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CONTINUATION OF STUDIES ON THERMOREGULATION OF FISH AND TURTLES IN THERMALLY STRESSED HABITATS

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ABSTRACT

Fundamental and realized climate spaces have been calculated for the turtle Chrysemys scripta. These allow us to make predictions about the effect of microclimate and thermal effluents on the behavior of these animals. We are finalizing a conceptual model to define the biophysical - behavioral thermoregulatory mechanisms employed by this turtle.

Operative environmental temperature (T_e) is a good predictor of the basking behavior of turtles. T_e is positively related to visible and thermal radiation and air temperature. A multiple regression equation

$$(T_e = 0.011R + 0.0025S + 1.53T + 0.0032V - 14.54)$$

where R = total radiation in Wm^{-2},

S = shortwave radiation from 300 - 3000 nm in Wm^{-2},

T = air temperature in ^oC and

V = wind speed in ms^{-1} ($r^2 = 0.78$)

defines the relationship of T_e to microclimate variables. Turtles generally do not bask until T_e exceeds 28^oC, thus implicating thermoregulation as a major factor in determining the basking behavior of C. scripta. A turtle basking on a log at noon experiences a T_e as high as 55^oC while a turtle floating at the surface of the water sees a T_e near water temperature.

Water temperature was very important in determining the distribution of largemouth bass, Micropterus salmoides, in a South Carolina reservoir receiving thermal effluent from a nuclear reactor. Bass were restricted in movement by lethal water temperatures and utilized a greater proportion of the reservoir in winter months as compared to summer months. Bass selected temperatures close to 30^oC and avoided temperatures above 31^oC.

Under normal, unheated conditions, bass dispersed throughout the reservoir

but were concentrated in six main areas (two shoreline locations, three coves, and one deep spring). During reactor operation, hot water at temperatures lethal to fish ($\sim 55^{o}C$), forced bass to retreat to refuges in two of the coves and the deep spring. Distribution of bass varied seasonally. During winter bass occupied larger areas in the refuges than during the summer because more cool water was present.

This study is the first in which multichannel radio transmitters were surgically implanted in free ranging fish, permitting the telemetry of temperatures from five parts of a fish's body and from its surrounding water. In general, body temperatures followed water temperatures closely, but rapidly changing temperatures produced lags between body temperatures and water of as much as $3.5^{o}C$. It appeared that skin exchanged heat fastest with water , heart second fastest and coelom and dorsal muscle exchanged heat with water at the slowest rates.

Theoretical calculations and experimental data confirm that air movement quickly strips away the boundary layer from turtles and similar shaped organisms up to 10 kg in mass. In still air, boundary layer thickness is inversely related to the difference in water vapor density at the surface of an object and in the free air beyond the boundary layer. For dry turtles and lizards this difference is small and the boundary layer is greater than for wet surfaces.

Fed and non fed turtles may spend the same amount of time basking under identical laboratory conditions. Experiments to determine if there is a thermophilic response to feeding in these animals are ongoing and will continue over the next two years.

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INTRODUCTION

The purpose of this research has been to determine quantitatively the mechanisms by which fish and turtles thermoregulate in response to thermal stress in their natural environment. During the 1979-80 project year significant progress has been made in all areas of our research and we have accomplished all of our objectives for the year. Particularly important contributions have included the first successful implantation of a multichannel, temperature sensing, radio transmitter into largemouth bass (*Micropterus salmoides*), the successful completion of our first series of field experiments on the behavioral thermoregulation of this fish, and the completion of our field studies on the relationship of operative environmental temperatures to the basking behavior of turtles (*Chrysemys scripta*). Excellent progress has been made in analyzing data and writing manuscripts. The addition of Edward Standora to the project in October, 1979 has resulted in a great improvement in the efficiency of our day to day laboratory operations and in our data handling - computer operations. More importantly, he has made very important contributions to our analysis of the fundamental and realized climate spaces of *C. scripta*. He has played an important role in our efforts to finalize our analysis of the biophysical - behavioral thermoregulatory mechanisms by which *C. scripta* adjusts to thermal effluents.

Specific objectives to be accomplished in this project year were to:

1.) Finish a definitive paper on the thermoregulatory mechanisms by which the turtle *Chrysemys scripta* adjusts to thermal effluents,

2.) Complete the first series of field studies on the behavioral thermoregulation of largemouth bass, *Micropterus salmoides*, analyze the data and plan the next set of experiments,

3.) Complete our analysis of operative environmental temperatures of

turtles,

4.) Continue theoretical calculations and attendant experiments on the effect of body size, physical characteristics and physiology on the thermoregulation of large ectotherms.

All of these objectives will have been met by September 30, 1980. Details are given below.

THERMOREGULATORY MECHANISMS OF TURTLES

Our analysis of the energy budgets and climate space of the turtle Chrysemys scripta was completed by the fall of 1979 and a working manuscript has been prepared. We also have completed a manuscript on the behavioral thermoregulation of turtles in a nuclear reactor cooling reservoir (Par Pond on the Savannah River Plant, Aiken, S.C.). This manuscript (Spotila et al. 1980a) is scheduled for submission in July 1980. It combined the data from our previous manuscripts on the microclimate of Par Pond and the response of turtles to thermal effluents in that reservoir. Completion of these manuscripts was the first phase of our effort to define the thermoregulatory mechanisms by which the turtle C. scripta adjusts to thermal effluents.

During the past year we have finished analyzing our field data from 1974 - 1977. We have also been analyzing more recent field data. At this time we are completing realized climate spaces for the turtle C. scripta. We superimpose the microclimatic conditions for which the animal was actually above water basking ($Q_{abs} + T_a$); plus the water temperatures it occupied (as if it was operating along the blackbody line of the climate space) over the theoretical or fundamental climate space as given by Foley (1976), thus producing a realized climate space (Fig. 1). Edward Standora is now completing this analysis. This approach provides a much clearer picture of the acutal ability of a turtle to exploit the thermal niches available in its environment. Standora, Foley and I

will now combine this information with that in our working manuscript on energy budgets and climate spaces to produce a paper on the fundamental and realized climate spaces of C. scripta by the end of this year. Rather than providing just another climate space paper we will make a more fundamental contribution by combining data from real animals and microclimates with our theoretical computations to provide biologically meaningful predictions. This completes the second phase of our effort. Joseph Schubauer has completed his master's thesis (June 1980) and has several manuscripts in preparation on the response of turtles (movements and population structure) to thermal effluents in Par Pond (Schubauer 1980).

With our backlog of field and laboratory data analyzed we are entering the final phase of our effort to develop a theoretical framework on which to base a behavioral - biophysical - ecological model of the thermoregulation of C. scripta. In August we will have a meeting of all the principals in our turtle studies and after an open exchange of ideas will finalize the outlines of our model. Then we will set about writing what we expect to be a definitive paper on the behavioral thermoregulation of this animal. The research of Kenneth Crawford on the effect of operative environmental temperature on the behavior of turtles will be very important in this final phase of our effort to define the thermoregulatory mechanisms employed by C. scripta. Crawford's research is detailed in the next section.

In summary, phase I of this year's turtle research saw the completion of a working manuscript on the energy budgets and climate space of C. scripta and a manuscript on the behavioral thermoregulation of turtles in Par Pond. Phase II involved the further analysis of field data to produce realized climate spaces and the combination of this analysis with the working manuscript to produce a paper on the fundamental and realized climate spaces of C. scripta.

Phase III involved the operative environmental temperature study (see next section) and the effort to formulate a model to define the thermoregulatory mechanisms employed by this turtle. Completion of these three phases completes the first objective of this year's research.

OPERATIVE ENVIRONMENTAL TEMPERATURE

Operative environmental temperature (T_e) (Bakken 1976, Bakken and Gates 1975, Bakken 1980) is a good predictor of the basking behavior of turtles. Kenneth Crawford has completed his analysis of the data from his T_e study of 1979 and has completed his thesis (Crawford 1980).

We have defined T_e as the "operative environmental temperature" *sensu stricto* (Bakken and Gates 1975, p. 261 and Bakken 1976, p. 351-352). That is "T_e may be identified as the temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal and exposed to the same microclimate. It is also equivalent to the temperature of a blackbody cavity producing the same thermal load on the animal as the actual nonblackbody microclimate, and therefore may be regarded as the true environmental temperature seen by that animal". (Bakken and Gates, p. 261, 1975). For an ectothermic turtle, with no pelage, T_e is the temperature of the environment as experienced by the animal and is an index of the thermal load placed on the animal by its environment.

Operative environmental temperature is a generalization of the <u>operative temperature</u> stress index developed by Winslow et al. (1937). While well suited for use with naked, ectotherms that exhibit low rates of evaporative water loss (turtles, lizards), it is not applicable to homeotherms that have pelage. In that case the proper thermal index is "standard operative temperature" (T_{es}). This index has been discussed by Bakken (1976), Robinson et al. (1976), and

Mahoney and King (1977). Recently Bakken (1980) has reviewed the evolution of the T_{es} term from the operative temperature concept of Winslow et al. (1937) and Gonzalez et al. (1974) and the standard operative temperature of Gagge (1940), Kerslake (1972) and Gonzalez et al. (1974). As now defined T_{es} is a direct index of sensible heat flux. Since it includes body temperature and the insulation of pelage in its definition it is most useful for homeothermic animals (Bakken 1980) and not readily applicable to ectotherms (Bakken 1976).

Since T_e is the "true" environmental temperature and is equivalent to the temperature of an inanimate model of an ectotherm we were able to measure T_e for a turtle by constructing a cast of the animal and using it as a "T_e thermometer". This was similar in concept to the use of the Vernon (1932) globe thermometer which was designed to measure the heat stress on a human in an indoor environment (Kerslake 1972, pp. 67-72). However, it was much superior in both theory and practice. Vernon's "thermometer" was a blackened copper toilet float and had nearly the same operative temperature as a human due to a similar relation between convection and radiation (Kerslake 1972). Crawford's T_e thermometers duplicated turtles in size, shape, radiative properties (absorptivity and emissivity), and substrate contact area. Therefore, they had the same T_e as real turtles and could be used with confidence without first undertaking a detailed energy budget analysis. Thus when he placed them in the same positions in the environment as occupied by turtles he could measure operative environmental temperatures on a continuous basis. The complex thermal environment (solar radiation, water temperature, wind speed, etc.) was simplified into an integrated temperature that gave the heat load on the animal. For example, a turtle basking on a log at noon saw a T_e as high as 55°C, while a turtle floating at the surface of the water saw a T_e near water temperature.

T_e is positively related to visible and thermal radiation and air temperature (Figs. 2 - 4). It is not obviously related to wind speed (Fig. 5). A

multiple regression equation describes the relationship of T_e to these microclimate parameters.

$$T_e = 0.011R + 0.0025S + 1.53T + 0.0032V - 14.54$$

where R = total radiation in Wm^{-2},

S = shortwave radiation from 300 - 3000 nm in Wm^{-2},

T = air temperature in ^oC and

V = wind speed in m s^{-1} ($r^2 = 0.78$)

Turtles, C. scripta, generally do not bask until $T_e > 28^oC$ (Fig. 6). This is not an artifact of our measurement system since we often measured $T_e < 28^oC$ (Fig. 7) and very few turtles basked at low T_e. Thus T_e was a good predictor of basking behavior. By computing T_e for our previous field data (1974 - 1977), using the equation given above, we were able to confirm the role of T_e in determining the basking behavior of turtles. Turtles in Susan's Swamp (point C, Fig. 8) in 1974 - 1976 basked when $T_e > 28^oC$ as predicted from Crawford's data (Fig. 9). Since the observations on basking behavior were made by one group of researchers who did not measure T_e and T_e was computed for those turtles by Crawford who did not make the original microclimate and behavioral observations, we have a blind test of our theory. We predicted that turtles would bask at T_e exceeding 28^oC. We computed T_e from independent data and plotted the number of basking turtles vs T_e. The turtles behaved as we had predicted giving us confidence in the utility of T_e as a predictive tool for turtle behavior and implicating thermoregulation as the major factor in determining the basking behavior of C. scripta. Crawford is now preparing a manuscript for publication on these results. His findings play an important role in our efforts to develop a model to predict the thermoregulatory behavior of this species.

