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Reprinted from TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY
Vol. 103, No. 4, October 1974
pp. 663–710

Distributional Ecology and Behavioral Thermoregulation of Fishes in Relation to Heated Effluent from a Power Plant at Lake Monona, Wisconsin

WILLIAM H. NEILL[1] AND JOHN J. MAGNUSON

Laboratory of Limnology, Department of Zoology,
University of Wisconsin, Madison, Wisconsin 53706

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[1] Present address: Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.

ABSTRACT

Cooling water for a 220-megawatt power plant is pumped from 5 m beneath Lake Monona's surface, heated about 10 C, and discharged into the littoral zone. Maximum temperatures in the effluent-outfall area approach 35 C in summer and 14 C in winter; unheated parts of the littoral zone rarely exceed 29 C.

To assess distributional responses of fishes to operation of the power plant, the outfall area and two reference areas were electrofished on 30 dates between 8 August 1968 and 21 August 1969. Some fishes avoided the outfall area; these were *Perca flavescens*, *Cottus bairdi*, subadult *Morone mississippiensis*, and subadult *Ictalurus melas*. Others were occasionally or usually concentrated in the outfall area relative to reference areas—*Lepisosteus osseus*, adult *Cyprinus carpio*, adult *M. mississippiensis*, young *Lepomis gibbosus*, *L. macrochirus*, and *Micropterus salmoides*. The tendency for fish of a given species and size to concentrate in or avoid the outfall area generally did not reverse from season to season or from day to night.

Any differences in growth rate of young fishes among outfall and reference areas were obscured by size-dependent movements of the fish.

In August 1970, body temperature of fishes in the outfall area varied with species and time of day. During afternoon, median temperatures of *Cyprinus carpio*, *Lepomis gibbosus*, *L. macrochirus*, and *Micropterus salmoides* were higher than 29 C, while those of *Morone mississippiensis*, *Ambloplites rupestris*, *Pomoxis nigromaculatus*, and *Perca flavescens* were lower than 29 C. At night, only *Lepisosteus osseus* and *C. carpio* had median body temperatures higher than 29 C.

Young *Lepomis macrochirus* collected during summer 1970 from the outfall area had estimated acclimation temperatures between 29.4 and 31.3 C, even though temperatures between 25 and 36 C were available. To have had acclimations between 29.4 and 31.3 C, the fish must have avoided exposure to temperatures higher than about 31.5 C. This conclusion agreed substantially with the distribution of body temperatures of young *L. macrochirus*; the highest body temperature among 31 specimens was 31.8 C.

Temperatures at which fishes lived in the outfall area during summer 1970 were positively correlated ($p < 0.01$) with the degree to which they were concentrated in the outfall area during the two previous summers. The strength of the correlation argued that, during summer, temperature was the primary factor governing not only distribution of fishes within the outfall area, but also the abundances of fishes in the outfall area relative to unheated parts of the littoral zone.

Moreover, integration of field and laboratory results suggested that fishes were distributed within the outfall area according to their different temperature preferenda. Preferred temperatures of six Lake Monona fishes were measured by allowing each of several specimens to behaviorally regulate the temperature of its tank. Midpoint of the preferred temperature range agreed well with the median body temperature recorded in the outfall area during afternoon (considering, in the case of *Perca flavescens*, that temperatures below 26.5 C were not available in the outfall area): *Cyprinus carpio*, 31.8 C (laboratory), 30.6 C (field); *Lepomis macrochirus*, 30.3, 29.4; *Micropterus salmoides*, 29.1, 29.7; *Pomoxis nigromaculatus*, 28.3, 28.3; *A. rupestris*, 27.3, 27.5; and *Perca flavescens*, 23.4, 27.1.

In other laboratory experiments, *Lepomis macrochirus* and *Perca flavescens* were required to partition time between an environment with preferred temperature and an environment with food but either warmer or cooler than the preferred temperature. Each species made forays for food into water with extreme temperatures. However, neither laboratory nor field results suggested that thermoregulatory behavior was overridden by feeding behavior, even though zooplanktonic food was more abundant in the outfall area than in unheated parts of the littoral zone.

INTRODUCTION

Rapid expansion of the steam-electric power industry has spurred concern for the potential impact of thermal effluents on aquatic ecosystems. As much as one-fifth of the total freshwater runoff in the United States will be needed for steam-electric cooling water by 1980 (Krenkel and Parker 1969).

Fishes, like other organisms, are profoundly affected by temperature. Extensive bibliographies by Kennedy and Mihursky (1967) and Raney and Menzel (1969) attest to the wealth of available information regarding direct and indirect actions of temperature on the survival, growth, metabolism, behavior, and reproduction of fishes. Yet, ecological study of fishes in habitats heated by power plants began only about 15 years ago in North America, and such investigations are still few and incomplete. Coutant (1970, p. 376), in reviewing both published and unpublished information on "thermal pollution," concluded:

> Most power plant surveys lack detail of observation and definition of goals sufficient to provide more than circumstantial evidence for ecological processes . . . laboratory experiments are often unrealistic simulations of complex phenomena. True predictability will require judicious application of data from both sources.

Our investigation sought to avoid the deficiencies mentioned by Coutant (1970) and, in so doing, contribute to knowledge of the ecological processes that occur in aquatic habitats receiving heated effluent.

The Standpoint

Behavioral regulation of environment has been an under-emphasized feature in the ecology of fishes. Fishes are mobile organisms, able to swim through their habitat at sustained speeds of a few body lengths per second (Bainbridge 1960). In aquatic organisms with lesser potential for voluntary movements, physiological adaptation is perhaps the primary strategy for coping with environmental variation. Physiological mechanisms allow fishes also to successfully occupy diverse habitats and tolerate temporal fluctuations of environment.

But, if the potentially available environment is heterogeneous, a fish can behaviorally regulate the conditions it must experience by spending more time in one subset of environment and less or no time in other subsets.

Temperature heterogeneity of some aquatic habitats is greatly increased by their reception of heated effluents from steam-electric plants. Although the fraction of habitat near the point of effluent discharge (outfall area) may be warmed by several degrees Celsius, temperatures throughout most of the receiving water mass typically are unaltered. For example, only about 0.3% of the water at a depth of 0.5 m in Lake Monona is warmed more than 1 C by effluent from a power plant; the percentage of total volume so warmed is much smaller.

In a habitat partly heated by thermal effluent, then, temperatures experienced by fishes depend on where they live within the habitat. If fishes were randomly moving particles, the number exposed to elevated temperatures and the time each individual is exposed would be small. Fishes typically are not randomly distributed within a habitat; rather, they tend to be concentrated in some areas and scarce or absent in others.

Thus, the effects of steam-electric power production on fishes must depend first on their behavioral responses to elevated temperatures and to other features of the outfall area. It matters little whether in the laboratory yellow perch (*Perca flavescens*), for example, can grow at 30 C or can survive 33 C for 1,000 min if yellow perch never occur in an outfall area where temperatures exceed 29 C. The more important question is whether yellow perch given a choice will invade water of a particular temperature and, if so, for how long and for what reasons, ecologically prudent or otherwise. Only when fish are likely to occur voluntarily or by necessity under certain conditions does it become ecologically important to know the consequences of that exposure—consequences relative to survival, growth, and reproduction.

Major Objectives

Conviction that the responses of fishes to environmental variation are first manifest in their distributions prescribed the primary goals of the investigation. Major objectives were to:

1. assess spatial and temporal aspects of fish distribution in the outfall area of a steam-electric power plant;
2. relate fish distributions to temperature by measuring the temperatures at which fishes live during summer in the outfall area;
3. evaluate the relationship between fish

distributions during summer and behavioral thermoregulation; and

4. explore the extent to which fish may alter thermoregulatory behavior in order to acquire an essential resource—food.

Statistical Treatment of Data

To analyze data from both field and laboratory, nonparametric techniques were used almost exclusively. Reasons for avoiding more traditional, parametric methods included:

1. uncertainty about the level of measurements (in most cases, the data probably were of ordinal strength),
2. uncertainty about the shapes of the sampling distributions, and
3. small sizes of samples.

Confidence intervals for medians were constructed in accordance with the method suggested by Mood and Graybill (1963, p. 406). All other nonparametric tests used in this work were described by Siegel (1956). Infrequent recourse to parametric statistics is indicated by the word "parametric" and follows the usage of Steel and Torrie (1960).

FIELD RESEARCH SITE: LAKE MONONA

Lake Monona, in Wisconsin's Dane County, provides water for cooling the condensers of a coal and gas fired, 220-megawatt power plant operated by the Madison Gas and Electric Company. Water is removed from the lake (1,400 ha, maximum depth 22.5 m) at two points, each 5 m below the surface and about 110 m offshore. After a 10 C rise in temperature during circulation through the condensers, water is returned to the lake at two surface outfalls located about 200 m apart on the shoreline. Heated effluent flows almost continuously from the primary outfall but does not flow from the secondary outfall during periods of low power production. A steel-slatted baffle at the secondary outfall diffuses the jet; the primary jet is unobstructed. Operating capacities of the circulation pumps total 6,850 liters/sec (Hoopes, Zeller, and Rohlich 1968).

The heated discharge produces an area considerably warmer than the shallow water along the remainder of the shoreline. The fraction of the littoral zone less than 2 m deep and heated more than 1 C is about 2 ha.

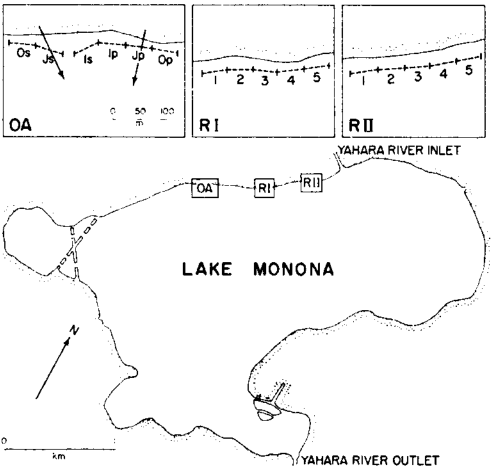

FIGURE 1.—Map of Lake Monona showing enlarged views of the outfall area (OA) and reference areas (RI and RII) with code letters for individual 50 m sampling transects (Os, Js, . . . , RII 5). Arrows indicate positions of the secondary jet (across transect Js) and primary jet (across transect Jp).

