Behavioral Thermoregulation by Fishes: A New Experimental Approach

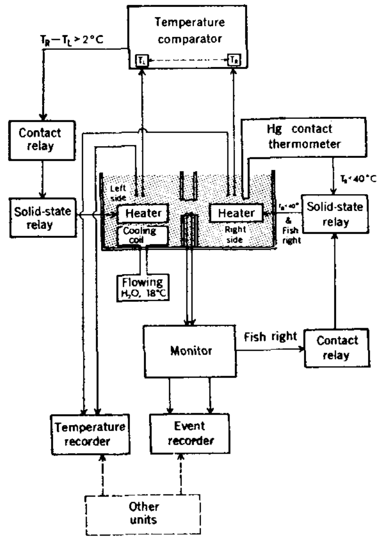
Abstract. *Electronic equipment allows fishes, by their spatial movements, to regulate the temperature in experimental tanks. Swimming into warmer water causes the temperature of the entire tank to increase; conversely, swimming into cooler water causes the temperature to decrease. The technique may be adapted for studying simultaneous behavioral regulation of temperature and nonthermal factors.*

Fishes, as mobile organisms living in heterothermal environments, can exercise substantial behavioral control over the temperatures they experience. They achieve this by swimming into, or remaining in, areas with certain temperatures and leaving, or avoiding, parts of the habitat with other temperatures.

Understanding how different fishes behave in heterothermal environments is crucial in predicting the ecological impact of heated effluents. Discharges from the rapidly expanding steam–electric power industry not only heat the receiving waters but do so unevenly, causing strong spatial variation in tempeature. Where fishes live in such waters largely determines what metabolic and ecological effects actually accrue.

Behavioral thermoregulation by fishes has been investigated primarily through two experimental techniques. The more

Fig. 1. An experimental system for study of behavioral thermoregulation in fishes. The right half of the tank warms at 3° to 5°C an hour (potentially to 40°C) whenever the fish is in the right half and cools at 3° to 5°C an hour whenever the fish is in the left half. The left half of the tank is always 2°C cooler than the right half. Thus, the fish always has available alternative temperatures 2°C apart.



conventional approach is to allow fish to "choose" temperatures by positioning themselves in a horizontal or vertical gradient of temperature (*1*). The second technique is to permit conditioned fish to control either the upper or the lower limit of temperature by activating a trigger (*2*); this method, in generalized form, was first applied for studying behavioral thermoregulation in terrestrial vertebrates (*3*).

Our technique incorporates features of both the earlier methods, but it is unique in several respects. Neither maintenance of temperature gradients in large volumes of water nor elaborate conditioning of experimental subjects is required. Data can be collected continuously and automatically, even in near-darkness; the form of the data is appropriate for direct processing by computer.

A fish can control environmental temperature by dividing his time between the halves of an appropriately equipped aquarium (Fig. 1). The fish is able to swim from one half to the other by passing through a tunnel in the partition that divides the tank. Passage of the fish is sensed by a pair of photocells in the tunnel; the direction of the passage is determined by the sequence in which the fish interrupts dim beams of light passing across the tunnel from positions opposite the photocells. The signal from the photocells is interpreted by a monitor (based on the bistable multivibrator of computer circuitry), recorded, and used to control heat transfer in the tank (*4*). Passage of the fish into one side (say, right) of the tank causes that side to begin warming at 3° to 5°C an hour. The warming of the right side ceases only when the fish swims to the other side; then the right side begins cooling at 3° to 5°C an hour. The temperature of the left side is kept 2°C lower than that of the right side by a comparator-relay circuit. Accordingly, the fish always has available alternative temperatures 2°C apart. Sequential testing and choosing of one temperature over the other results in thermoregulation; thus, the fish serves as its own thermostat.

Young fishes of six species have successfully regulated temperature in the apparatus described above. The record of one specimen of each species is presented in Fig. 2 (*5, 6*) to exemplify, without typifying, regulatory performances during trials lasting 3 days. Temperatures between 18° and 40°C were potentially available in each case. Sufficient data were collected to demonstrate that regulated temperatures varied significantly among species and were in accord with temperature distributions of the same species in a lake receiving heated effluent (*7*).

In a subsequent experiment, a naive bluegill (*Lepomis macrochirus*) was required to regulate the temperature of a tank with no differential between halves. The fish maintained a temperature re-