FIELD STUDIES ON LARGEMOUTH BASS

Claire Ross examined the behavioral mechanisms which allow largemouth bass

Micropterus salmoides to survive under adverse temperature conditions in a South Carolina reservoir (Pond C, Fig. 8) receiving thermal effluent from a nuclear reactor. Water temperature was very important in determining the distribution of largemouth bass and bluegill (Lepomis macrochirus) in the reservoir. Bass were restricted in range by lethal water temperatures and utilized a greater proportion of the reservoir in winter months as compared to summer months. Bass selected temperatures close to 30°C and avoided temperatures above 31°C.

Temperature and Distribution

Under normal unheated conditions, bass spread throughout the reservoir. Reduced reactor water flow lowered the water level throughout the reservoir and temperatures were normal. Ross located bass by fishing with artificial lures and by electroshocking. She found that although fish were dispersed in all parts of the reservoir, they were concentrated in six main areas (Fig. 10).

Bass and bluegills were found along both shorelines just outside Sanctuary Cove, but much of the shoreline between this area and Powerline Refuge was devoid of bass. Powerline Refuge, at a depth of 10 m, was one of the deepest locations in the reservoir. The deep, cooler water always contained a relatively large number of bass. The western shore near Powerline Refuge was shadowed with trees. Bass were usually caught along this shoreline. The northeastern shore was more shallow but contained an abundance of dead trees and stumps. This area was representative of typical bass habitat and supported a moderate number of Pond C bass. The greatest concentration of all species and sizes of fish was located in Canal Cove. Fish congregated at the inflow area where the reactor cooling water spilled over the rock-lined canal into the reservoir. This was the deepest area within the cove (7 m). Many large bass and bluegill were caught by electroshocking. Many smaller fish were also present between and

around the rocks at the mouth of the canal. Small bass and bluegill occupied the shallow shoreline areas near Boat Dock Cove, often in schools of about 10 to 50 fish. Larger fish resided in the deeper water. Fish in Canal Cove and Sanctuary Cove appeared tightly aggregated but not schooled.

Commencement of reactor operation resulted in increased water flow and then the release of hot water into Canal Cove (approximately 55°C). No dead fish appeared immediately after the reactor resumed operation. Presumably, the fish left the area before water temperatures became lethal. Although surface temperatures at Powerline Refuge were 45°C, the deeper, cooler water offered refuge to some bass. Boat Dock Refuge was located away from the main hot water current. There was a cool stream at the back (west) end of the cove which cooled the water enough for scanty bass habitation. The only other spot supportive of fish at this time was Sanctuary Cove. Bass assembled here in substantial numbers. Although surface water ranged in temperature from 33°C to 40°C in summer, cooler water entered Sanctuary Cove from three streams. This cooler, heavier water sank to the bottom and provided cool spots throughout the cove (Fig. 11). Channels, apparently dug by alligators as they moved through the area, provided cool water pathways which led from two of the streams through Sanctuary Cove to the deeper water beyond. Smaller fish confined themselves to shorelines in small groups of up to 10 fish. Adult bass inhabited areas in the aquatic vegetation and under floating boards. Bass were sometimes crowded two to five abreast under the boards. Adults also occupied specific shoreline areas which were shaded by overhanging trees and bushes. Adult bluegills populated the warmer (32 - 42°C) water outside Sanctuary Cove in Coves 2 and 3 (Fig. 10). The remaining water channels in Pond C were barren of fish. These observations were consistent with the reports of Clugston (1973) and Siler (1975) but expand their findings by providing more detailed observations of fish locations and behavior. Details are contained in a master's

thesis (Ross, 1980).

Distribution of bass varied seasonally. For example, during late winter, bass occupied larger areas in the refuges than during summer (Fig. 12). This was directly related to water temperature. During this period (early March) bass were found only in those areas which provided a temperature below 31°C. Even if surface temperature was as high as 37°C, bass could apparently survive by spending at least part of their time at much lower temperatures. Because of cooler ambient temperatures and increased stream flow, the refuge areas contained greater amounts of cool water than during the summer. This heavier water flowed under the heated effluent and provided larger areas that had temperatures suitable for bass habitation.

The importance of temperatures of 31°C or lower to bass was also indicated by the body temperatures of 11 bass caught in Sanctuary Cove in March 1980. Mean stomach temperature was 29.6°C with a range from 25.0°C to 31.0°C. Although these bass had temperatures from 10 to 34°C available to them in the refuge area most of them were operating at a temperature of 29 to 31°C. Clugston (1973) found a preferred temperature of 27 to 30°C for adult Pond C bass and Siler (1975), using gill nets in Pond C, caught bass in water of 27 to 35°C under heated, winter conditions. Body temperatures of these bass were not known. In other studies Coutant (1975) reported preferred temperature and optimum growth rate at 27°C for adult bass in Tennessee lakes, Dendy (1946) listed the thermal preferendum of bass in the field as 26 to 28°C and Warden and Lorio (1973) found diurnal movement of bass decreased and nocturnal movement increased at temperatures above 27°C. Upper avoidance temperatures of 30°C were reported for Par Pond bass by Clugston while 29°C was found for largemouth bass in Tennessee (Coutant 1975). At this time it appears that bass in Pond C have similar preference and avoidance temperatures as bass from other areas.

When confined to the refuge areas bass and bluegill experienced a wide variety of temperatures. If they swam towards the main portion of the reservoir they quickly encountered lethal temperatures even in late winter. If they remained in an area like Sanctuary Cove they encountered considerable vertical and horizontal variation in temperature. Gradients of 15°C were common from the bottom to surface in water 0.5 - 0.9 m deep. A large bass could easily experience 15°C at its ventral surface and 20°C or more at its dorsal surface while remaining motionless. By swimming a short distance, this bass could quickly go from a water temperature of 14°C to 32°C. By moving along alligator channels a bass could reach Coves 2 and 3 where bottom temperatures ranged from 22.5 to 31.0°C in early March.

Temperature Telemetry

This study is the first in which multichannel radio transmitters were surgically implanted in fish, permitting the telemetry of temperatures from five parts of a fish's body and from its surrounding water. Fish were unrestrained and moved freely in their natural habitat in Pond C. From the shore or from a boat it was possible to follow their movement from as far away as 300 m. Muscle, skin, heart, two coelom temperatures and water temperature were transmitted every two minutes and recorded at varying intervals. Upon release, and whenever possible at other times, data were recorded continuously. At times when bass remained in one area, data were taken every 15 minutes.

A total of five bass were successfully implanted with transmitters. Of these five, two bass were tracked at normal temperatures, and three at heated temperatures. In general, body temperatures followed water temperatures closely but rapidly changing temperatures produced lags between body temperatures and water of as much as 3.5°C. A typical data set (Fig. 13) shows that a fish in

Sanctuary Cove swam into both cool and warm water but avoided water temperatures greater than 32°C or less than 20°C. When this fish made quick excursions into warm water (↓Fig. 14) dorsal muscle temperature lagged as much as 3.2°C behind water temperature. When the fish returned to cooler water (↑Fig. 14) dorsal muscle temperature was just reaching that warmer water temperature. Later when the fish made a longer trip into warm water and then returned to a cool area, dorsal muscle temperature continued to heat due to thermal lag, even while the exterior of the fish was cooling (second↓Fig. 14). This pattern continued throughout this track and was also apparent for the coelom (Fig. 15) and heart (Fig. 16). This fish left warm water when its exterior was exposed to temperatures near 31°C even though dorsal muscle temperature was 27.3°C, coelom temperature was 27.1°C and heart was 28.1°C. When this fish encountered large changes in water temperature its internal body compartments showed considerable lag in temperature. It appeared to be responding behaviorally to high water temperature well before (e.g. 30 min., Fig. 14) its body compartments equilibrated to water temperature. This is of interest because the bass continued to heat internally evenwhen it entered cooler water. Other bass showed similar thermal responses. Large temperature differentials (1.0 - 3.0°C) occurred most often when bass were crossing a cove or traversing the reservoir, swimming through many different water temperatures in a relatively short time.

The close relationship between bass body and water temperature is expected of small poikilotherms because of limited heat storage capacity and conductive heat exchange with the water (Spotila 1980). It appears that skin temperature exchanges heat fastest with water, heart second fastest, and coelom and dorsal muscle exchanges heat with water at about the slowest rates.

Kubb (1979) found rates of heat exchange in bass were fastest in the heart, slowest in the mid-gut region, and intermediate in the brain. The heart and

midgut rates would agree with those suggested by this study but the hypothesis of Kubb and Spotila (1980), that heart temperature may limit the exploitive behavior of bass, cannot be supported by this data. It appears that skin temperature may provide the stimulus for the bass to seek different temperature water. At external temperatures of 30 to 31°C (water), the bass entered cooler water. Even though the bass avoided water temperature above 31°C, body temperatures rose to 31.3°C. It would seem that the bass would also have had to "know" its thermal time constant to consistently keep its internal body temperature below lethal levels, otherwise heat lag within its body would result in a continued rise in body temperature even after the fish entered cooler water. This rise above external temperature is not always a set rate of temperature change, but is dependent on the size of the fish (Kubb and Spotila 1980), amount of time spent in a particular temperature, and the steepness of the thermal gradient. To prevent internal compartments from reaching lethal temperatures, the bass must seek cooler water far in advance of the anticipated critical internal temperature. Heat exchange is fastest at the skin surface and so it seems likely that sensors located here would receive immediate reinforcement for thermoregulatory behaviors. Crawshaw (1979) reported that the ability to sense changes in peripheral temperature is well-developed in ectotherms. This is supported by the findings of Bardach (1956) and Dizon et al. (1974, 1976). Peripheral temperature sensors have been implicated in the regulation of body temperature in ectotherms (Myhre and Hammel 1969, Crawshaw and Hammel 1971, 1974).

Habitat Selection and Behavior

Habitat selection by Pond C bass involves more than avoidance of lethal temperatures. Pond C bass are restricted in range by water temperature. Bass must constantly respond behaviorally and physiologically to minimize adverse effects caused by physical stresses placed on them by this extreme and

unpredictable environment while satisfying their biological requirements such as feeding, spawning, defense of territory, maintenance of position in dominance heirarchies, and avoidance of predation. The physiological effects caused by continuously fluctuating environments must be offset by compensatory mechanisms. The motivation for temperature selection and reasons for deviations from anticipated physiological optima must be strong behavioral preferences. For example, although a bass telemetered under heated conditions could have achieved a preferred temperature between 20 and 31°C, it behaved as though using Neill's (1979) reactive mechanism of thermoregulation by moving away from undesirable temperatures. Coutant (1975) found habitat preference for stumps and rock outcrops by bass overruled optimum temperature selection. Reynolds (1977) pointed out that non-thermal stimuli may provide the adaptive or ecological value for such deviations. We conclude from our study of Pond C bass that behavioral stimuli interacted with optimal temperature selection of the bass under heated and normothermic conditions and that these bass selected an optimal habitat rather than an optimal temperature.

