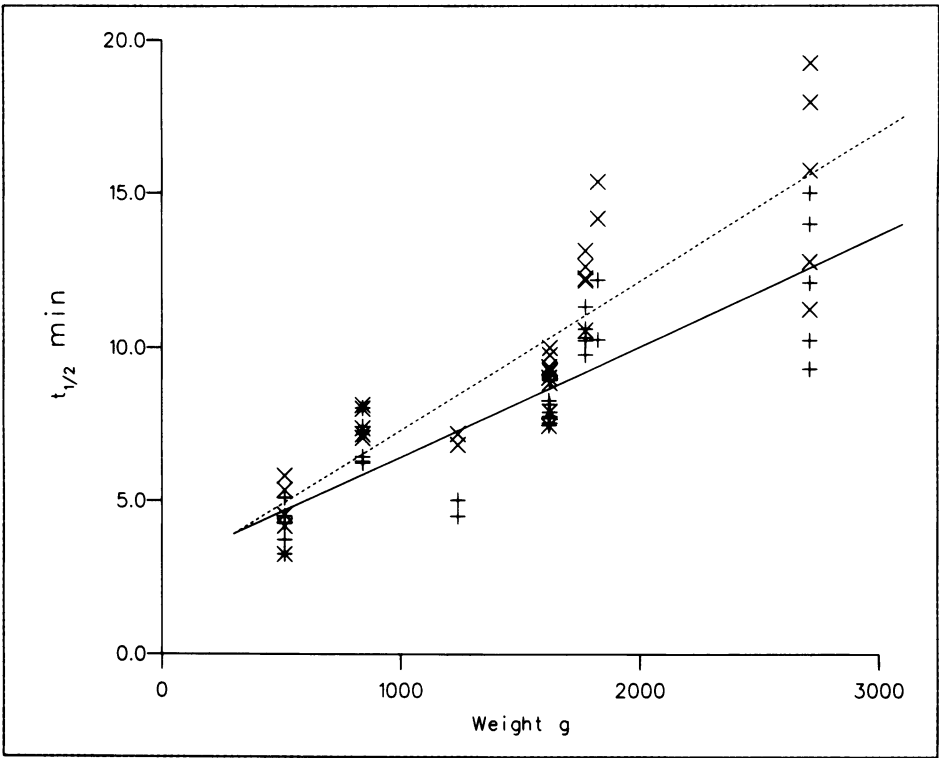


FIG. 4.—Linear fits of temperature change halftimes, $t_{1/2}$, to fish weight for the step-change experiments. Sample sizes, symbols, and line types are as in fig. 2. The fitted lines are $t_{1/2L} = 0.00485W + 2.45$ ($r^2 = .75$, $P < .0001$) and $t_{1/2D} = 0.00359W + 2.83$ ($r^2 = .83$, $P < .0001$).

respectively, of the variation in actual core temperature.

The values of k_h , k_c , and L used in figure 6 were chosen from the ranges observed in the temperature step-change experiments so that equation (3) accounted for as much of the variation in core temperature as possible. With these parameter choices, the model explained 98%, 99%, and 99% of the variation in core temperature in experi-

ments 1, 2, and 3, respectively. Table 4 summarizes the goodness of fit obtained with these optimal parameters and with the average parameter values.