During winter, a plywood baffle supported by floating booms extends 2.5 m beneath the surface to surround 4.5 ha of the lake, including the outfall area. In midwinter, the baffled area is mostly free of ice except during the coldest weather. The baffle was installed in 1968 during the last week of November and removed the last week of February 1969.

Research effort was concentrated in the littoral zone near the effluent outfalls, termed outfall area or OA, and in two reference areas (Fig. 1). Reference areas I and II (RI and RII) were located about 600 and 1,300 m northeast of the outfall area and were more similar to the outfall area in bottom slope and type, aquatic vegetation, and exposure to winds than other locations. However, reference areas had more sand and less coarse gravel and rubble than the outfall area. The bottom in the outfall area was also more irregular and had a steeper slope. A channel about 2.5 m deep extended out from the primary outfall. The secondary jet passed over a sandy bar, 0.6 m deep, approximately 40 m offshore. The dominant macrophyte in outfall and reference areas was watermilfoil (*Myrio-*

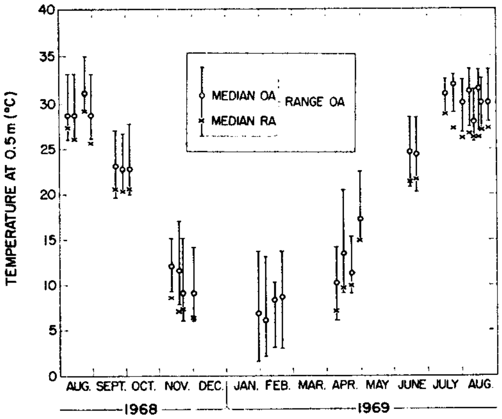

FIGURE 2.—Median temperatures of the outfall area and reference areas and range of temperature in the outfall area during each afternoon of fish sampling, 8 August 1968 to 21 August 1969.

phyllum), which sometimes was covered with growths of the filamentous alga *Cladophora*. However, the reference areas had more wild celery (*Vallisneria*) and common elodea (*Elodea*) than the outfall area.

Sixteen sampling transects were established, five in each reference area and six in the outfall area (Fig. 1). Each transect, 50 m long, was parallel to shore and along the 1–1.5 m bottom-contour interval. Transects Js and Jp spanned the secondary and primary jets, respectively; the other transects in the outfall area were positioned inside (Is and Ip) and outside (Os and Op) the area bounded by the jets. Transects were marked at each end by numbered buoys or by structures on shore.

WATER TEMPERATURE IN THE STUDY AREAS OF LAKE MONONA

Water temperatures were systematically measured during each phase of the investigation of fish distribution. As fishes were sampled, temperatures 0.5 m below the surface were continuously recorded with a Rustrak Thermistor Probe Recorder[2] (model 133). Temperatures at other depths were measured with an electronic thermometer of the Wheatstone-bridge type.

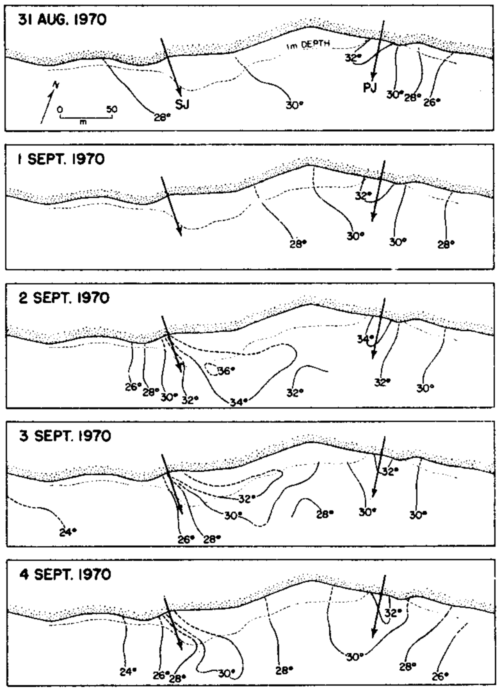

FIGURE 3.—Distribution of temperature at 0.5 m beneath the surface in the outfall area on five successive afternoons, 31 August–4 September 1970.

Water temperatures (0.5 m) in the reference areas were 25–30 C in August 1968 and, following the winter minimum, returned to similar levels in July and August 1969 (Fig. 2). The two reference areas had essentially identical temperatures. Minimum recorded temperature in the outfall area was similar to reference area temperatures on each sampling date. However, median and maximum temperatures in the outfall area exceeded reference area temperature by 2–4 C and 6–8 C, respectively, on most sampling dates. Temperatures at night were generally less than 2 C below those recorded during afternoon on the same date.

Median temperatures of transects on the same afternoon or evening varied less than 1 C within the reference areas but as much as 8.5 C in the outfall area. The transect across the primary jet (Jp) was 4–8 C warmer than the reference areas. Temperatures between the two jets (Ip and Is) were often fairly uniform and 3–5 C higher than those

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[2] Reference to trade names does not imply endorsement by The University of Wisconsin or by the National Marine Fisheries Service, NOAA.

of reference areas. The transect across the secondary jet (Js) was often cooler than that spanning the primary jet, even when heated effluent was flowing from the secondary outfall. Outside the jets, water temperature abruptly approached that of the reference areas.

Although some locations in the outfall area were consistently warmer than others, distribution of temperature varied greatly from day to day (Fig. 3) because of changes in wind velocity and variation in rates of effluent discharge. For example, on two consecutive afternoons about 18% and 66% of water at 0.5 m depth in the outfall area was warmer than 30 C (Fig. 3, 1 and 2 September 1970).

The outfall area was vertically stratified with respect to temperature (e.g., Fig. 4). Although water 0.5 m beneath the surface was usually less than 1 C cooler than surface water, water temperature at 1 m was often 3 C lower than at 0.5 m. (Surface and 1-m temperatures in the reference areas seldom differed by even 1 C.) Vertical stratification, always poorly defined near the jets, deteriorated throughout the outfall area when strong onshore winds promoted mixing.

DISTRIBUTION OF FISHES AMONG THE STUDY AREAS OF LAKE MONONA

Objectives

Electrofishing surveys were conducted in each study area to determine whether the different fishes of the littoral zone were relatively concentrated or scarce in the outfall area and whether the degree of concentration varied from day to night and from season to season.

Sampling Gear, Procedures, and Schedule

Fishes were captured with an electrofishing apparatus mounted on a pontoon barge (Fig. 5). Electricity (220 V-AC, 60 Hz) was supplied by a gasoline powered generator to three electrodes made from copper tubing 2.5 cm in diameter. The electrodes were suspended from booms projecting from the front of the barge; each electrode was weighted so that it hung vertically 1.4 m into the water. Immediately behind the electrodes, a push net with a 1- × 1.3-m rectangular opening collected stunned fishes from the top meter of water; the 2.5-m-long net of 6-mm mesh netting was lined in the final 1 m (purse) with 3-mm mesh netting (Fig. 5).

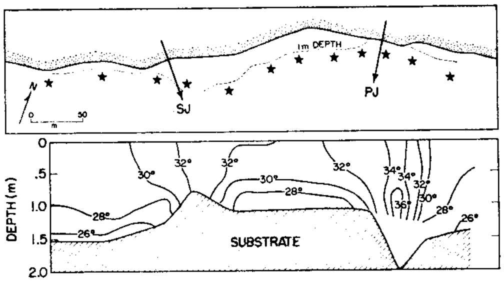

FIGURE 4.—Vertical distribution of temperature in the outfall area (afternoon, 17 August 1970). Stars on the plane view mark the locations where temperatures were measured.

The sampling unit was one electrofishing run along a transect. During each 30- to 60-sec run, water temperature 0.5 m beneath the surface was continuously recorded, and water depth was measured several times.

Generally, all captured fishes were either preserved in 10% formalin or immediately identified, measured for total length, and released. However, catches of young bluegill (*Lepomis macrochirus*) were so large during summer and early fall 1968 that to preserve all of them was impractical. Bluegill less than 75 mm long from most night samples between 8 August and 30 November 1968 were disregarded. Except from 29 January to 19 June 1969, bluegill less than 75 mm long that were not actually in the purse of the net were disregarded. Larger bluegill and all other fishes were recorded, regardless of their final position within the net.