The successful completion of this study signals that we have met the first three research objectives for this year. It has also raised several important questions concerning the thermoregulation of bass in Pond C. These are: 1. What are the behavioral mechanisms by which these fish adjust to the sudden influx of lethal hot water when the reactor becomes operational? 2. What is the homing ability and site fixity of bass in the three sanctuary areas (do Sanctuary Cove bass always return there when hot water enters the reservoir?) 3. What is the response of bass to multiple stresses (overcrowding, predation, high temperatures) when they are confined to small refuge areas for long periods of time?, and 4. What is the role of thermal sensors and heat transfer properties of bass in determining the behavioral response of these fish to water temperatures? We have designed several experiments to address these questions over the

next three years. These are detailed in our research proposal which accompanies this report.

EFFECT OF BODY SIZE, PHYSICAL CHARACTERISTICS AND PHYSIOLOGY ON THE THERMOREGULATION OF LARGE ECTOTHERMS

Boundary Layer Studies

We have continued our theoretical calculations on the effects of body size on thermoregulation. Reanalysis of our data and that of Tracy and Sotherland (1979) by us and them has clarified the role of boundary layer resistance in the evaporation of water from biological surfaces. Using bird eggs as a model system we demonstrated that air movement quickly strips away the boundary layer from eggs, turtles and similar shaped organisms up to 10 kg in mass. At a wind speed of 100 cm s^{-1} the boundary layer resistance (r_b) of a 10 kg sphere is 15 times less than in still air and at 400 cm s^{-1} it drops to almost zero (Spotila et al. 1980b). An apparent contradiction between theoretical calculations by Tracy and Sotherland and our experimental data has been resolved. In still air, boundary layer thickness is inversely related to the difference in water vapor density at the surface of an object and in the free air beyond the boundary layer. For bird eggs, turtles with dry shells, and lizards this difference is small because internal resistance is large and the concentration of water molecules at the surface is small. Thus boundary layer thickness is greater and r_b is larger. Therefore, while our agar replicas are excellent models for the measurement of boundary layer thickness and r_b for biological surfaces in moving air, they underestimate r_b and boundary layer thickness under conditions that are predominantely affected by natural convection.

Nutritional Status and Basking Behavior of Turtles

We have demonstrated that basking is an important thermoregulatory behavior

in turtles (C. scripta) under natural conditions (Spotila et al. 1980). Since Gatten (1974) reported that recently fed C. scripta had a higher preferred body temperature (29.1°C) than non fed individuals (24.6°C) we hypothesized that fed turtles should bask more often and/or for longer periods of time than non fed animals, resulting in higher body temperature through time. As a first step in testing this hypothesis we have completed one phase of a laboratory experiment to determine the effect of feeding on the basking behavior of C. scripta.

Ten C. scripta were held in each of two isolated enclosures (25°C) with free access to water, dry substrate and a light-heat source above the dry substrate. One group was fed a diet of meat and vegetables while the other was not fed. Behavior was filmed during the light phase of a LD 12:12 photoperiod during the six weeks of the experiment. Preliminary data analysis suggests that there was no statistical difference in basking times between the fed and non fed groups during the first replication. The second replication is underway and definitive results will be available upon its completion. However, it seems that our turtles are not acting as expected if feeding causes a thermophilic response.

This raises some important questions. Many authors have reported that lizards and snakes (Regal 1966) and turtles (Moll and Legler 1971) initiate or prolong thermophilic behavior and basking, in response to feeding. Body temperatures are elevated above fasting levels for recently fed snakes (Benedict 1932, Regal 1966, Kitchell 1969, McGinnis and Moore 1969, Goodman 1971, Saint Girons 1975, Van Mierop and Barnard 1976) a lizard (Witten and Heatwole 1978), turtles (Gatten 1974, Schuett and Gatten 1980) and crocodilians (Lang 1979). Others have reported no response in an iguanid lizard (Case 1976), aquatic turtles (Boyer 1965) and a crododilian (Diefenbach 1975). The exact relationship between feeding, basking behavior and body temperature is therefore unclear. Parmenter (1978) reported that C. scripta had an optimum ingestion rate at 29°C.

That is the preferred body temperature for fed animals (Gatten 1974). The majority of the evidence suggests that feeding should cause a thermophilic response in turtles and other reptiles although this response may be affected by other factors such as heterogeneity in the thermal environment, acclimation or water temperature, social interactions, past history, health, enzyme kinetics, etc. We plan to investigate the interrelationships of some of these factors in the thermoregulatory behavior of C. scripta.

Our first action will be to complete the current experiment and analyze that data. Then we will conduct a series of experiments on the basking behavior and body temperatures of fed and non fed C. scripta acclimated at 10, 20, 30, and 35°C in an environmental chamber containing a heat-light source, dry substrate and water. We expect fed turtles to bask more often and have a higher body temperature than non fed animals, especially at lower ambient temperatures (10 and 20°C). Finally we will begin to study digestive efficiency and enzyme efficiency of turtles held at these temperatures. These experiments will be conducted over the next three years and are described in more detail in the renewal proposal that accompanies this report.

CONCLUDING COMMENTS

During this year we have published five articles (Gibbons et al. 1979a, Gibbons et al. 1979b, Kubb and Spotila 1980, Paladino et al. 1980, Spotila et al. 1979) and one note (Schubauer et al. 1980), two articles are in press (Davis et al, 1980, Spotila et al. 1980b) and six are in preparation or submitted for review. Four master's theses were completed (Crawford 1980, Ross 1980, Schubauer 1980 and Weinheimer 1980). In December 1979 we presented two papers at the American Society of Zoology meeting in Tampa, Florida. This summer we are presenting four papers at the joint meeting of the Herpetologists League and Society for the Study of Amphibians and Reptiles.

Cooperation with the Savannah River Ecology Laboratory (SREL) continues to be an important factor in our field research. This year we have worked very closely with Dr. J. W. Gibbons and members of his laboratory. We continue our working contacts with Drs. John Giesy and I. L. Brisbin. Edward Standora who conducted his Ph.D. research at SREL has joined our laboratory and made very significant contributions to our research efforts this year. By maintaining this cooperative effort we have increased the effectiveness of our research effort and contributed to the research goals of SREL. Claire Ross was supported in part by a SREL graduate research support fellowship while Kenneth Crawford was supported by this contract. Two of our published papers were coauthored with members of the SREL staff as are two of the manuscripts in preparation.

The project director, James R. Spotila, spent 100% of his time on this project during the month of June 1980. He spent 33% of his time on this project during the 1979-80 academic year.

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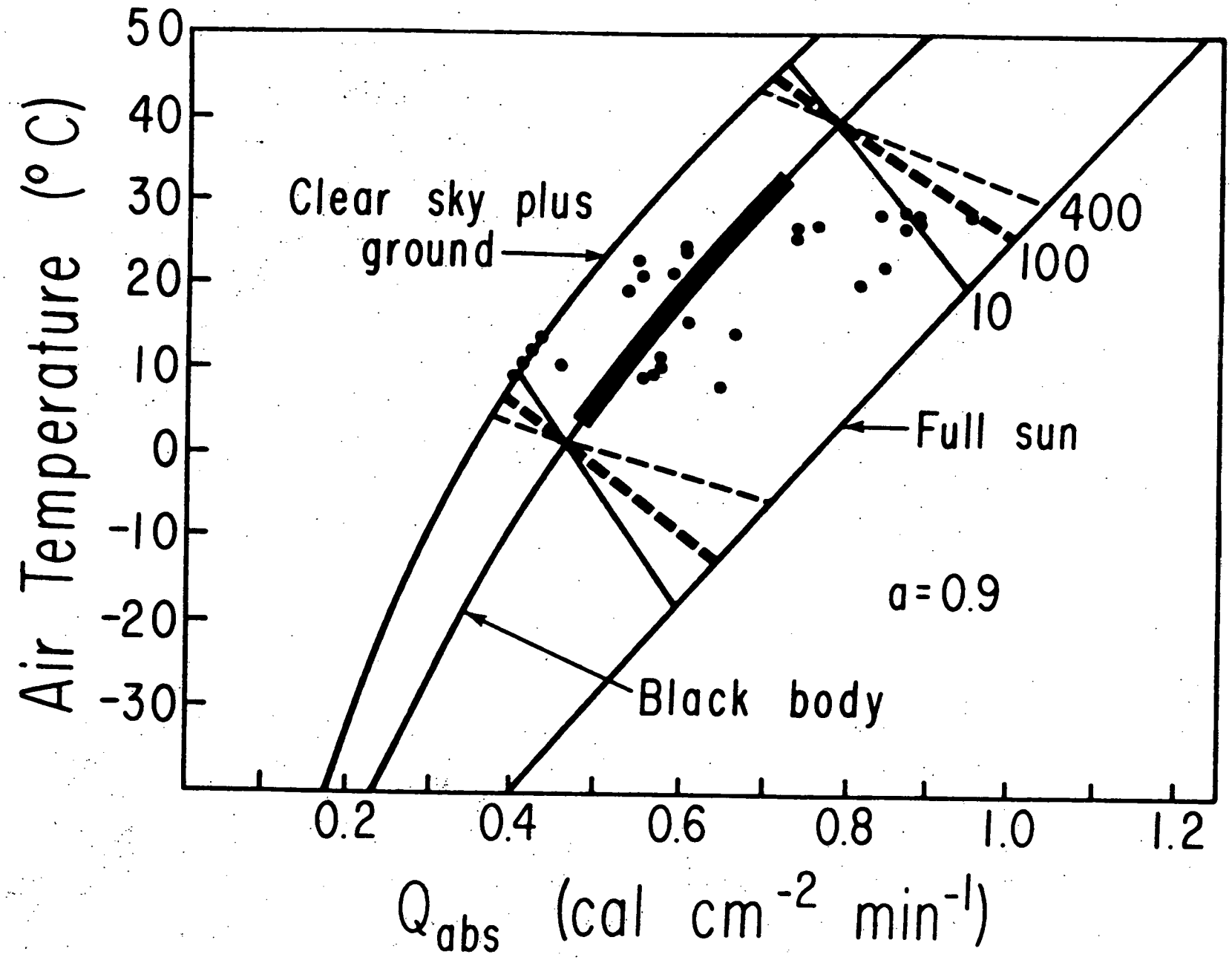

Figure 1. Realized climate space for the turtle Chrsemys scripta. Dots indicate conditions during which basking was observed. The wide area on the blackbody line represents water temperatures experienced by the turtles. Solid and dashed lines marked 10, 100, and 400 indicate limits to the fundamental climate space as affected by wind, (cm s^{-1}).