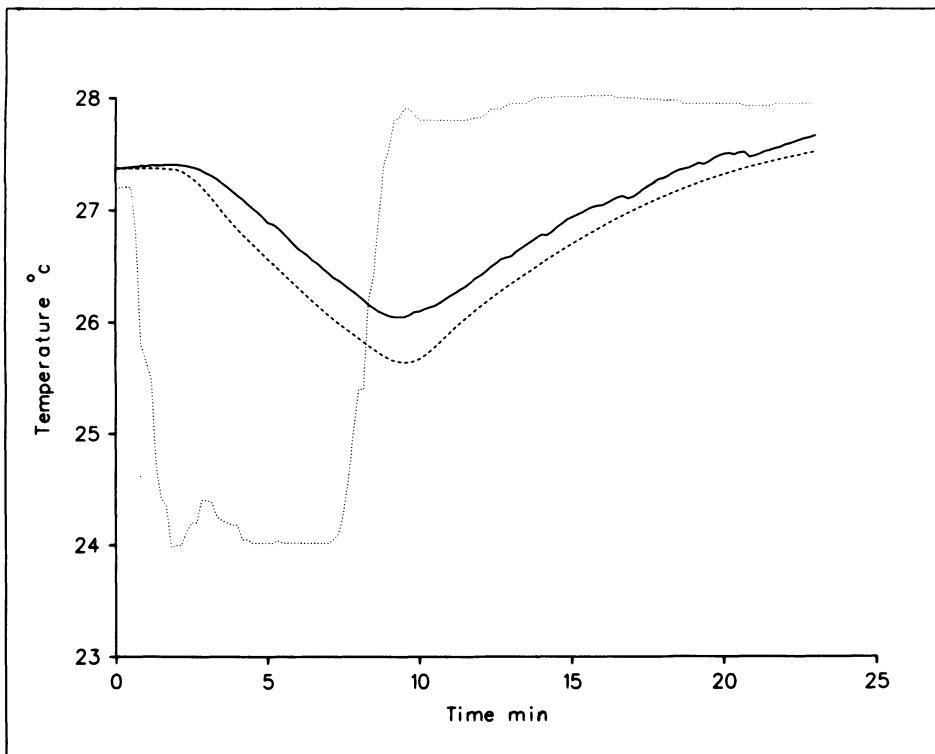
DISCUSSION

As in Fechhelm and Neill (1982), for bluegill and *Tilapia*, we estimated the model parameters k and L (heat exchange

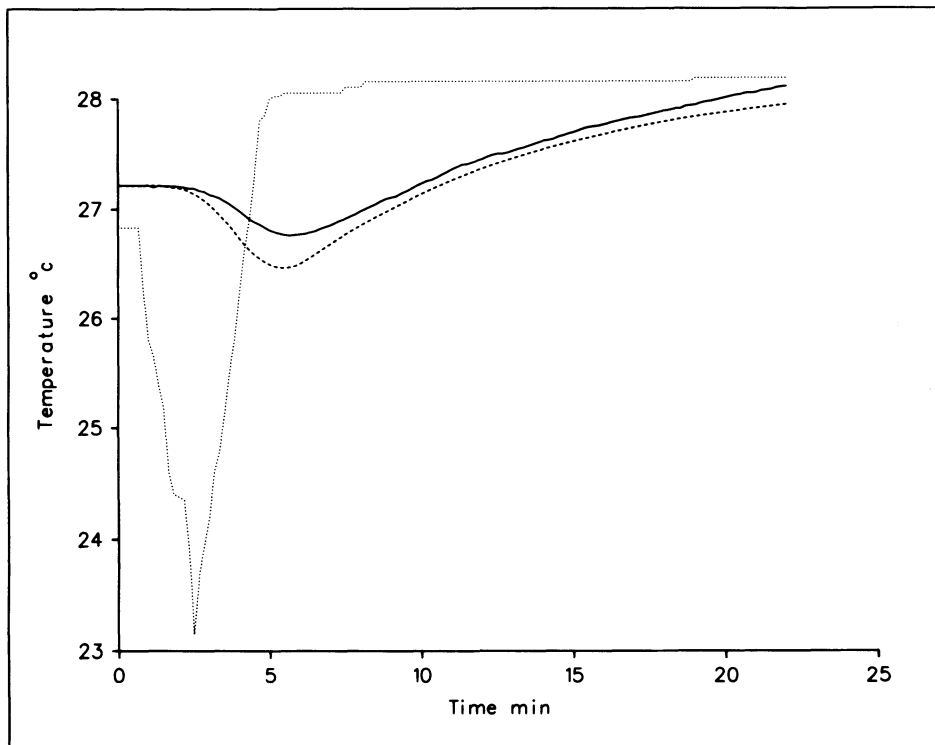
TABLE 3
THERMAL EXCHANGE PARAMETERS OF FISH 13 MEASURED BY TEMPERATURE EXCHANGE EXPERIMENTS CONDUCTED WHEN FISH IS ALIVE AND AFTER DEATH