Most larger fishes to be released were marked in 1968 by a fin-punch distinctive for the area of capture, or in 1969 by a

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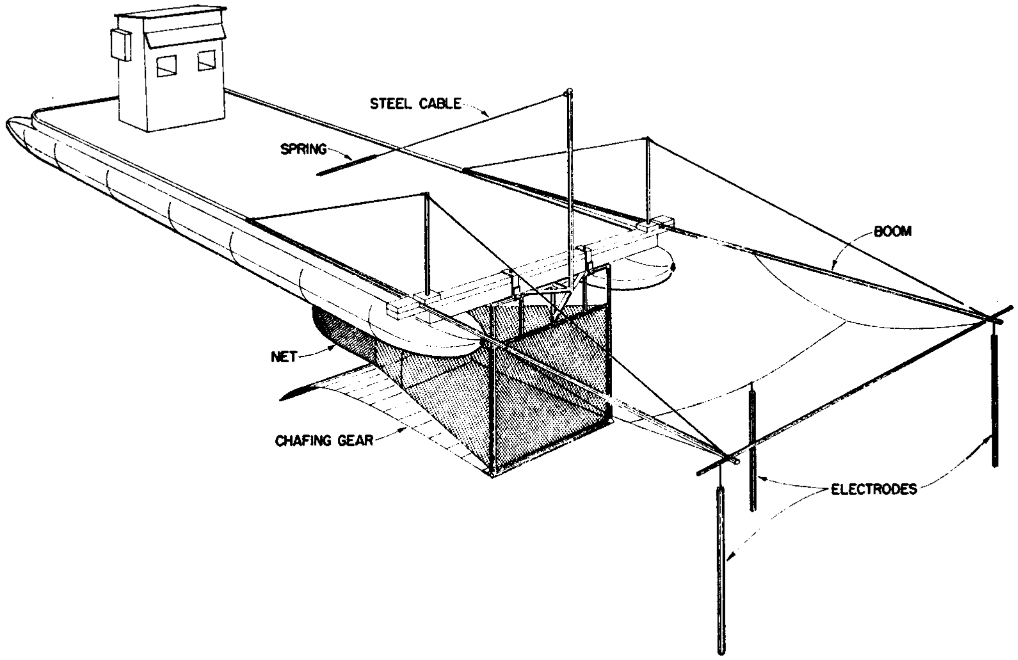
FIGURE 5.—Diagram of the barge rigged for electrofishing and a detailed view of the push net.


STEEL CABLE
SPRING
BOOM
NET
CHAFING GEAR
ELECTRODES

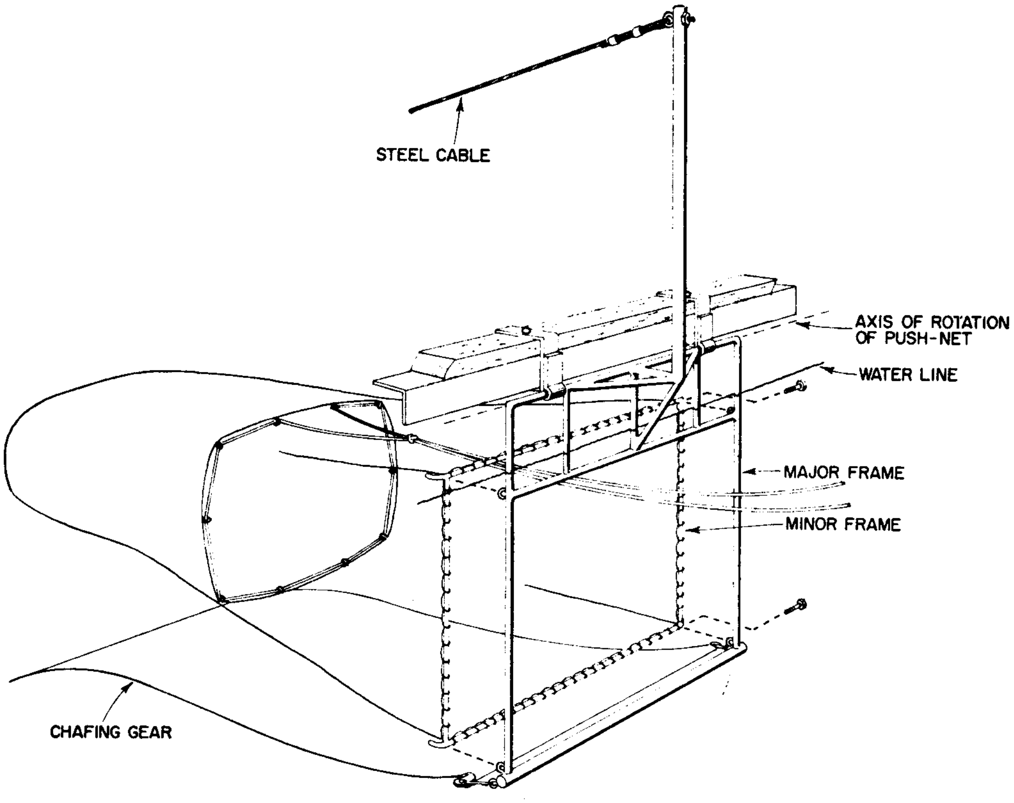

STEEL CABLE
AXIS OF ROTATION OF PUSH-NET
WATER LINE
MAJOR FRAME
MINOR FRAME
CHAFING GEAR

TABLE 1.—*Species, lengths, and numbers of fish caught from the study areas of Lake Monona during electrofishing surveys, 8 August 1968 to 21 August 1969*

Species		Length class identification	Range of total lengths (mm)	Total number caught
Common name	Scientific name			
Longnose gar	*Lepisosteus osseus* (Linnaeus)	—	365–846	43[a]
Northern pike	*Esox lucius* Linnaeus	—	229–531	2
Carp	*Cyprinus carpio* Linnaeus	small	8–123	160
Carp	*Cyprinus carpio* Linnaeus	large	163–737	96
Golden shiner	*Notemigonus crysoleucas* (Mitchill)	—	17–115	21
Emerald shiner	*Notropis atherinoides* Rafinesque	—	80	1
Spottail shiner	*Notropis hudsonius* (Clinton)	—	98–100	3
Bluntnose minnow	*Pimephales notatus* (Rafinesque)	—	17–68	20
White sucker	*Catostomus commersoni* (Lacépède)	—	403–460	4
Bigmouth buffalo	*Ictiobus cyprinellus* (Valenciennes)	—	440–600	7
Black bullhead	*Ictalurus melas* (Rafinesque)	small	33–150	165
Black bullhead	*Ictalurus melas* (Rafinesque)	large	151–265	46
Yellow bullhead	*Ictalurus natalis* (Lesueur)	—	226–245	2
Brown bullhead	*Ictalurus nebulosus* (Lesueur)	—	63–230	12
Banded killifish	*Fundulus diaphanus* (Lesueur)	—	38–64	2
Brook silverside	*Labidesthes sicculus* (Cope)	—	8–97	413
Brook stickleback	*Culaea inconstans* (Kirtland)	—	29	1
White bass	*Morone chrysops* (Rafinesque)	—	17–294	33
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	small	13–50	417
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	medium	51–99	187
Yellow bass	*Morone mississippiensis* Jordan and Eigenmann	large	107–256	287
Rock bass	*Ambloplites rupestris* (Rafinesque)	small	10–48	120
Rock bass	*Ambloplites rupestris* (Rafinesque)	large	51–210	54
Green sunfish	*Lepomis cyanellus* Rafinesque	—	19–166	17
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)	small	12–75	149
Pumpkinseed	*Lepomis gibbosus* (Linnaeus)	large	76–170	136
Bluegill	*Lepomis macrochirus* Rafinesque	small	28–75	19,154
Bluegill	*Lepomis macrochirus* Rafinesque	medium	76–100	237
Bluegill	*Lepomis macrochirus* Rafinesque	large	101–224	848
Largemouth bass	*Micropterus salmoides* (Lacépède)	—	51–311	77
White crappie	*Pomoxis annularis* Rafinesque	—	114–247	10
Black crappie	*Pomoxis nigromaculatus* (Lesueur)	small	12–75	853
Black crappie	*Pomoxis nigromaculatus* (Lesueur)	large	76–249	81
Iowa darter	*Etheostoma exile* (Girard)	—	23–89	65
Johnny darter	*Etheostoma nigrum* Rafinesque	—	65	1
Yellow perch	*Perca flavescens* (Mitchill)	small	46–99	285
Yellow perch	*Perca flavescens* (Mitchill)	large	101–286	99
Logperch	*Percina caprodes* (Rafinesque)	—	35–117	44
Walleye	*Stizostedion vitreum vitreum* (Mitchill)	—	13–585	41
Freshwater drum	*Aplodinotus grunniens* Rafinesque	—	68–420	53
Mottled sculpin	*Cottus bairdi* Girard	—	31–83	93

[a] Includes sighted as well as captured longnose gar.

numbered anchor tag (Floy Anchor Tag, FD-67) inserted into the epaxial musculature beneath the dorsal fin.

Fish distributions were surveyed on 30 dates from 8 August 1968 to 21 August 1969. Generally, each transect was sampled twice on every date, once during the afternoon [1230–1730 CST (central standard time)] and again after dark (1830–2400 CST). However, the reference areas were not sampled during January and February 1969 because ice covered them.

Analytical Treatment of Fish-Catch Data

Analyses of distributions were based on catch per unit effort (catch/effort). Catch data were categorized by species, length class, season, time of day, and location of capture. Individuals of each species were pooled into one, two, or three length classes, the number