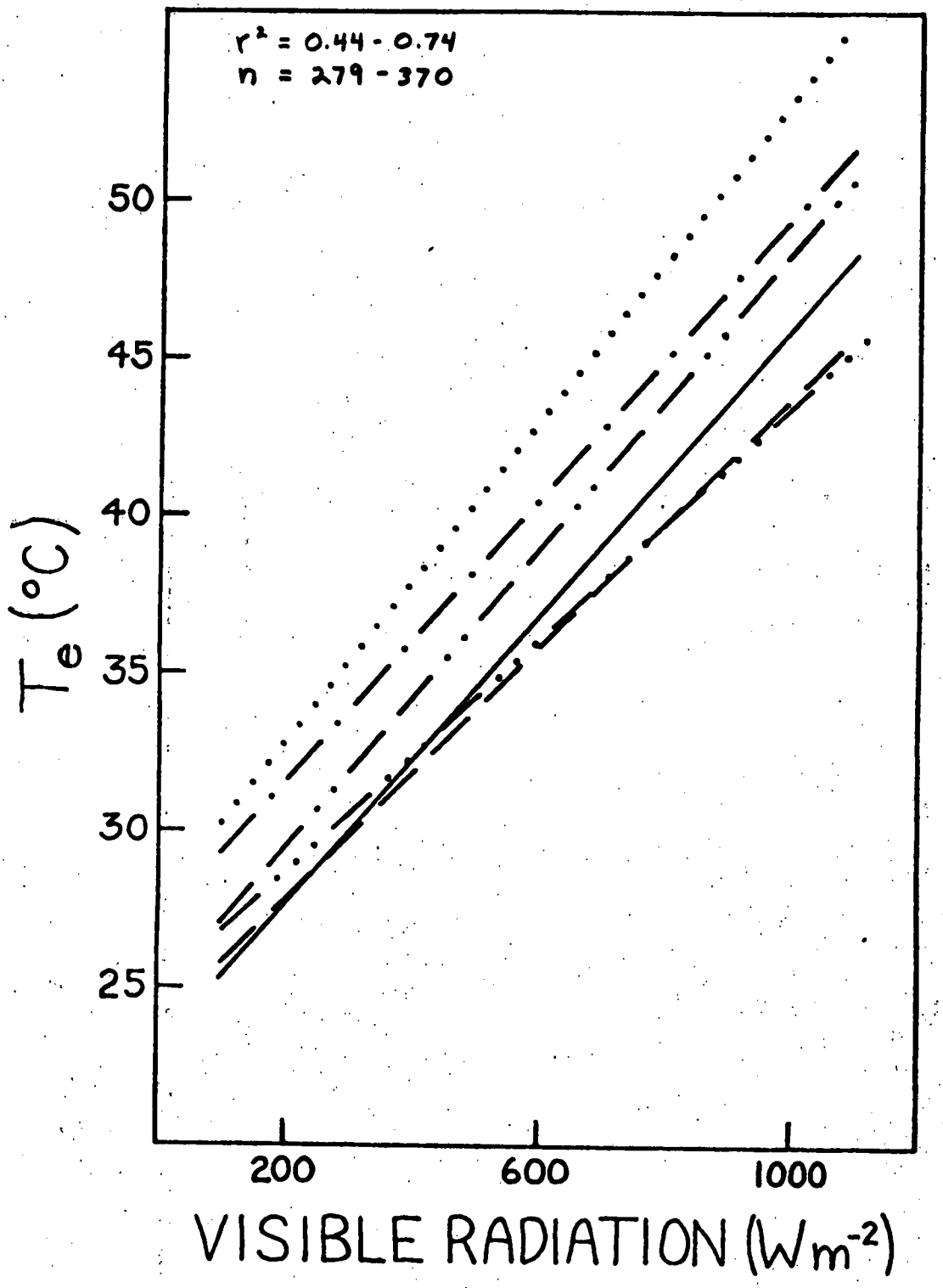

Figure 2. Linear regressions of Operative Environmental Temperature of the turtle C. scripta as a function of visible radiation for six hollow copper models painted black. Measurements were made in South Carolina in 1979 and 1980.

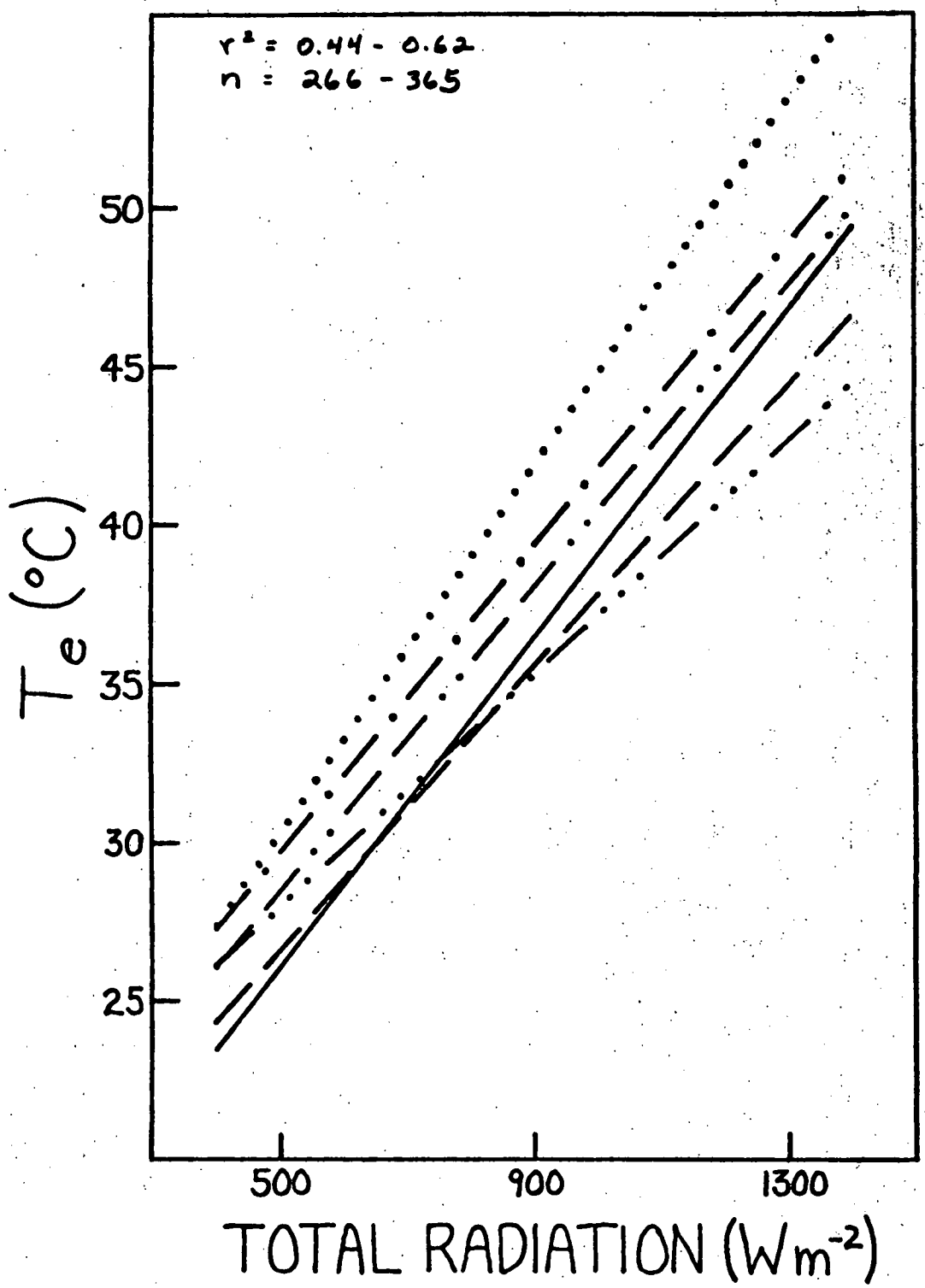

Figure 3. Linear regressions of Operative Environmental Temperature of the turtle C. scripta as a function of total radiation for six hollow copper models painted black. Measurements were made in South Carolina in 1979 and 1980.

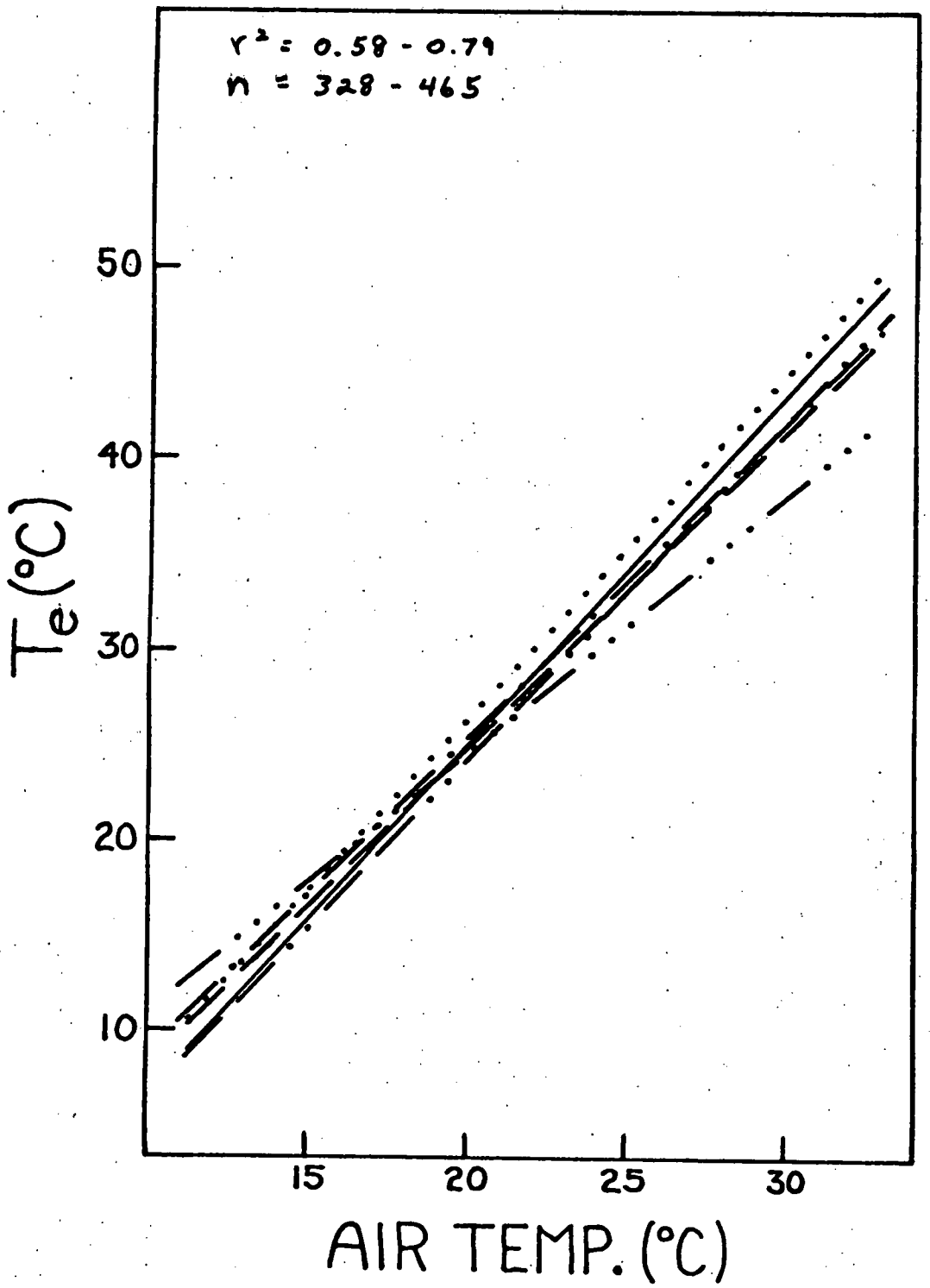

Figure 4. Linear regressions of Operative Environmental Temperature of the turtle C. scripta as a function of air temperature for six hollow copper models painted black. Measurements were made in South Carolina in 1979 and 1980.