STATUS	DIREC- TION	n	K (min ⁻¹)			L (min)			t _{1/2} (min)		
			Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Live	C	6	.0835	.0058	.0768–.0927	.84	.24	.44–1.15	9.17	.74	7.91–10.0
Dead	C	2	.0324	.0004	.0321–.0326	9.32	1.72	8.11–10.54	30.72	1.49	29.67–31.77
Live	H	6	.0930	.0038	.0853–.930	.77	.54	.24–1.76	8.23	.64	7.54–9.08
Dead	H	2	.0325	.0005	.0322–.0329	10.46	.67	9.98–10.94	31.77	.34	31.52–32.01
Live	H & C	12	.0883	.0068	.0768–.0950	.80	.40	.24– 1.76	8.67	.82	7.54–10.0
Dead	H & C	4	.0325	.0004	.0321–.0329	9.89	1.25	8.11–10.94	31.25	1.07	29.67–32.01

NOTE.—The symbols are the same as described in table 2.

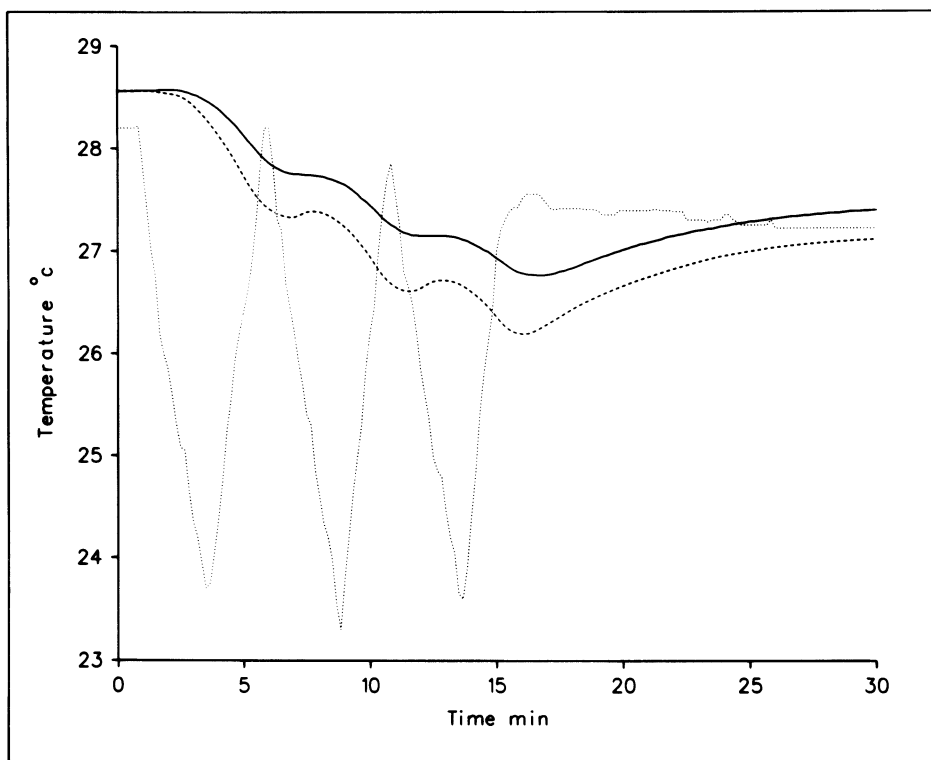


a



b

FIG. 5a-c.—Simulation of the response of body temperature of fish 104 to three different continuously varying ambient temperature regimes. The values of k_h , k_c , and L (0.130 min^{-1} , 0.111 min^{-1} , and 1.38 min , respectively) were the averages obtained for fish 104 in the temperature step-change experiments. The dotted line represents ambient temperature, the solid line is actual fish core temperature, and the dashed line is fish core temperature predicted by the model.