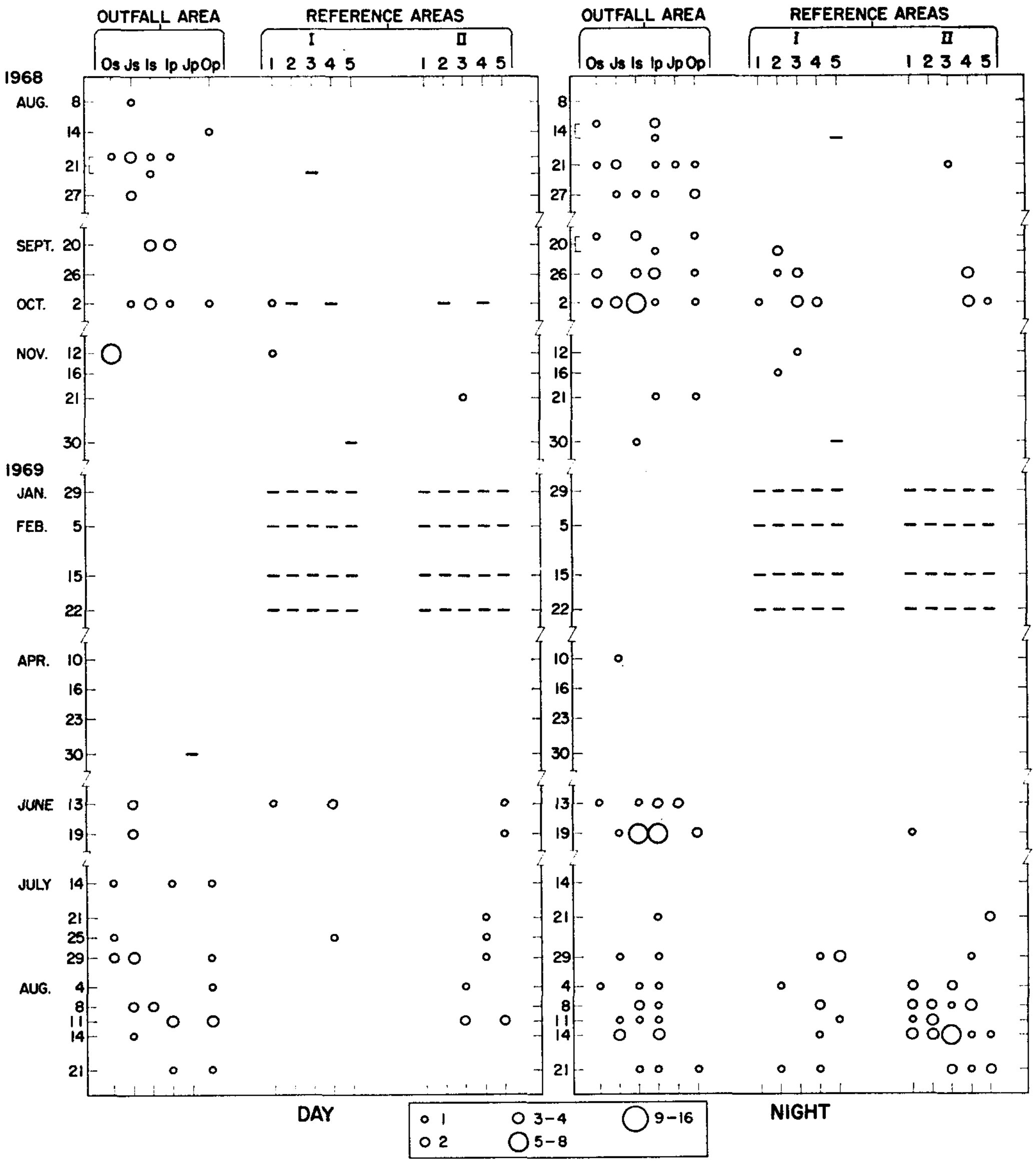


FIGURE 6.—Number of medium bluegill caught from each electrofishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.

of classes increasing with the number of specimens (Table 1). Two length classes approximately separated yearling and younger fish from those older than 1 year; three length classes approximately separated age 0, age I, and older fish. Sampling dates clustered temporally and thermally into seven seasonal periods: (1) August 1968, (2) September–October 1968, (3) November 1968, (4) January–February 1969, (5) April 1969, (6) June 1969, and (7) July–August 1969 (Fig. 2). The minimum and maximum time inter-

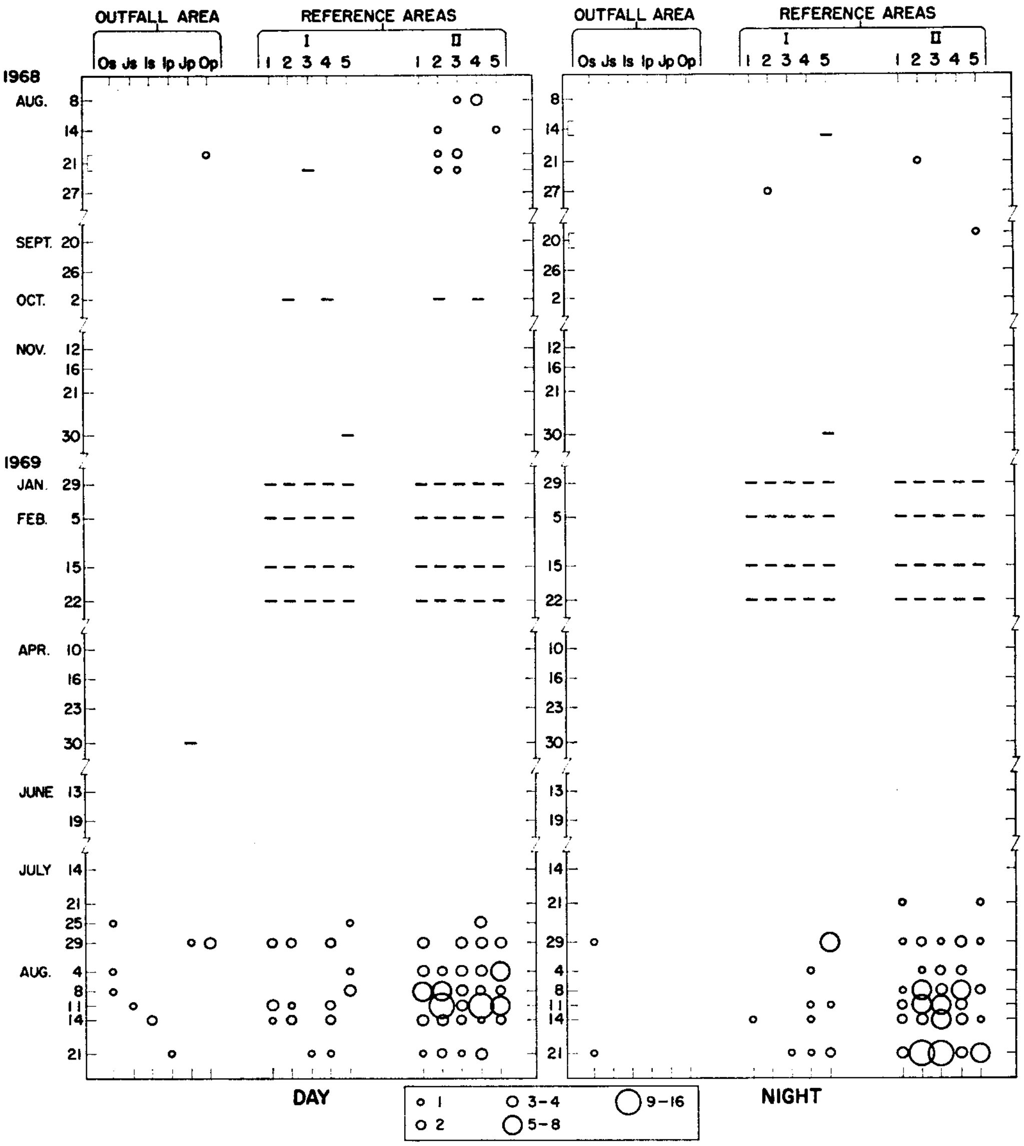


FIGURE 7.—Number of small yellow perch caught from each electrofishing run between 8 August 1968 and 21 August 1969, by time of day, date, and transect. Number of fish is indicated by size of circle, according to scale at bottom of figure. A short horizontal line indicates that no sampling effort was expended; a blank indicates no catch.

vals between successive sampling dates of any period were 3 and 9 days. Reference area temperatures were between 25 and 30 C during August 1968 and July–August 1969, between 20 and 22 C during September–October 1968 and June 1969, between 6 and 15 C during November 1968 and April 1969, and between 0 and 4 C during January–February 1969 (Fig. 2). Within each season, day and night catches were considered separately.

For each category of catch, catch/effort from the outfall area was compared statistically with that from the combined reference areas. The null hypothesis that catch/effort from the outfall area equaled catch/effort from the reference areas was assessed by the Kolmogorov-Smirnov one-sample test, a distribution-free analysis for goodness of fit. Statements concerning different abundances of fishes between areas are inferences based on significant ($p \leqslant 0.05$) differences in catch/effort.

Catches of most fishes varied greatly with season and time of day (e.g., Figs. 6 and 7). Young fishes were represented mostly in summer and fall samples; larger individuals of many species were caught more frequently at night than during afternoon. Thus, for any one species and length class, comparison of catch/effort between outfall and reference areas was limited to only certain of the seasonal-diel periods. Comparisons between areas were automatically precluded for the January–February 1969 period because the reference areas were not sampled.

Abundance of Fishes in the Outfall Area Relative to Reference Areas

Of the 31 species collected, 11 were unevenly distributed between outfall and reference areas during at least one seasonal-diel period (Fig. 8).

Longnose gar (*Lepisosteus osseus*) were conspicuously concentrated in the outfall area at night during both summers. A small fraction of individuals, once stunned, actually entered the push net; most longnose gar swam erratically and violently out of the electrical field, escaping capture. Beginning in 1969, we systematically tallied longnose gar only seen by the push net operator as well as those actually caught. These data indicated that longnose gar were more abundant in the outfall area than in the reference areas at night in July–August 1969. The same was undoubtedly true in August 1968, although few quantitative data were collected. Few longnose gar were seen or caught during other sampling periods. All captured longnose gar and probably all those only sighted exceeded 350 mm in length.

Large carp (*Cyprinus carpio*) were more abundant in the outfall area than in the reference areas during August 1968, day and night; September–October 1968, day and night; November 1968, night; and July–August 1969, night. In contrast, during both day and night in August 1968 and again in July–August 1969, small fish (most <25 mm long) tended to be less abundant in the outfall area than in the reference areas, the ratio of catch/effort from the outfall area to catch/effort from the reference areas never exceeding 0.67. But during any one seasonal-diel period, catch/effort of small carp from the outfall area did not differ significantly from that in the combined reference areas.

Small black bullhead (*Ictalurus melas*) were more abundant in the reference areas than in the outfall area during November 1968, day and night. During both summers, large schools of age 0 black bullhead were frequently seen in the reference areas but rarely in the outfall area.