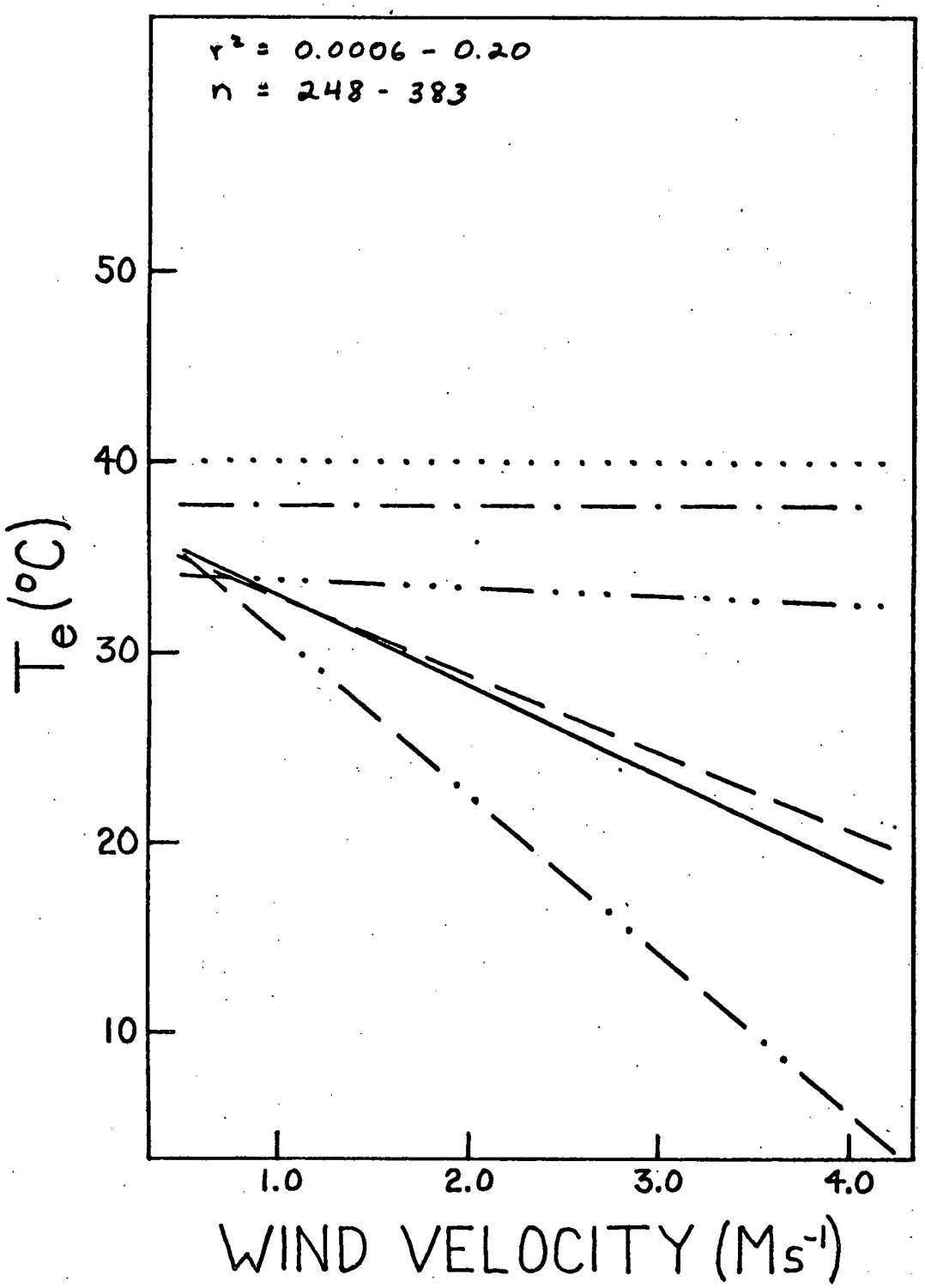

Figure 5. Linear regressions of Operative Environmental Temperatures of the turtle C. scripta as a function of wind velocity for six hollow copper models painted black. Measurements were made in South Carolina in 1979 and 1980.

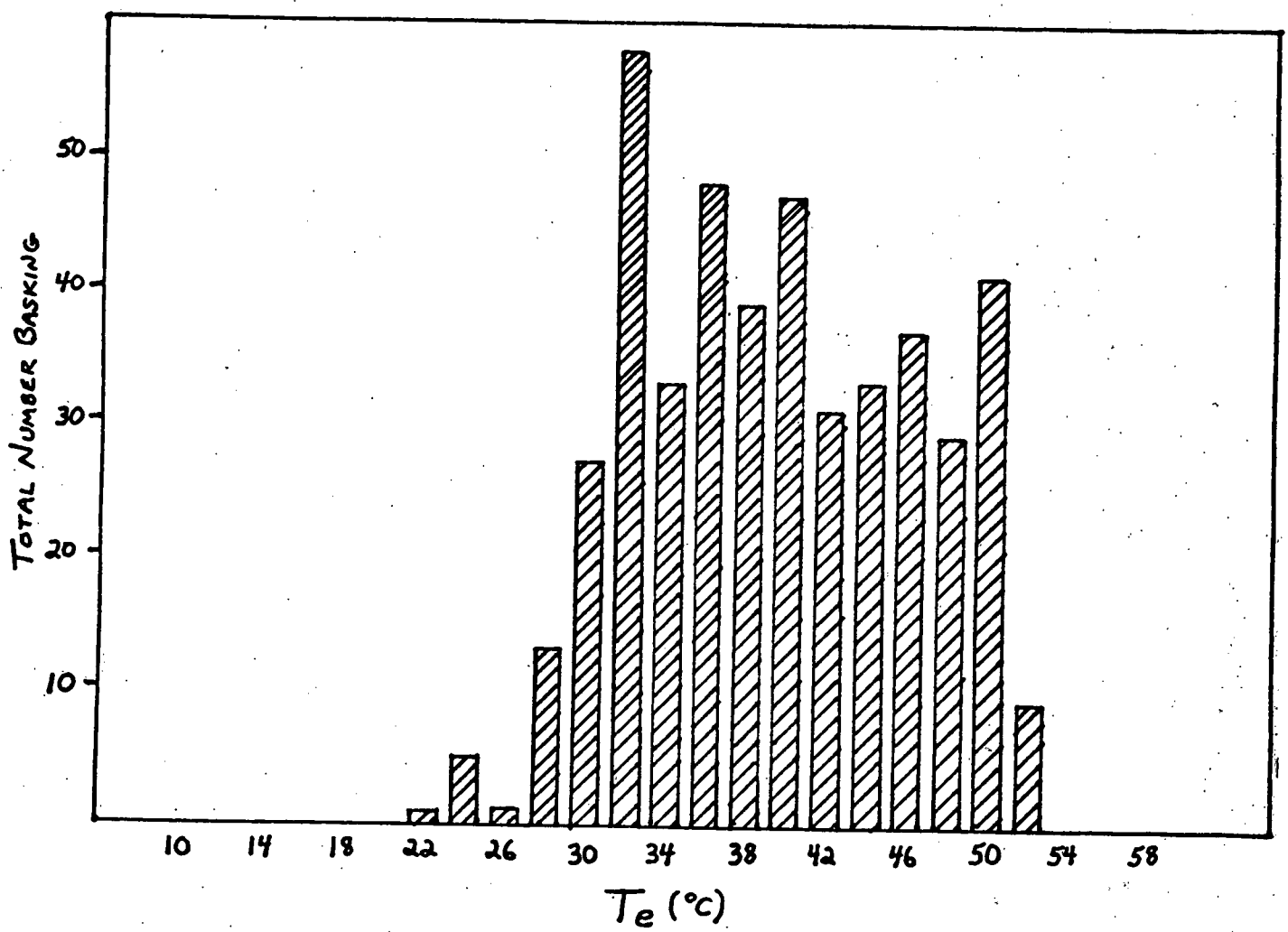

Figure 6. Histogram of the total number of turtles observed basking in South Carolina and their associated operative environmental temperatures. Temperatures are grouped by 2°C intervals. Measurements were made in 1979 and 1980.

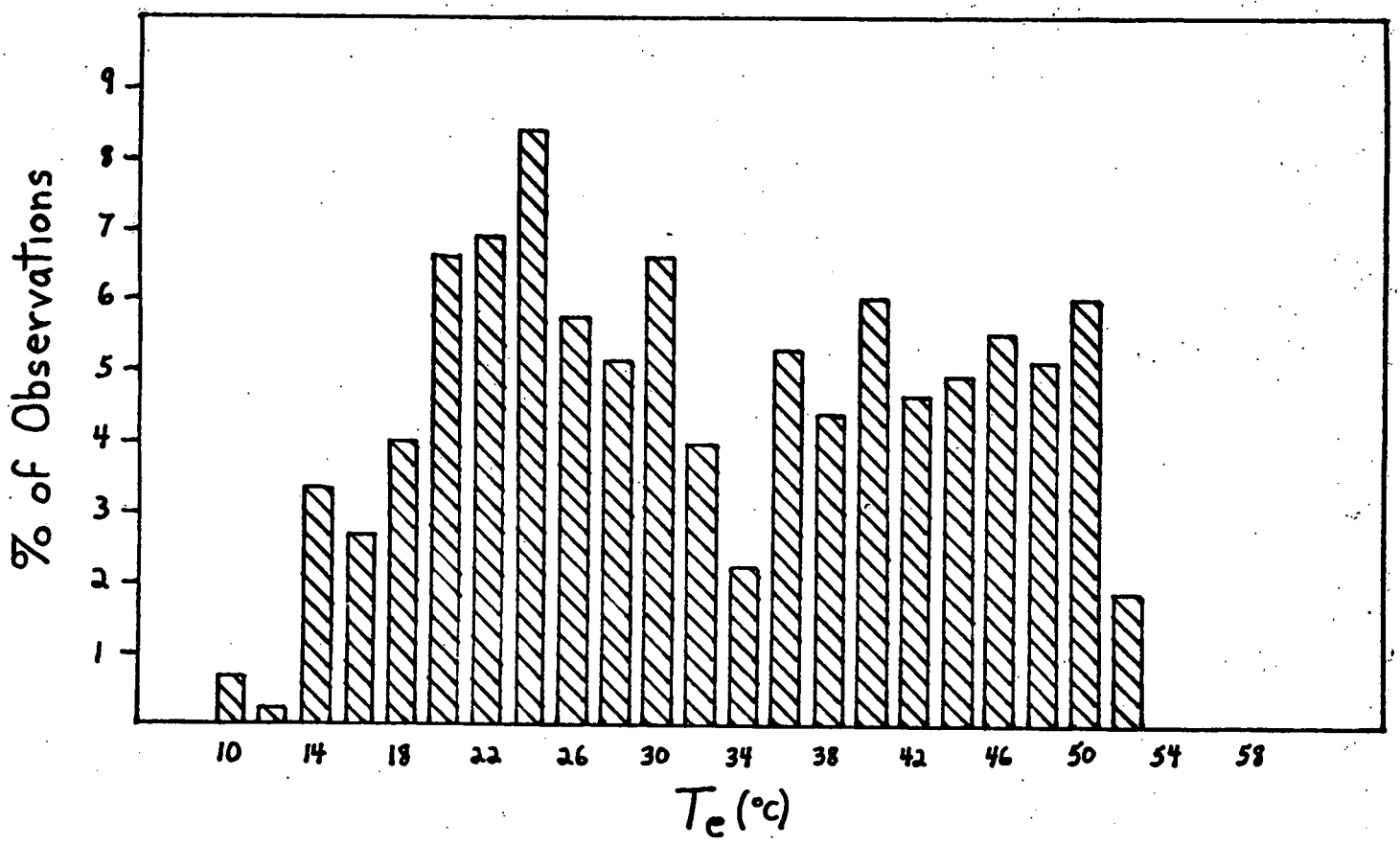

Figure 7. Histogram of the frequencies of observed operative environmental temperatures for blackened models of turtles. Measurements were made in South Carolina in 1979 and 1980.