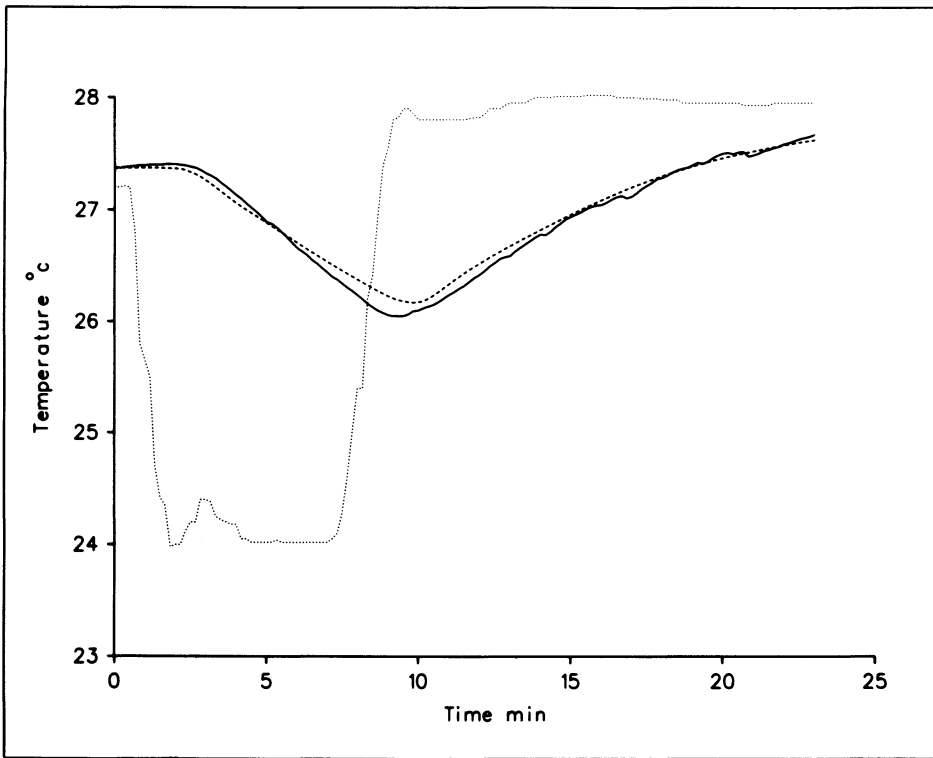
C

FIG. 5 (Continued)