Large yellow bass (*Morone mississippiensis*) were more abundant by day in the outfall area than in the reference areas during April 1969, June 1969, and July–August 1969. But at night their abundances in outfall and reference areas did not differ significantly during August 1968, September–October 1968, April 1969, or July–August 1969, even though sample size was relatively large, exceeding 40 fish during each season. Catch/effort was higher at night than during the day. Small and medium-sized yellow bass were more abundant, day and night, in reference areas than in the outfall area during July–August 1969.

Large yellow bass in the outfall area were concentrated near the discharge jets, particularly during the day. Although runs across the two jets constituted only 33% of sampling effort in the outfall area, they produced 96% (25 of 26 fish) and 66% (63 of 95 fish) of the large yellow bass caught in the outfall area during day and night, respectively. During late winter and spring 1969, adult yellow bass (in addition to bluegill and black crappie) were conspicuously concentrated at the primary outfall during the daylight hours; these fish were not effectively sampled by electrofishing.

Small rock bass (*Ambloplites rupestris*) were more abundant in the outfall area than in the reference areas during July–August

1969, day and night. Of 77 specimens caught from the outfall area during July–August 1969, the two coolest transects, Op and Os, yielded 33 and 30 fish, respectively. The remaining 14 fish were all caught from Js, the southwest end of which was generally cooler than water between or in the jets.

Although 29 and 73 large pumpkinseed (*Lepomis gibbosus*) were caught during day and night sampling in July–August 1969, outfall and reference area catch/effort did not differ significantly. Small pumpkinseed were more abundant in the outfall area than in reference areas during both day and night in August 1968 and during afternoon in September–October 1968.

Bluegill were caught much more frequently than any other species; 848 large, 237 medium, and over 19,000 small specimens were taken.

Large and medium-sized bluegill were more abundant by day in the outfall area than in the reference areas during August 1968, September–October 1968, November 1968, and July–August 1969. Large bluegill were more abundant at night in the outfall area than in the reference areas during all seasonal periods except August 1968 and July–August 1969; at night, medium-sized bluegill were more abundant in the outfall area than in the reference areas during August 1968, September–October 1968, and June 1969.

Small bluegill were more abundant, both day and night, in the outfall area than in the reference areas during August 1968 and July–August 1969, and, at least by day, in September–October 1968 and June 1969, as well. In November 1968, however, young bluegill during the day were more abundant in reference areas than in the outfall area.

During both years age 0 bluegill were taken in progressively increasing numbers as summer advanced, but mid-August catches in 1969 were only about 20% of those in 1968. Catch/effort in 1968 declined during November from the maximum reached in September. Reference area I produced a much smaller fraction of the total young bluegill catch in July–August 1969 than in August 1968.

Largemouth bass (*Micropterus salmoides*) were more abundant by day in the outfall area than in the reference areas during September–October 1968 and July–August 1969. Largemouth bass were more evenly distributed among areas at night.

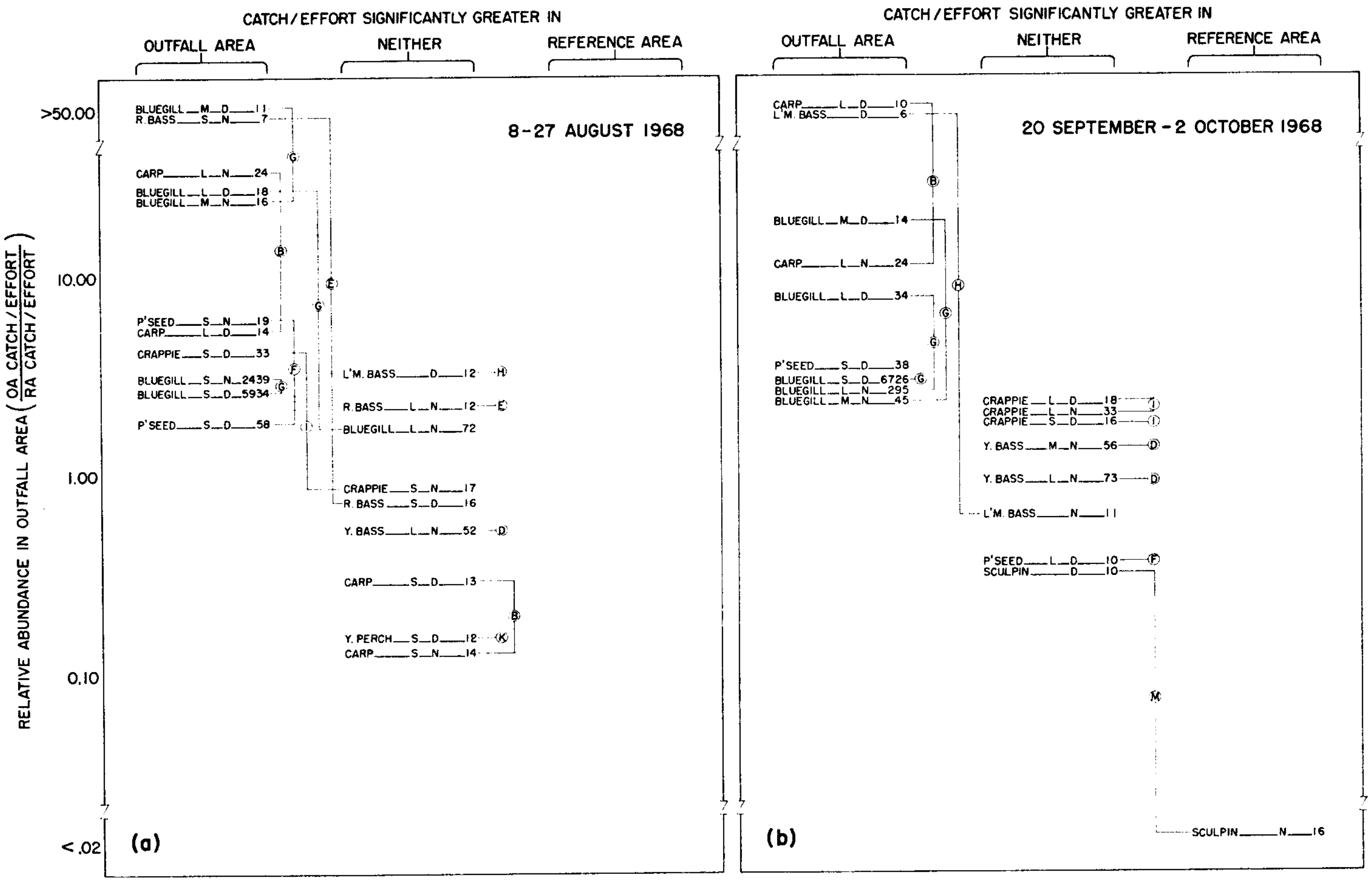
Small black crappie (*Pomoxis nigromaculatus*) were more abundant by day in the outfall area than in reference areas in August 1968, but they were more abundant in the reference areas during both day and night in July–August 1969. Large fish tended to be more abundant in the outfall area than in the reference areas during September–October 1968, but neither day nor night catches differed significantly between areas.

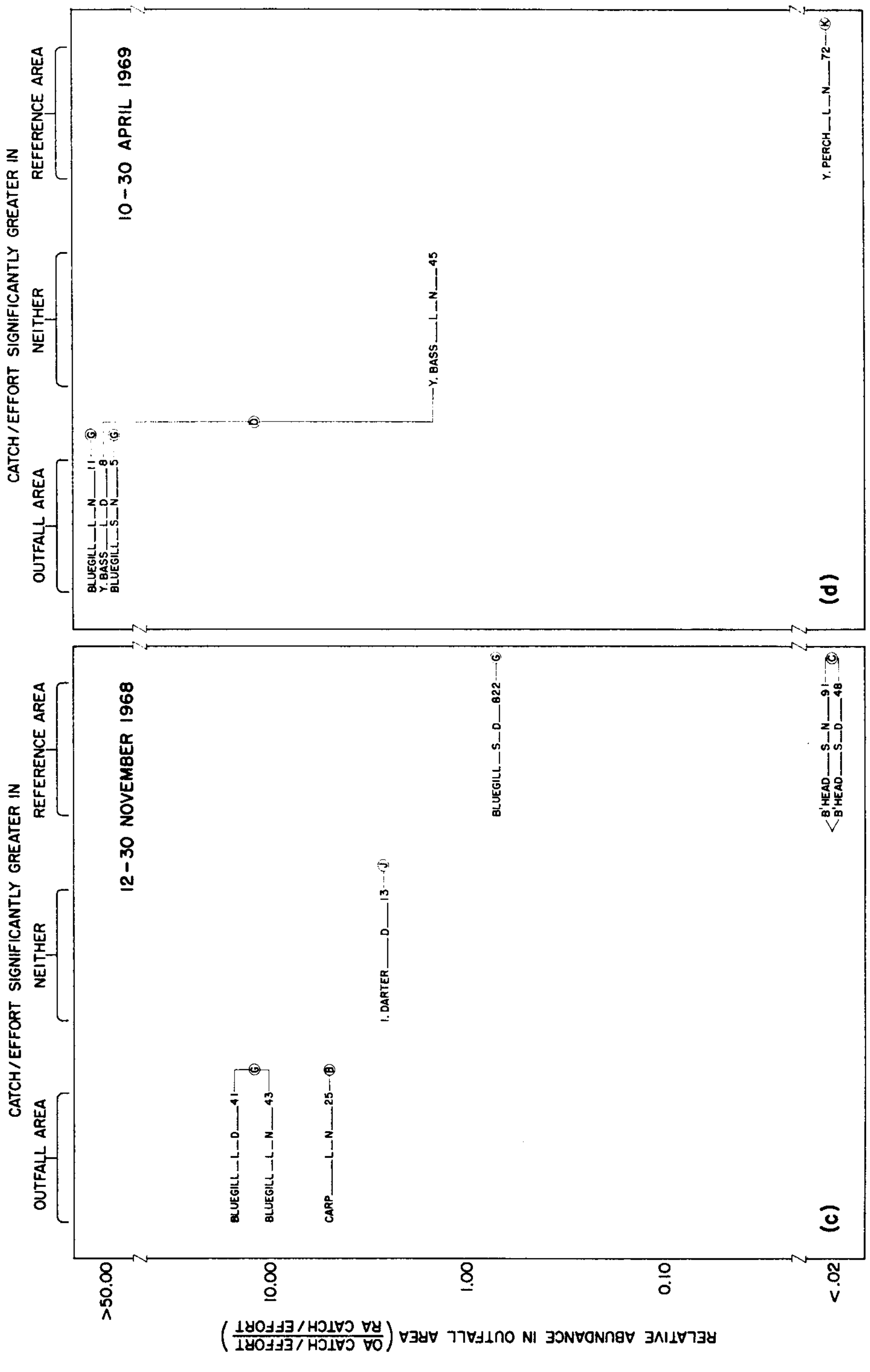
Few large yellow perch were taken, except at night during April 1969. All of these were caught from the reference areas; RII produced more fish than RI. All specimens examined were ripe males. Yellow perch egg masses