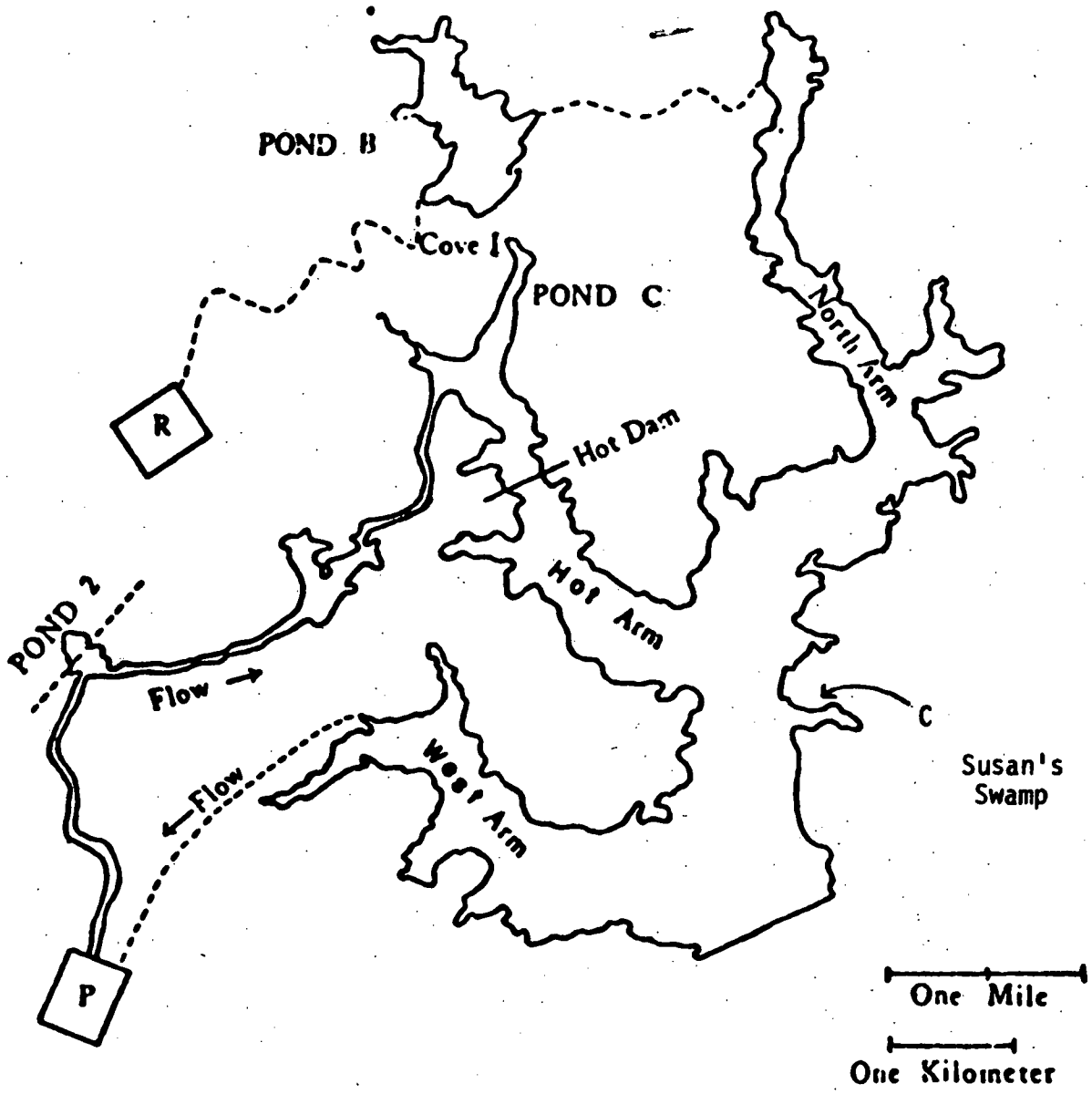

Figure 8 PAR pond reservoir system on Savannah River Plant. PAR pond is 1120 ha and Pond C is 76 ha. Cove I (sanctuary cove) is located at the far northern end of Pond C. It remains near ambient while the rest of Pond C is > 50°C in the summer.

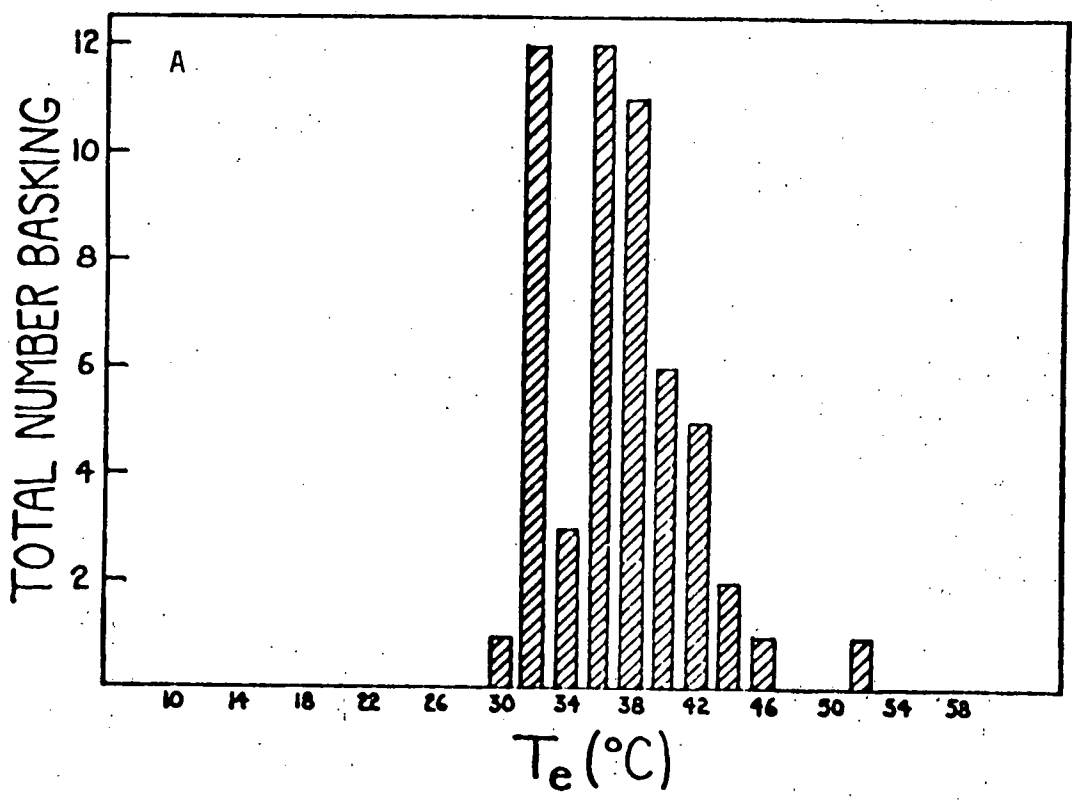

Figure 9A. Histogram of the total number of turtles observed basking at Susan's Swamp on Par Pond and their associated operative environmental temperatures. Temperatures are grouped by 2°C intervals. T_e's are calculated from a multiple regression equation generated from 1979 and 1980 data. This figure is based on observations made in 1976.

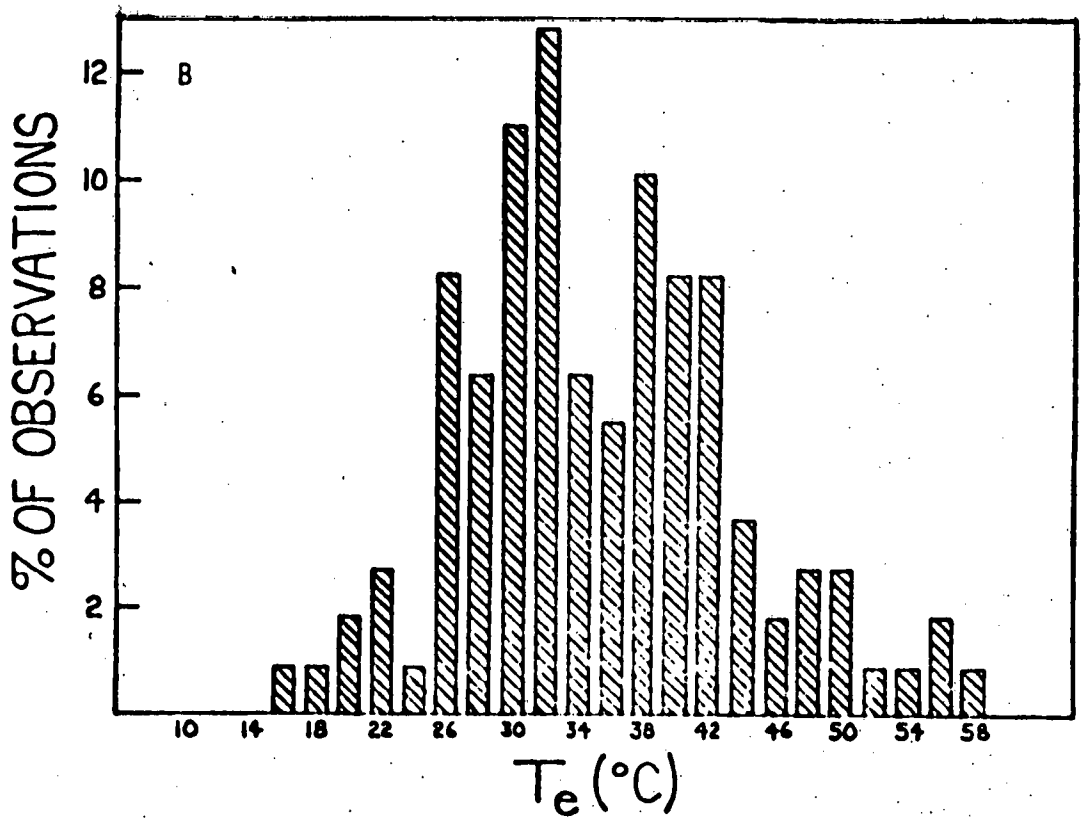

Figure 9B. Histogram of the frequencies of operative environmental temperatures calculated for Susan's Swamp data using the multiple regression equation generated from 1979 and 1980 data. This figure is based on observations made in 1976.

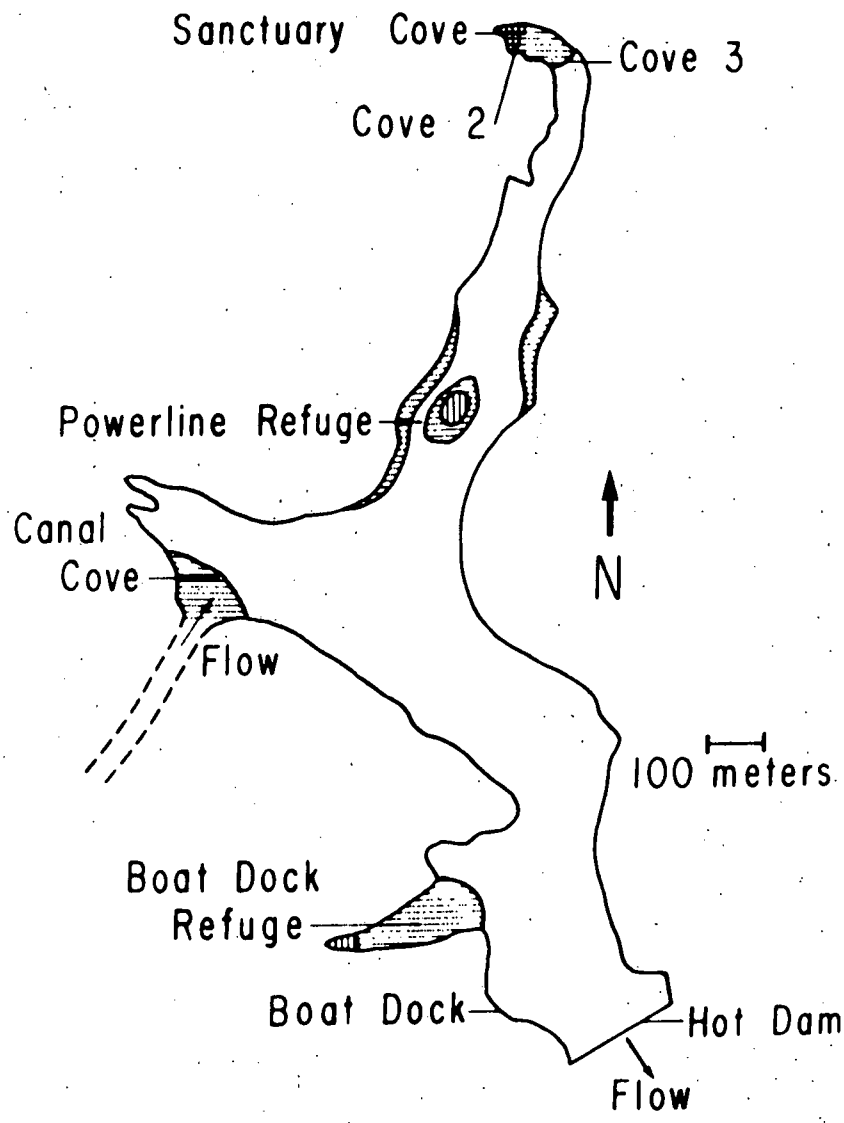

Figure 10. Distributions of fish in Pond C, June - November, 1979. Horizontal slashes indicate ambient distribution, vertical slashes indicate heated distribution.