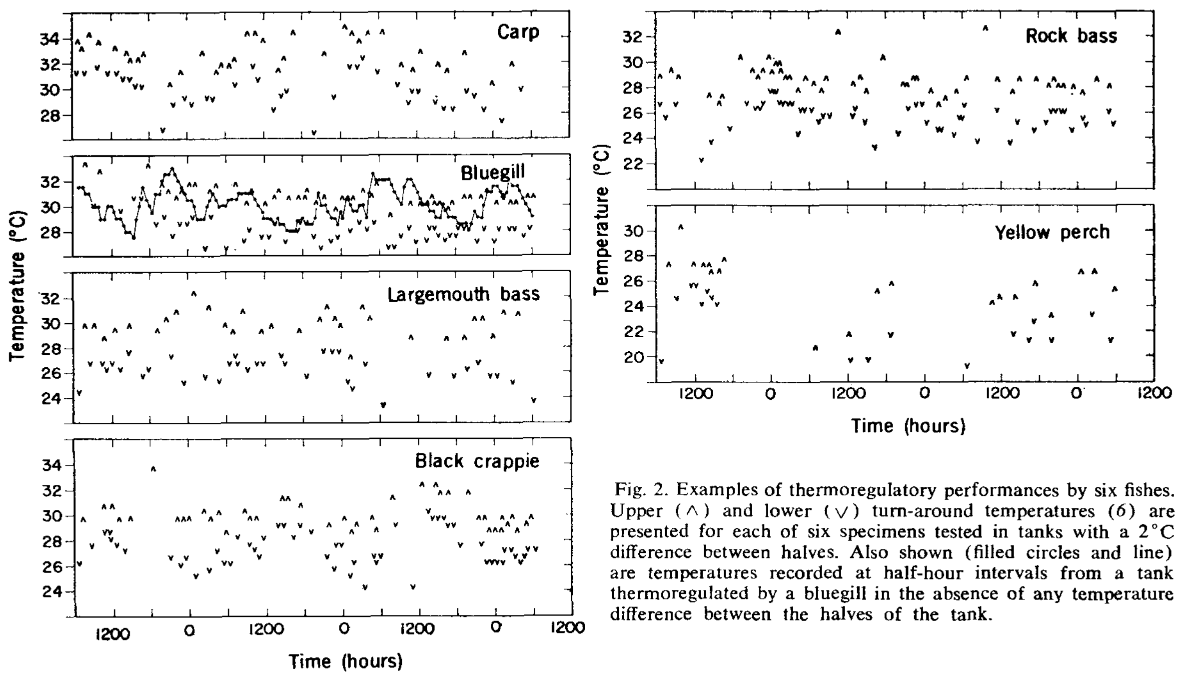


Fig. 2. Examples of thermoregulatory performances by six fishes. Upper (∧) and lower (∨) turn-around temperatures (*6*) are presented for each of six specimens tested in tanks with a 2°C difference between halves. Also shown (filled circles and line) are temperatures recorded at half-hour intervals from a tank thermoregulated by a bluegill in the absence of any temperature difference between the halves of the tank.

gime similar to that regulated by other bluegills in tanks with a 2°C difference between sides (Fig. 2). Successful regulation in a tank without a temperature differential indicated that the bluegill learned to associate changes in its spatial position with eventual (but not immediate) changes in temperature.

We believe that our experimental system is amenable to several other modifications that may increase its versatility. If the tunnel is essentially curved on itself to form a doughnut-shaped swimming space, behavioral thermoregulation by continuously swimming fishes of the open sea, such as tunas (*8*), can be studied. Swimming direction (clockwise, counterclockwise) can control the direction of temperature change; swimming speed can control the rate of temperature change. Thus, fishes could be required to thermoregulate in continuous, gentle (0.1°C per 100 m) gradients of temperature in space that are simulated by changes in temperature through time.

Simultaneous behavioral regulation of temperature and a second, nonthermal factor may be investigated by using a tank with four compartments and two monitors. Concentrations of soluble substances (such as O_2, salts, pollutants) can be regulated by a fish-controlled mixing valve; light intensity can be regulated by fish-controlled dimmer circuitry. Movements of the fish in one dimension would regulate temperature and, in the other, the second variable (*9*). Such an approach would make it possible to measure the joint preferendum for two independently varying factors.

WILLIAM H. NEILL
Honolulu Laboratory,
Southwest Fisheries Center,
National Marine Fisheries Service,
Honolulu, Hawaii 96812
JOHN J. MAGNUSON
GERALD G. CHIPMAN
Laboratory of Limnology,
University of Wisconsin,
Madison 53706

References and Notes

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2. P. N. Rozin and J. Mayer, *Science* **134**, 942 (1961).
3. B. Weiss and V. G. Laties, *J. Comp. Physiol. Psychol.* **53**, 603 (1960).
4. The circuit diagram of the monitor and other details are available on request from the authors.
5. The specimens 50 to 100 mm long that provided the data for Fig. 2 were taken from waters near Madison, Wisconsin, and were acclimated to 22°C prior to experiments.
6. The upper turn-around temperatures were local temperature maximums recorded from the warmer side of the tank. The *i*th local maximum, U_i, was the highest temperature recorded along the time sequence such that U_i was separated from adjacent maximums, U_{i-1} and U_{i+1}, by temperatures at least 0.5°C less than $\min(U_{i-1}, U_i)$ and $\min(U_i, U_{i+1})$, respectively. The lower turn-around temperatures were the corresponding local minimums recorded from the cooler side of the tank. The *i*th local minimum, L_i, was the lowest temperature recorded along the time sequence such that L_i was separated from adjacent minimums, L_{i-1} and L_{i+1}, by temperatures at least 0.5°C greater than $\max(L_{i-1}, L_i)$ and $\max(L_i, L_{i+1})$, respectively.
7. W. H. Neill, thesis, University of Wisconsin (1971).
8. Work proposed by the first two authors and A. Dizon for execution at the Honolulu Laboratory of the Southwest Fisheries Center, National Marine Fisheries Service.
9. Systems analogous to those described here may be used to study behavioral regulation of nonthermal factors at various constant temperatures.
10. Development of the method described here and its initial application were part of a thesis submitted by W.H.N. to the graduate faculty of the University of Wisconsin, Madison, in 1971, in partial fulfillment of the requirements for the Ph.D. degree. The work was done at the Laboratory of Limnology and was supported in part by funds from the Wisconsin Utilities Association and the Office of Water Resources Research, Department of the Interior (MG OWRR B-028-Wis—WRC 70-010M). We gratefully acknowledge the technical assistance of Thomas C. Byles and Bruce K. Quirk.

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