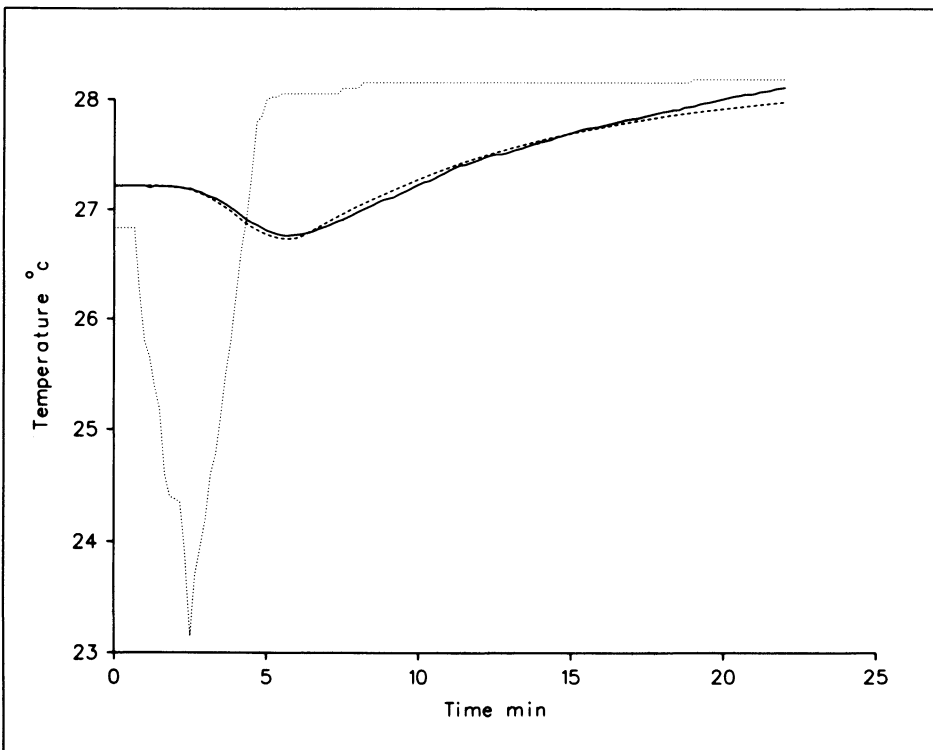
rate and lag time, respectively) for largemouth bass from temperature step-change experiments. However, we believe that our procedure is more direct than that of Fechtelmann and Neill (1982). We used nonlinear regression to fit the two-parameter equation (5) directly to the entire time series of core-body temperatures in each experiment, simultaneously estimating k and L and yielding an estimate of r^2 for the entire estimation procedure. In contrast, Fechtelmann and Neill (1982) first edited their time series to remove the initial lag period and data recorded after 80% of the body temperature adjustment was completed. The remaining data were then fitted with linear regression to the log-transformed equation $\ln|T_e - T_b(t)| = \ln|T_e - T_b(0)| - kt$ (where $||$ = absolute value). A third step was necessary to derive L , which was calculated as the mean difference between the time when each T_b was actually measured and the time predicted for that value of T_b by the linear regression equation. The r^2 values reported by Fechtelmann and Neill (1982) ($r^2 > .99$ for each of 80 experiments) are therefore

somewhat inflated relative to ours ($r^2 > .97$ for each of 66 experiments); their r^2 values consider errors in fitting only one parameter, k , to part of the original time series, whereas our procedure gives an overall r^2 for fitting both parameters to an entire time series. In either study, the consistently high r^2 values indicate the adequacy of model (5) for describing the response of body temperature to a sudden temperature change.

Although the data from each of our step-change experiments were well fitted by model (5) ($r^2 > .97$ in all cases), individual fish showed significant variation in the parameters k and L across several experiments. The coefficients of variation (CV) in k , calculated from table 2, ranged from 2% for k_h of fish 7 to 21% for k_c of fish 5; the average CV was 10%. For L , CVs ranged from 3% for L_c of fish 102 to 143% for L_c of fish 7, with a mean CV of 48%. Fechtelmann and Neill (1982) also noted greater variation in their estimates of L ; however, their estimates of both parameters were more precise than ours. The CVs of their mean k values ranged from 2% to 8% (average CV