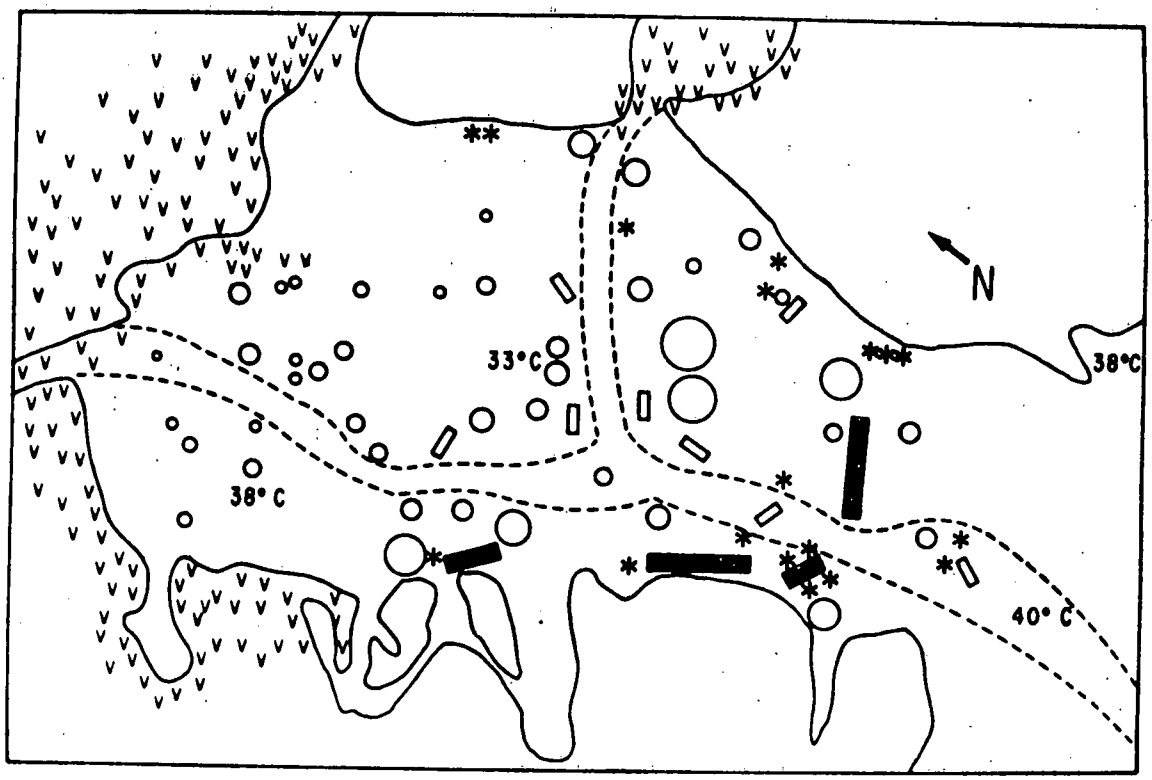

Figure 11. Sanctuary Cove bass locations, summer 1979, heated conditions. Bass positions are marked by (*), floating boards by (▭), stumps by (O), swamp by (v), and submerged logs and planks by (▬). Temperatures were measured 5 cm under the water surface. Dashed lines indicate channels created by alligators.

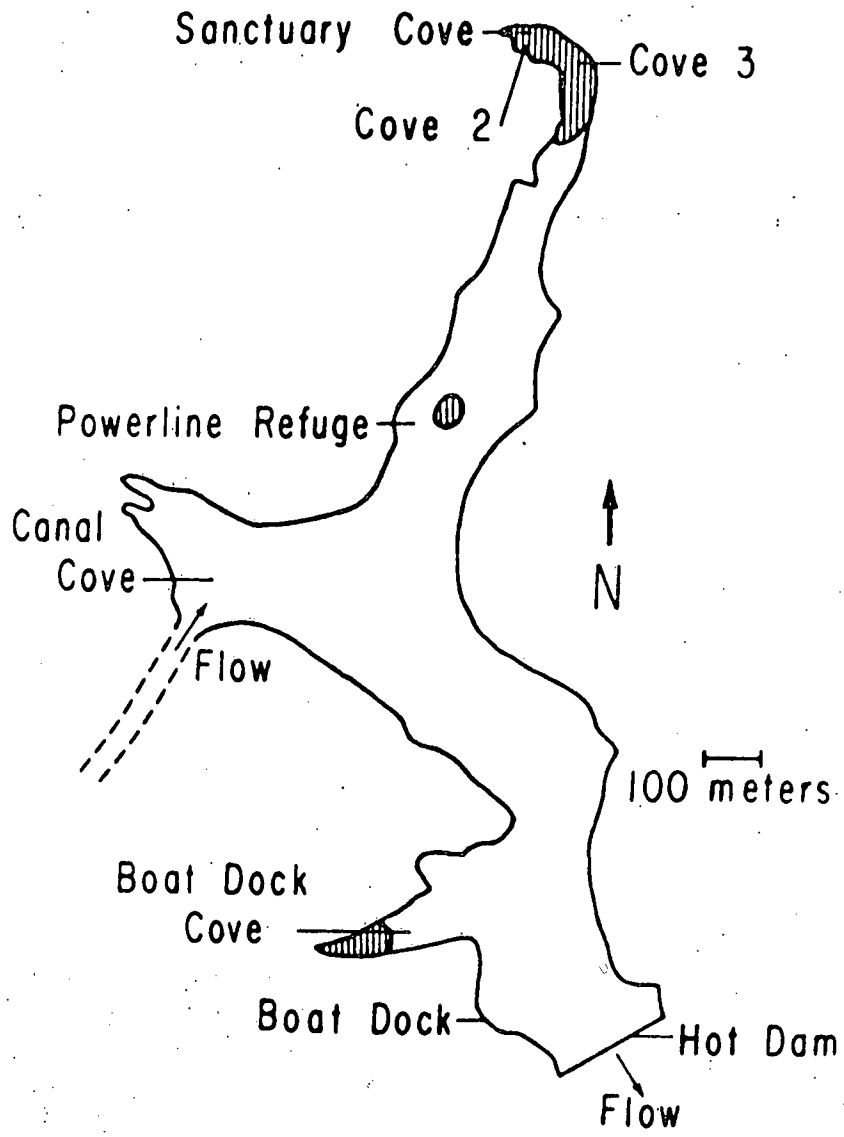

Figure 12 Distributions of fish in Pond C, March 1980. Vertical slashes indicate heated distribution of fish. As compared to summer months, bass were dispersed farther down the northern channel.

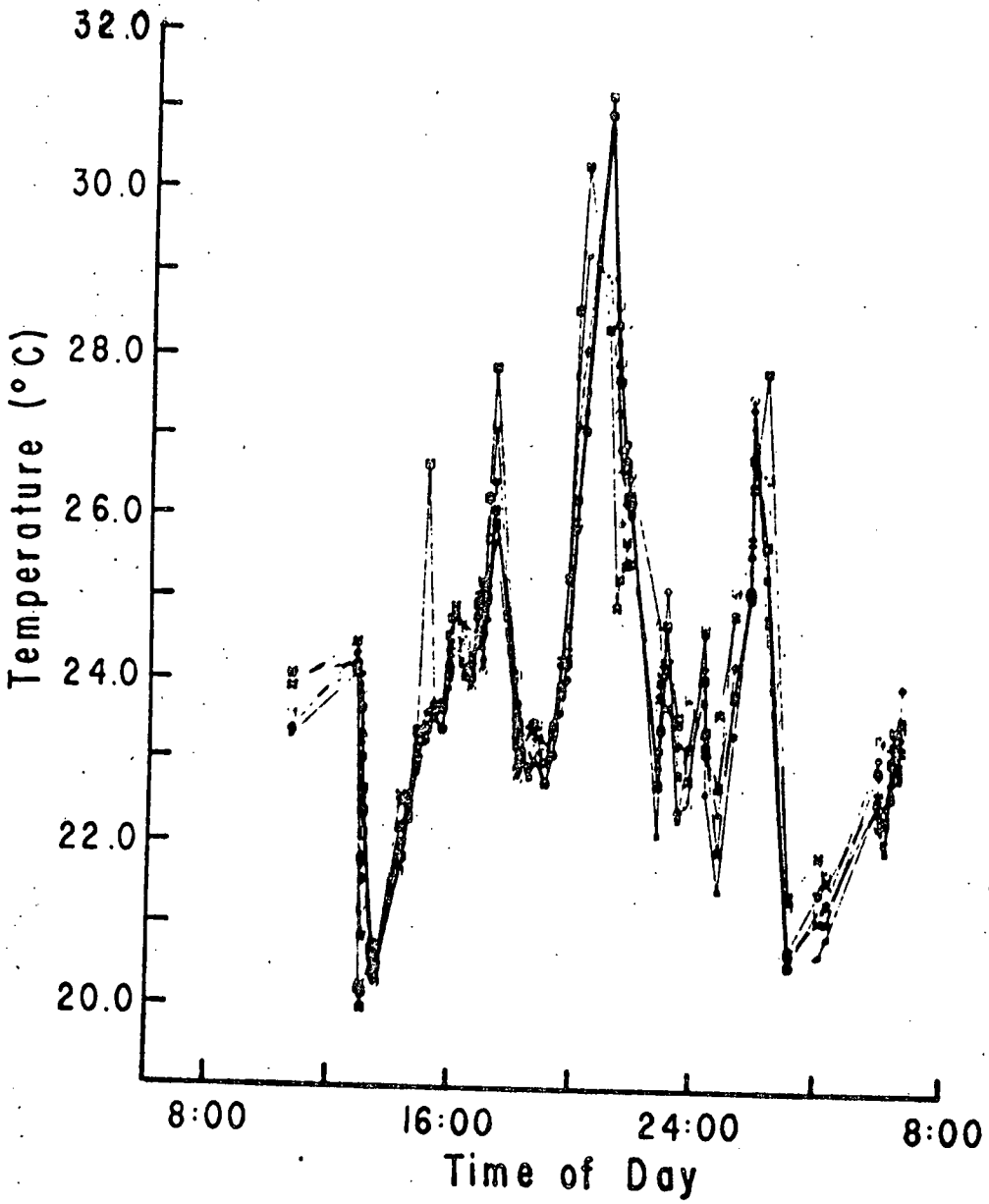

Figure 13 Dorsal muscle (*), skin (○), coelom 1 (⊗), heart (⊕), water (⊠), and coelom 2 (□) temperatures for a bass tracked during heated conditions in Sanctuary Cove.