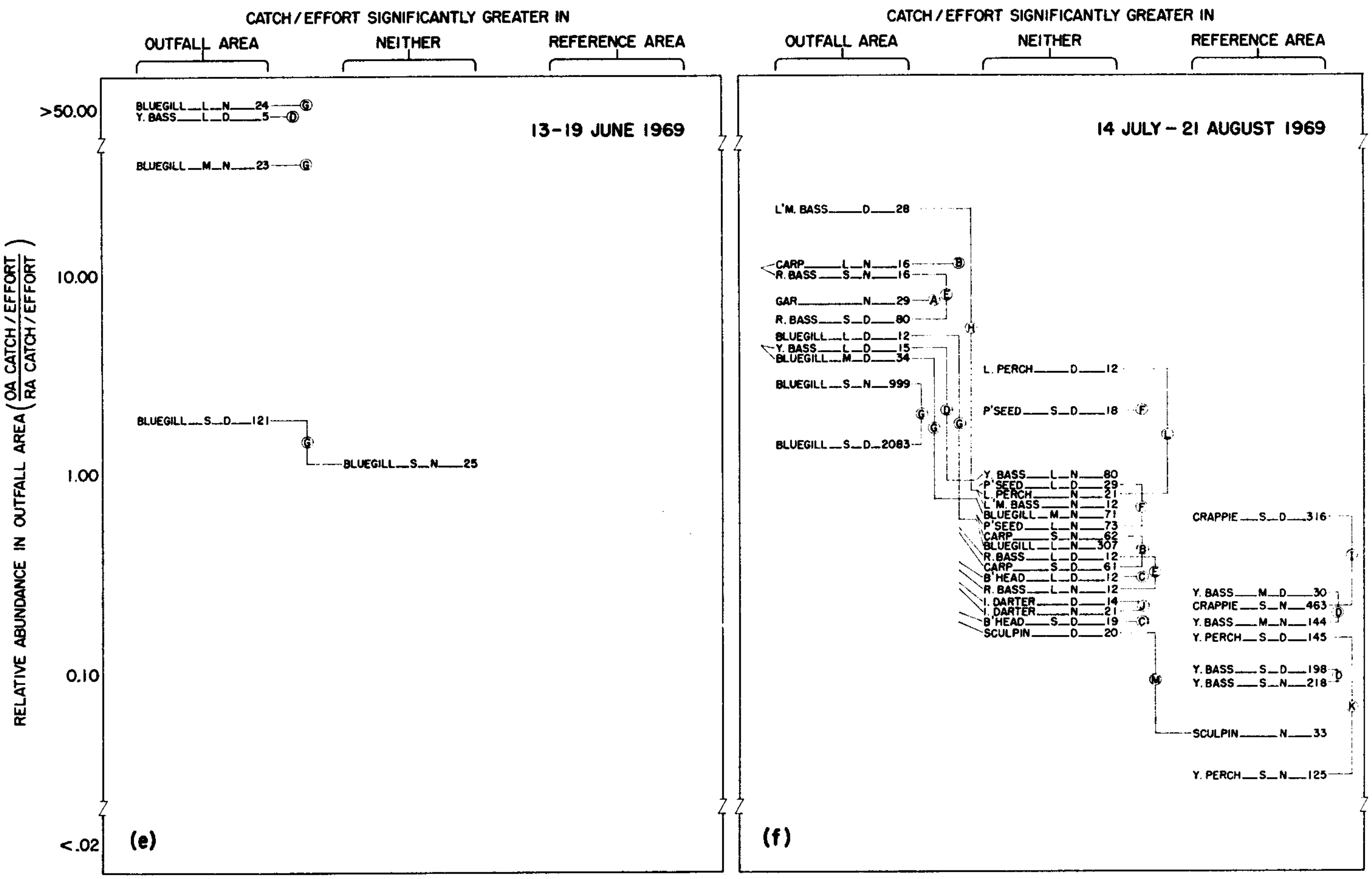
→

FIGURE 8.—Comparison of electrofishing catch/effort between outfall and combined reference areas by season: (a) August 1968, (b) September–October 1968, (c) November 1968, (d) April 1969, (e) June 1969, (f) July–August 1969. The vertical position of each entry is a measure of the degree to which fish were concentrated in the outfall area relative to reference areas; the horizontal position of each entry indicates whether catch/effort from the outfall area was statistically greater than, not different from, or less than catch/effort from the reference areas (Kolmogorov-Smirnov one-sample test; probability level, 0.05). Each entry consists of fish of one species and length class (L = large, M = medium, S = small, no letter = all lengths; see Table 1 for identification of length classes) caught during one time of day (D = afternoon, N = night); the number of fish follows the code letter for time of day. Lines from entries extend to encircled letters (see below) and connect day and night entries for fish of the same species-length category if both day and night data were obtained.

A	Longnose gar
B	Carp
C	Black bullhead
D	Yellow bass
E	Rock bass
F	Pumpkinseed
G	Bluegill
H	Largemouth bass
I	Black crappie
J	Iowa darter
K	Yellow perch
L	Logperch
M	Mottled sculpin


CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH/EFFORT / RA CATCH/EFFORT)
>50.00
10.00
1.00
0.10
<.02
8-27 AUGUST 1968
BLUEGILL—M—D—11
R BASS—S—N—7
CARP—L—N—24
BLUEGILL—L—D—18
BLUEGILL—M—N—16
P'SEED—S—N—19
CARP—L—D—14
CRAPPIE—S—D—33
BLUEGILL—S—N—2439
BLUEGILL—S—D—5934
P'SEED—S—D—58
L'M. BASS—D—12
R. BASS—L—N—12
BLUEGILL—L—N—72
CRAPPIE—S—N—17
R. BASS—S—D—16
Y. BASS—L—N—52
CARP—S—D—13
Y. PERCH—S—D—12
CARP—S—N—14
G
B
E
G
F
G
I
H
E
D
B
K
(a)
20 SEPTEMBER - 2 OCTOBER 1968
CARP—L—D—10
L'M. BASS—D—6
BLUEGILL—M—D—14
CARP—L—N—24
BLUEGILL—L—D—34
P'SEED—S—D—38
BLUEGILL—S—D—6726
BLUEGILL—L—N—295
BLUEGILL—M—N—45
CRAPPIE—L—D—18
CRAPPIE—L—N—33
CRAPPIE—S—D—16
Y. BASS—M—N—56
Y. BASS—L—N—73
L'M. BASS—N—11
P'SEED—L—D—10
SCULPIN—D—10
SCULPIN—N—16
B
H
G
G
G
J
I
D
D
F
M
(b)


CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
12-30 NOVEMBER 1968
BLUEGILL—L—D—41 G
BLUEGILL—L—N—43
CARP—L—N—25 B
I. DARTER—D—13 J
BLUEGILL—S—D—822 G
< B'HEAD—S—N—91 C
< B'HEAD—S—D—48
(c)
CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
10-30 APRIL 1969
BLUEGILL—L—N—11 G
Y. BASS—L—D—8 D
BLUEGILL—S—N—5 G
Y. BASS—L—N—45
Y. PERCH—L—N—72 K
(d)
>50.00
10.00
1.00
0.10
<.02
RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH/EFFORT / RA CATCH/EFFORT)


CATCH/EFFORT SIGNIFICANTLY GREATER IN
OUTFALL AREA
NEITHER
REFERENCE AREA
RELATIVE ABUNDANCE IN OUTFALL AREA (OA CATCH/EFFORT / RA CATCH/EFFORT)
>50.00
10.00
1.00
0.10
<.02
(e)
13-19 JUNE 1969
BLUEGILL_L_N_24 G
Y. BASS_L_D_5 D
BLUEGILL_M_N_23 G
BLUEGILL_S_D_121
G
BLUEGILL_S_N_25
(f)
14 JULY - 21 AUGUST 1969
L'M. BASS_D_28
CARP_L_N_16 B
R. BASS_S_N_16
GAR_N_29 A E
R. BASS_S_D_80
H
BLUEGILL_L_D_12
Y. BASS_L_D_15
BLUEGILL_M_D_34
BLUEGILL_S_N_999
G
D
G
G
BLUEGILL_S_D_2083
L. PERCH_D_12
P'SEED_S_D_18 F
L
Y. BASS_L_N_80
P'SEED_L_D_29
L. PERCH_N_21
L'M. BASS_N_12
BLUEGILL_M_N_71
P'SEED_L_N_73
CARP_S_N_62
BLUEGILL_L_N_307
R. BASS_L_D_12
CARP_S_D_61
B'HEAD_L_D_12
R. BASS_L_N_12
I. DARTER_D_14
I. DARTER_N_21
B'HEAD_S_D_19
SCULPIN_D_20
F
B
C
E
J
C
M
CRAPPIE_S_D_316
I
Y. BASS_M_D_30
CRAPPIE_S_N_463
Y. BASS_M_N_144
Y. PERCH_S_D_145
D
Y. BASS_S_D_198
Y. BASS_S_N_218
D
K
SCULPIN_N_33
Y. PERCH_S_N_125

were frequently observed during April in both reference areas. Small yellow perch were more abundant in the reference areas (primarily RII) than in the outfall area during both day and night in July–August 1969 (Fig. 7).