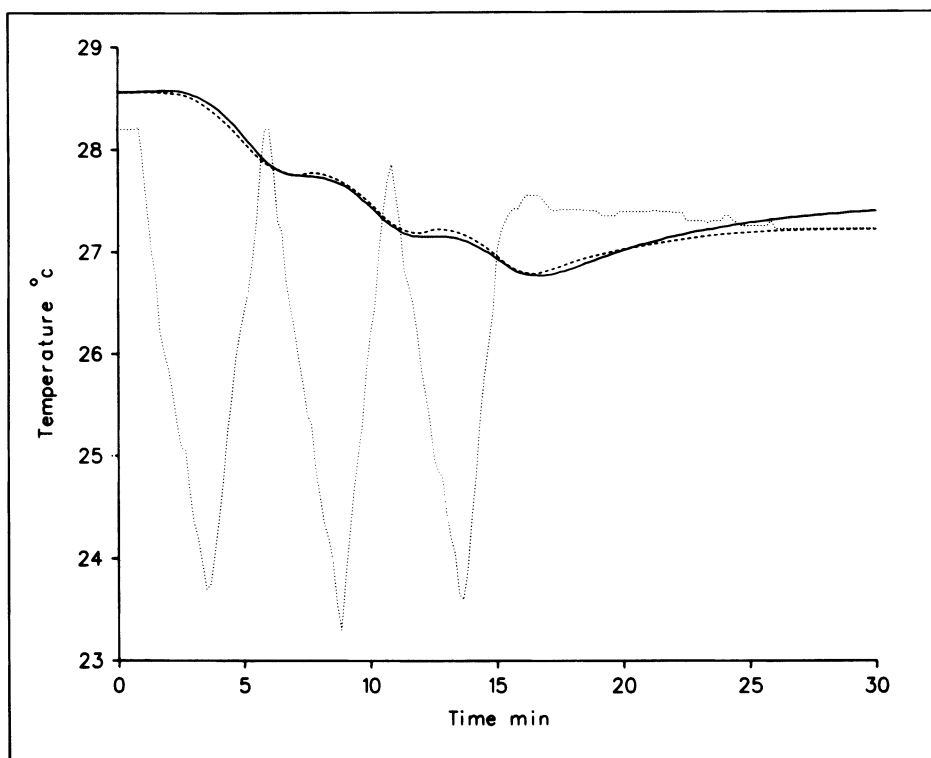


a



b

FIG. 6a-c.—Simulation of the response of body temperature of fish 104 to three different continuously varying ambient temperature regimes. The values of k_h , k_c , and L (0.132 min^{-1} , 0.066 min^{-1} , and 1.50 min , respectively) were chosen for best fit from the ranges observed for fish 104 in the temperature step-change experiments. Line types are as in fig. 5.



c

FIG. 6 (Continued)

= 5%), whereas their mean L values had CVs between 6% and 39%, with an average CV of 16%. Our estimates show greater variability, in part because replicate experiments on a given fish were done on dif-

ferent days, whereas Fechhelm and Neill (1982) performed all experiments on a given fish on the same day. Day-to-day variation in our estimates may have simple causes, such as changes in the position of

TABLE 4
QUALITY-OF-FIT MEASUREMENTS FOR CYCLING TEMPERATURE SIMULATIONS

EXPERIMENT AND PARAMETER SET ^a	ABSOLUTE ERROR °C			VARIANCE EXPLAINED (%)
	Mean	Maximum	90th Percentile	
1 (139):				
Average23	.44	.38	73
Optimal06	.18	.11	98
2 (133):				
Average12	.32	.25	89
Optimal04	.13	.09	99
3 (181):				
Average35	.61	.54	52
Optimal24	.18	.13	98
1, 2, 3 (453):				
Average24	.61
Optimal05	.18

NOTE.—Numbers in parentheses are N 's.

^a The average and optimal parameter sets are described in the legends of figs. 5 and 6.

the stomach tag, or may suggest that thermal exchange parameters vary with the changing physiological status of the fish. Fechhelm and Neill (1982) also confined their fish to prevent activity, but we did not. Differential activity among replicates probably contributed to the higher variability in our estimates since activity would tend to elevate heart rate and increase blood flow.

Despite the variability in parameter estimates, certain trends are clearly evident. The present results indicate that largemouth bass exchange heat at a faster rate when warming than when cooling, with an average k_h/k_c ratio of 1.31 for all fish. This effect has been reported in other fishes by Stauffer et al. (1975), Crawshaw (1976), Beitingner et al. (1977), Reynolds (1977), Spigarelli et al. (1977), and Fechhelm and Neill (1982). In a previous study of largemouth bass, Venables (1976) measured $k_h = 0.094$ and $k_c = 0.072$ for a 1,440 g fish, giving $k_h/k_c = 1.31$, exactly as above. However, Kubbe, Spotila, and Pendergast (1980) found no difference in largemouth warming and cooling rates. The differences in warming and cooling rates have been variously attributed to endogenous heat production, variations in blood flow, and heart rate hysteresis that depends on the direction of temperature change.

Longer lag times for warming conditions than for cooling have been reported by Fechhelm and Neill (1982). In the present study, warming lag for largemouth bass was significantly greater than cooling lag, with an average L_h/L_c ratio of 1.59. This observation warrants further study to elucidate the physiological mechanisms that paradoxically seem to delay the onset of body temperature adjustment while simultaneously raising the rate of heat exchange when warming and cooling conditions are contrasted.