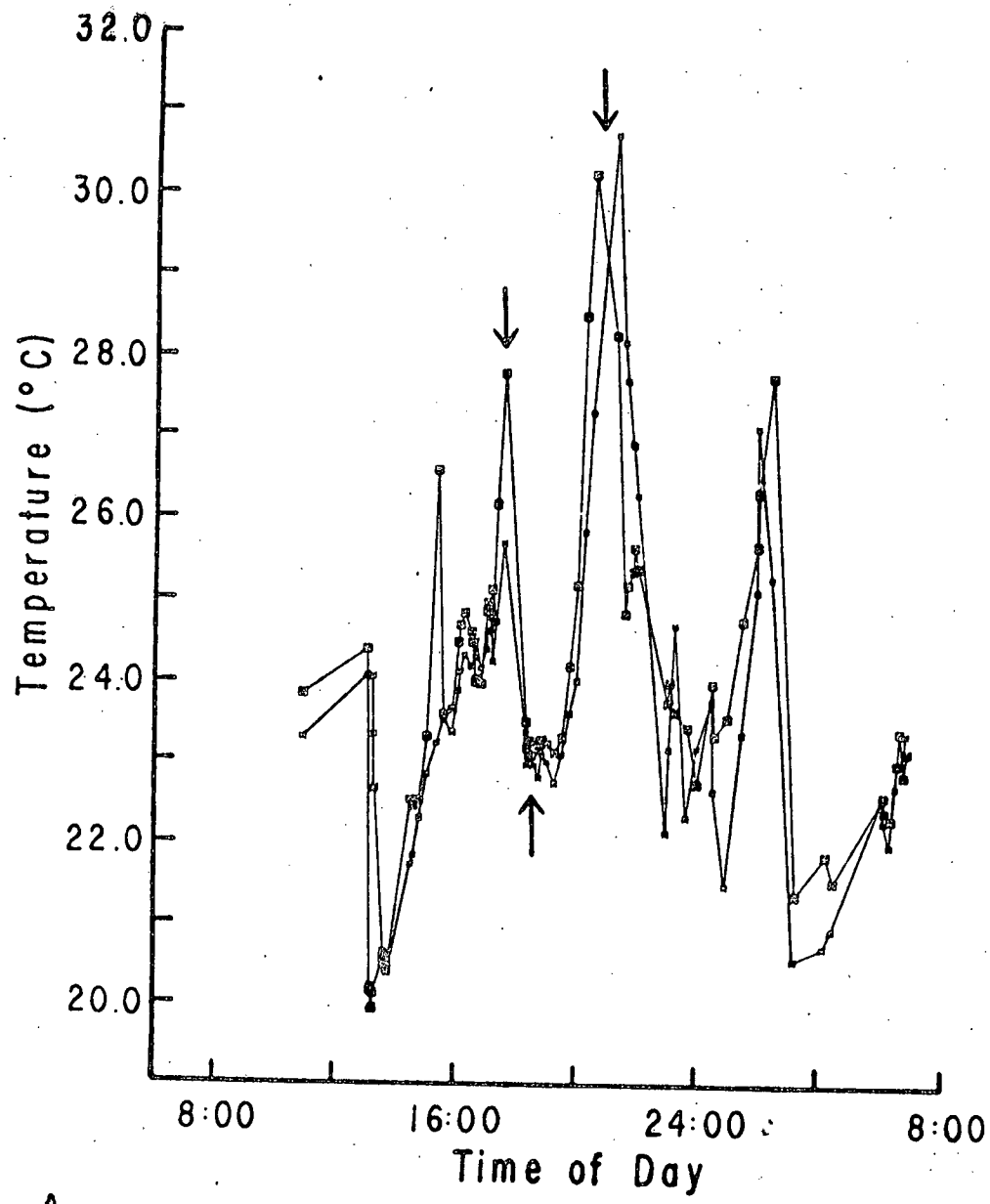

Figure 14 Comparison of dorsal muscle (*) and water (⊠) temperatures in a bass tracked during heated conditions in Sanctuary Cove.

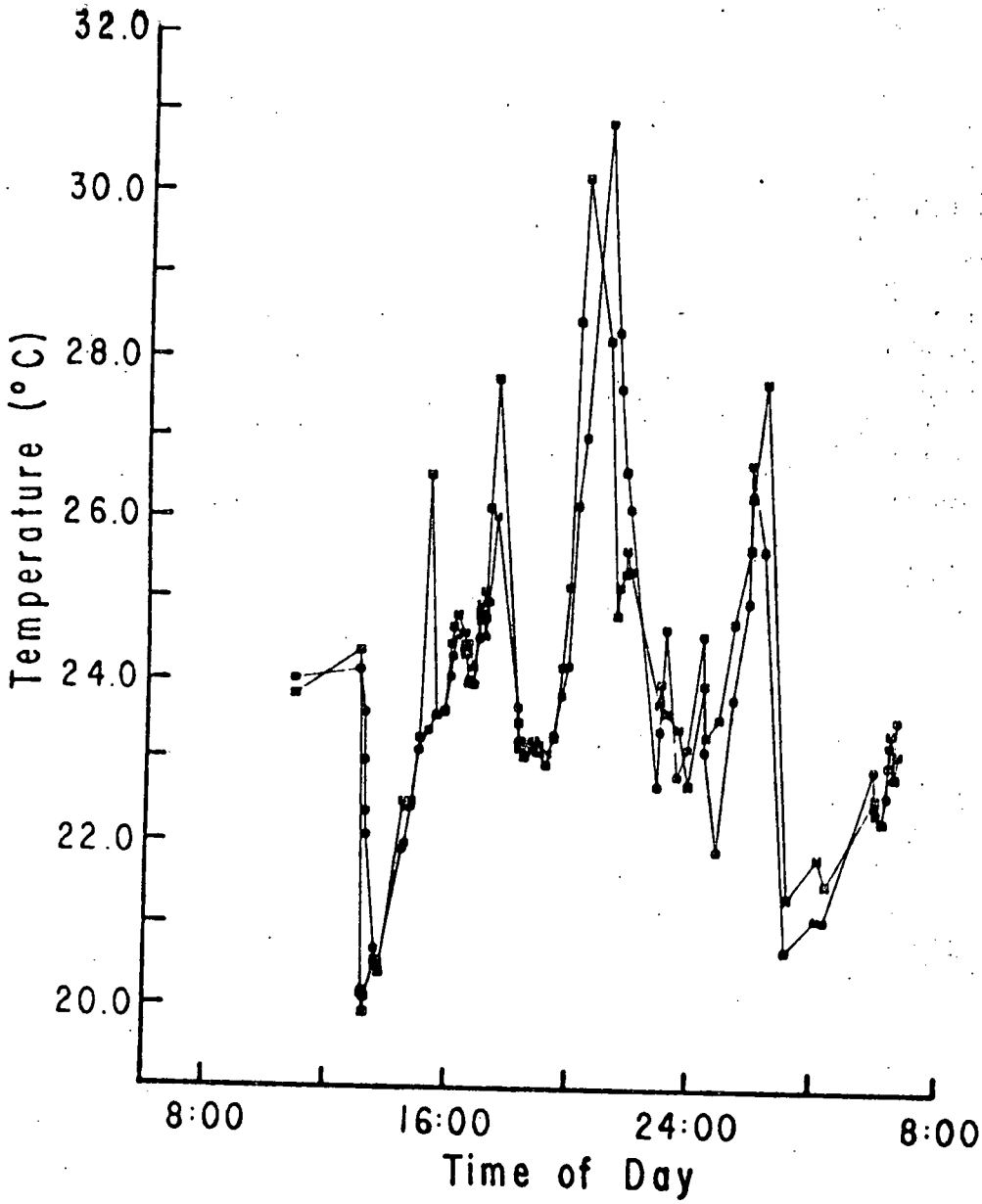

Figure 15 Comparison of coelom (⊗) and water (⊠) temperatures for a bass tracked during heated conditions in Sanctuary Cove.

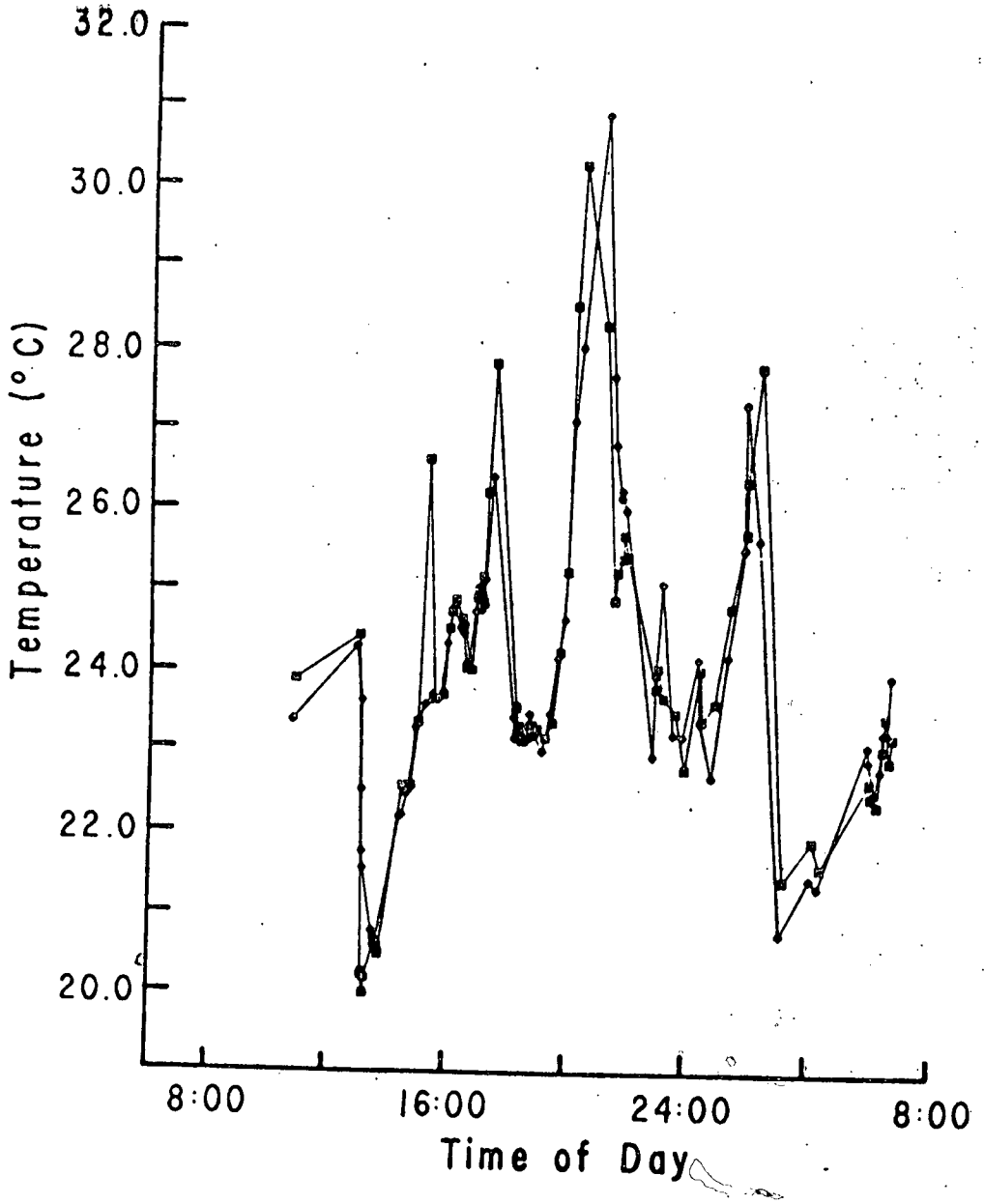

Figure 16 Comparison of heart (⊕) and water (⊠) temperatures in a bass tracked during heated conditions in Sanctuary Cove.