Mottled sculpin (*Cottus bairdi*) were more abundant in the reference areas than in the outfall area at night during September–October 1968 and during both day and night in July–August 1969.

Although 20 other species (approximately 800 individuals) were caught, catch data did not strongly indicate nonuniformity in their spatial distributions. Brook silverside (*Labidesthes sicculus*) were probably concentrated in the outfall area during summer and early fall. Large schools of brook silverside were regularly observed near the primary jet, but these small fish were seldom stunned by the electrical field and usually escaped the push net. Seven bigmouth buffalo (*Ictiobus cyprinellus*) were caught during fall 1968; all were taken in runs across the primary jet. We saw other bigmouth buffalo swimming in the primary discharge plume but never elsewhere.

The extent to which littoral distributions of Lake Monona fishes were biased in favor of or against the outfall area may be summarized by segregating several response types. Segregation is achieved by a dichotomous key used in the same manner as those constructed for taxonomic identifications:

1a Catch/effort not significantly different between outfall and reference areas during any seasonal-diel period 2
1b Catch/effort significantly different between outfall and reference areas during at least one seasonal-diel period 3
2a Fewer than 20 specimens caught during any seasonal-diel period .... Rare types
  Northern pike (*Esox lucius*)
  Golden shiner (*Notemigonus crysoleucas*)
  Emerald shiner (*Notropis atherinoides*)
  Spottail shiner (*Notropis hudsonius*)
  Bluntnose minnow (*Pimephales notatus*)
  White sucker (*Catostomus commersoni*)
  Bigmouth buffalo
  Black bullhead, large
  Yellow bullhead (*Ictalurus natalis*)
  Brown bullhead (*Ictalurus nebulosus*)
  Banded killifish (*Fundulus diaphanus*)
  White bass (*Morone chrysops*)
  Rock bass, large
  Brook stickleback (*Culaea inconstans*)
  Green sunfish (*Lepomis cyanellus*)
  White crappie (*Pomoxis annularis*)
  Johnny darter (*Etheostoma nigrum*)
  Walleye (*Stizostedion vitreum vitreum*)
  Freshwater drum (*Aplodinotus grunniens*)
2b At least 20 specimens caught during some seasonal-diel period .... Indifferent types
  Carp, small
  Pumpkinseed, large
  Black crappie, large
  Iowa darter (*Etheostoma exile*)
  Logperch (*Percina caprodes*)
3a Catch/effort in the reference areas never significantly less than in the outfall area .... Reference-area types
  Black bullhead, small
  Yellow bass, small & medium
  Yellow perch, small & large
  Mottled sculpin
3b Catch/effort in the outfall area significantly greater than in the reference areas during at least one seasonal-diel period 4
4a Catch/effort in the reference areas significantly greater than in the outfall area during at least one seasonal-diel period .... Mixed types
  Bluegill, small
  Black crappie, small
4b Catch/effort in the outfall area never significantly less than in the reference areas .... Outfall-area types
  Longnose gar
  Carp, large
  Yellow bass, large
  Rock bass, small
  Pumpkinseed, small
  Bluegill, medium & large
  Largemouth bass

The key perhaps misrepresents the responses of some fishes. Small carp were probably more abundant during summer in the reference areas. Small bluegill were more abundant in the reference areas in November 1968 but were more abundant in the outfall area during most other seasons. Large black crappie were probably more abundant in outfall than in reference areas during September–October 1968. Thus, small carp may have been a reference-area type, whereas both small bluegill and large black crappie were probably outfall-area types.

There were no reference data with which to compare catches in the outfall area during January–February 1969, but electrofishing and visual observation suggested that fishes present in the outfall area were few compared with numbers there at other seasons. Twenty-four day and 24 night runs yielded only 31 specimens representing six species: 13 bluegill, 10 brook silverside, 3 Iowa darter, 2 carp, 2 golden shiner, and 1 yellow bass. Aquatic vegetation was essentially absent from the entire outfall area during winter.

Recapture of Marked Fishes

Although 934 fishes were fin-punched during 1968 and 1,726 more were tagged in 1969, we had recaptured only eight marked specimens by 1 July 1970. Forty-two tagged specimens were caught and reported to us by fishermen. Of 14 yellow bass and 21 bluegill reported by fishermen, 10 and 12 fish, respectively, were caught more than 1 km from the tagging location. These data verified that we were not catching and re-catching the same individuals. They also supported our general impression that residence times of larger fishes in the sampling areas were short—1 week or less.

Distribution of Lake Monona Fish Compared with That of Fishes in Other Heated Waters

Little published literature exists on the distributions of fishes in other waters receiving heated effluent (Raney and Menzel 1969; Coutant 1970). No published field study and only a fraction of the report literature with which we are acquainted deal with a lake environment or an ichthyofauna very similar to that of Lake Monona. However, most information now available suggests that whatever the habitat type and ichthyofaunal composition, some species avoid effluent outfall areas while others concentrate there.

Alabaster and Downing (1966) observed that fish distributions were little altered by effluents that warmed only the surface layers of several British rivers; but, in the more thoroughly mixed River Trent, bream (*Abramis brama*), tench (*Tinca tinca*), and carp lived in the warmest water available (about 28 C), while roach (*Rutilus rutilus*) and gudgeon (*Gobio gobio*) avoided water warmer than 26 C. Trembley (1961) reported that satinfin shiner (*Notropis analostanus*), banded killifish, American eel (*Anguilla rostrata*), redbreast sunfish (*Lepomis auritus*), and bluegill occurred during summer at temperatures above 32 C in the effluent lagoon of a power plant on the Delaware River, Pennsylvania. During cooler weather, the lagoon was inhabited by additional species, including golden shiner, brown bullhead, largemouth bass, black crappie, pumpkinseed, and rock bass. During summer in the Wabash River (Indiana) carp, buffalo (*Ictiobus* sp.), longnose gar, and channel catfish (*Ictalurus punctatus*) were among species concentrated below a heated effluent outfall (>30 C), but river carpsucker (*Carpiodes carpio*), redhorse (*Moxostoma* sp.), spotted bass (*Micropterus punctulatus*), longear sunfish (*Lepomis megalotis*), and sauger (*Stizostedion canadense*) were more abundant upstream from the outfall (Gammon 1970). Carp, buffalo, and channel catfish, but also river carpsucker and longear sunfish, occurred in summer at temperatures exceeding 33 C in an effluent canal discharging into the White River, Indiana (Proffitt 1969). Threadfin shad (*Dorosoma petenense*), sauger, skipjack herring (*Alosa chrysochloris*), and channel catfish concentrated in a heated discharge harbor on Kentucky Lake, Tennessee, during winter and spring (Dryer and Benson 1957). In marine environments, too, some fishes apparently concentrate near heated discharge outfalls, while others seem less abundant than in unheated areas (Allen, Boydstun, and Garcia 1970).

Insofar as similarity of species compositions allowed comparison, responses of adult fishes in Lake Monona were similar to their responses at other sites. Longnose gar, carp, bigmouth buffalo, bluegill, largemouth bass, black crappie, pumpkinseed, and rock bass—all recorded from other heated waters—did not avoid the outfall area of Lake Monona, although actual concentrations of adult black crappie, pumpkinseed, and rock bass were not demonstrated in the outfall area. At other sites, distributional data have not been collected for those fishes that avoided the outfall area of Lake Monona.

We are aware of no quantitative information on the distributions of young fishes relative to heated discharges, except for those data we collected in Lake Monona, nor have nocturnal distributions of fishes at other sites been investigated. But perhaps size and diel differences like those observed in Lake Monona are typical of fish distributions in heated environments.

Three field studies (Dryer and Benson 1957; Trembley 1961; Proffitt 1969) suffered a common deficiency: suitable reference sites, with which the discharge area could be

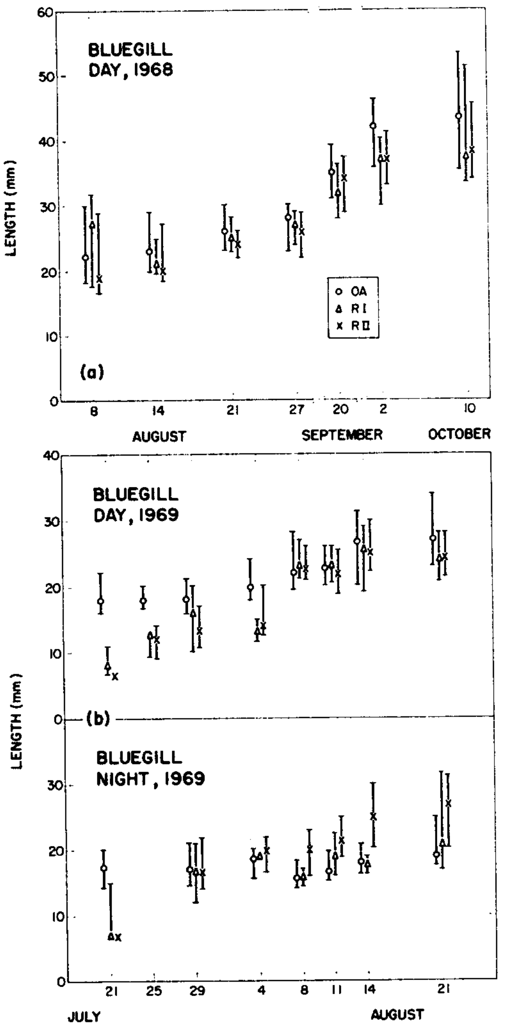


FIGURE 9.—Length-frequency distributions of age 0 bluegill collected from each study area, 8 August–10 October 1968 (a), and 21 July–21 August 1969 (b). Medians are indicated by point symbols; vertical lines are interquartile ranges. Sample size was at least 10 fish in each case during 1968 and at least five fish in most cases during 1969.

compared, were unavailable. Therefore, responses of fishes to the discharge area at one season could only be judged by those during some other season or reconciled with general impressions of fish distributions in the body of water as a whole. Thus, "... a remarkably common phenomenon, i.e., the attraction of fish to warmed water (from power plants) during cooler months and repulsion by thermal extremes in the peak of summer" (Coutant 1970, p. 367) must be interpreted with some caution.