The powers -0.51 and -0.62 fitted for the relationship of k to body weight in warming and cooling fish (fig. 3) are in close agreement with the value of -0.59 calculated by Fechhelm and Neill (1982) for pooled cooling and warming experiments on bluegill and *Tilapia* and with similar values from other studies also cited by Fechhelm and Neill (1982). Unlike Fechhelm and Neill (1982), who reported no significant relationships between size and

lag time, our results show that lag time is positively related to size. Of several regression equations fitted, the most predictive one related L to an exponential function of body length.

We had hoped that relationships between the thermal exchange parameters and body size could be developed with sufficient accuracy to allow parameter estimation from such curves, obviating the need for direct measurements in step-change trials for each fish. Although all the relationships were statistically significant (see figs. 3–5), the portions of unexplained variance were substantial (approximately 20% for relating k to weight and 43% for relating L to length), indicating that other factors besides size contribute significantly to determining thermal exchange parameters.

The experiments comparing temperature adjustment in fish 13 before and after death suggested that about 28% of heat transfer was mediated by conduction. Beitingner et al. (1977) concluded that conduction accounts for about 80% of the heat exchange in gizzard shad. Much of the difference between these results can be explained by the fact that our fish (weight = 1,623 g) was much larger than theirs (mean weight = 131 g). One would expect conduction to decrease in importance as weight increases since this process depends on surface area, which is smaller relative to mass in larger fish (Niimi 1975).

Our results confirm the effectiveness of the model (Eq. [3]) proposed by Fechhelm and Neill (1982) for simulating body-core temperature changes in fish subjected to continuously varying ambient temperature. Both studies indicate that average parameters measured in replicated step-change trials can be used with equation (4) to predict responses to more complex temperature regimes. Quantitative measures of accuracy were similar in the two studies, with Fechhelm and Neill (1982) reporting maximum absolute errors between 0.14 and 0.67 C (mean = 0.13 C), whereas we obtained maximum absolute errors between 0.32 and 0.61 C (mean = 0.24 C).

Both studies also observed that further improvement in model performance was possible by replacing the average parameter values with other values from within the ranges observed in step-change trials. By choosing such optimal parameters, Fech-

helm and Neill (1982) were able to reduce maximum absolute errors to 0.04 to 0.20 C, whereas our optimal parameters for fish 104 reduced maximum errors to 0.13–0.18 C.

Despite their use of less precise numerical techniques (discrete time, linear approximation vs. our simulation of [4] as a continuous process), Fechhelm and Neill (1982) obtain slightly more accurate model predictions. This probably results from the fact that they performed step-change and cycling temperature experiments for a fish on the same day whereas our experiments were done on different days, giving us more variable parameter estimates. Since many applications of this model, particularly in field studies, would not permit step-change calibration experiments immediately before or after observing fish in some ambient regime, our accuracies more closely reflect those practically attainable in such studies. In cases where parameters cannot be measured by step-change experiments, crude estimates could be calculated from relationships between parameters and body size, as in figures 3 and 4. However, this would further reduce the accuracy of equation (4) in predicting body temperature since such relationships do not explain all

the variation in measured heat exchange parameters.

In summary, we have shown that models such as (4) can be combined with estimates of heat exchange rates and lag times from step-change experiments to give predictions of body-core temperature under variable ambient temperatures. Such predictions are qualitatively accurate in estimating the timing and direction of temperature changes and are quantitatively good, explaining 50%–80% of observed variation in body temperature when ambient temperature is varied over 5 C. Reasonable parameters can also be selected that make predicted body temperatures virtually coincident with measured ones; however, day-to-day variations in parameters with physiological status make selection of such optimal values problematic. If very high levels of accuracy are needed, further work must be done to relate model parameters more closely with other factors that may explain more of this day-to-day variation and enable better parameter estimation. One possible approach to this would be the detailed investigation of circulatory processes and the effects of temperature on these processes that has been suggested by Fechhelm and Neill (1982).

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