Whatever occurs seasonally in heated discharge areas may also occur simultaneously in other similar, but unheated, parts of the habitat. For example, apparent abundances of several fishes fluctuated seasonally in the outfall area of Lake Monona, but similar fluctuations occurred simultaneously in the reference areas. Ratios of outfall to reference area catch/effort fluctuated to a lesser extent. Only among small bluegill and small black crappie were there significant reversals in the ratio from one season to another. In the black crappie, reversal occurred from one summer to the next, a change that could not be attributed to temperature. Young bluegill were more abundant in the outfall area during both summers but were more abundant in the reference areas during a colder season, November 1968. In Lake Monona, fishes did not differentially avoid the outfall area during summer to a much greater extent than at other seasons. Nor were the numbers of fish present in the outfall area during January–February 1969 as great as in summer.

Whatever difficulties arise in the assessment of fish abundances in outfall areas in the absence of suitable control sites, there can be little doubt that some spectacular concentrations of fishes do occur in direct response to the operation of power plants. For example, Dryer and Benson (1957) observed fish concentrations during winter and spring in a heated discharge harbor on Kentucky Lake, Tennessee; threadfin shad were so abundant that they hampered boating by clogging the cooling systems of outboard motors. But even this example is somewhat confusing because threadfin shad also concentrated in the unheated inlet harbor, clogging the intake screens of the power plant's cooling system.

SIZE DISTRIBUTIONS OF AGE 0 FISHES IN THE STUDY AREAS OF LAKE MONONA

To determine if sizes of age 0 fishes differed among outfall and reference areas, lengths and weights were obtained from specimens collected during electrofishing surveys of 1968 and 1969. By comparing sizes of fish caught on successive sampling dates from each area, we hoped to ascertain whether or not young fishes of the outfall area grew at different rates or differed in condition relative to their counterparts in the reference areas.

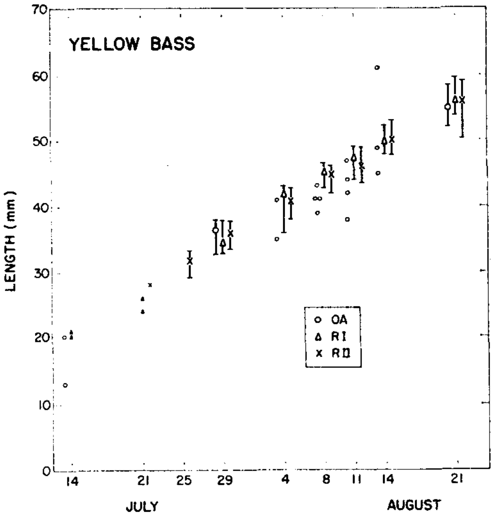


FIGURE 10.—Length-frequency distributions of age 0 yellow bass collected during afternoon and evening from each study area, 14 July–21 August 1969. Point symbols and vertical lines indicate the median and interquartile range for each sample of five or more fish. Smaller point symbols show lengths of individuals from samples of fewer than five fish.

Length-Frequency Distributions of Age 0 Bluegill, Yellow Bass, and Black Crappie

Adequate samples, generally of 20 or more fish, allowed interareal comparison of bluegill length distributions on several dates during summer and fall 1968 and summer 1969. Afternoon and evening distributions during 1969 were considered separately; only afternoon data from 1968 were available.

During summer 1969, enough age 0 yellow bass and black crappie were collected for interareal comparisons of length distributions. Data from afternoon and evening samples were pooled to establish, for each species, a single length-frequency distribution for each area on each date.

Length distributions of age 0 bluegill differed among outfall and reference areas. During afternoon in both 1968 and 1969, age 0 bluegill from the outfall area were generally longer than those from either reference area; RI and RII fish had similar length distributions (Fig. 9). Among the study areas, length-frequency distributions differed more consistently at their upper ends than at their lower ends. In both years, the 75th percentile and median lengths varied significantly among areas (Friedman two-way AOV; $p < 0.05$), but in neither year was there a significant difference among 25th percentile lengths (Friedman two-way AOV; 1968: $p = 0.10$; 1969: $p = 0.24$).

Median lengths of age 0 bluegill caught at night in 1969 differed from those obtained during afternoon (sign test; $p < 0.05$; Fig. 9b). After 29 July, RII fish taken at night had greater median lengths than those from OA and RI (randomization test; $p < 0.05$), which were similar in length. On each date in August, the median length of RII fish at night was greater or only slightly less than during the day, but median lengths of OA and RI fish were less at night by as much as 8 mm and in only one case (RI, 4 August) ever greater at night than during the afternoon. From 21 July to 21 August, median lengths of night-caught bluegill from OA scarcely changed, being 16 to 19 mm on every date. Similarly, after 29 July, there was little tendency for increase in median lengths of RI bluegill caught at night.

Neither age 0 yellow bass nor age 0 black crappie were consistently longer in one area than in another during 1969 (Figs. 10 and 11). On 21 August 1969, the single date when more than 10 yellow bass were taken from each area, median lengths of fish from OA, RI, and RII did not differ significantly (extension of median test; $p = 0.75$). OA and RII supplied most of the age 0 black crappie caught during 1969. When median lengths of black crappie from OA and RII were paired by date from 14 July to 21 August (except 25 July when only two fish were caught in RII), application of the Wilcoxon test indicated no significant ($p > 0.05$) difference between areas.

Growth and movements.—The general increase in fish lengths as summer progressed (Figs. 9–11) was primarily the result of

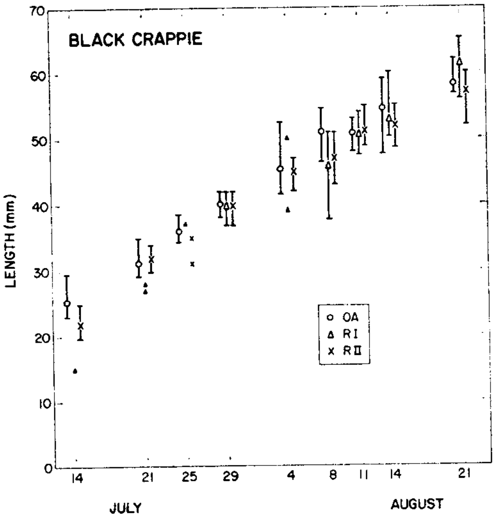


FIGURE 11.—Length-frequency distributions of age 0 black crappie collected during afternoon and evening from each study area, 14 July–21 August 1969. Point symbols and vertical lines indicate the median and interquartile range for each sample of five or more fish. Smaller point symbols show lengths of individuals from samples of fewer than five fish.

growth. Growth rates of age 0 fishes may have differed among areas, but any difference was obscured by other processes, particularly size-dependent movements of the fish.

At night, larger age 0 bluegill moved away from sampling locations in OA and RI to a greater extent than from those in RII. Because median lengths of fish from both OA and RI were less at night, movements perpendicular to shore rather than along shore were indicated. Diel onshore-offshore movements by larger bluegill fry have been postulated by Werner (1967). The smaller day-night difference in lengths of RII fish may have been related to the more gradual bottom slope in RII. Whatever the cause of apparent offshore movements, they were not directly related to operation of the power plant because it scarcely affected RI.

The apparent importance of size-differential movements on diel changes in age 0 bluegill length distributions suggested that persistent afternoon differences in fish lengths among areas were not entirely or even primarily due to interareal differences in growth rate. Larger age 0 bluegill may have been attracted to the outfall area from adjacent areas. Certainly, larger catches of age 0 bluegill from the outfall area than from reference areas implied active concentration of fish in the outfall area. It seems reasonable that larger fish, being more mobile than smaller fish, would have been differentially concentrated.

Comparison with age 0 fishes in other waters.—In no other system receiving thermal effluent have length distributions of age 0 fishes been investigated. However, data are available on rates of length increase for age 0 bluegill, yellow bass, and black crappie in unheated waters.

Median lengths of age 0 bluegill caught during afternoon from Lake Monona increased at rates commensurate with those observed for other populations, about 0.5 mm/day. Age 0 bluegill measured by Krumholz (1949) increased between 12 and 25 mm total length at 0.1 to 0.6 mm/day. Werner (1969) estimated that young bluegill grew 0.4 mm/day in an Indiana hatchery pond. But, on 14 August during both 1968 and 1969, age 0 bluegill from Lake Monona were 3–5 mm shorter than a 10-yr average computed for age 0 bluegill in Clear Lake, Iowa (Ridenhour 1960).

On 14 August 1969, Lake Monona age 0 yellow bass were about 5 mm shorter but age 0 black crappie about 5 mm longer than 10-yr averages for these species on 14 August in Clear Lake, Iowa (Ridenhour 1960).

Although the authors just cited have assumed that changes in average length of fish from date to date were due primarily to growth, their data, like those from Lake Monona, were potentially confounded by length-dependent recruitment, mortality, and movements of the fish.

Length-Weight Relationships of Age 0 Bluegill

Length-weight relationships of bluegill were examined for evidence of differences in condition between fish in outfall and reference areas. Specimens collected during four afternoons in 1968 and during afternoons and evenings on three dates in 1969 were removed individually from the preservative, blotted on a paper towel, weighed, and then measured. Weight and total length of each fish were

TABLE 2.—*Weight of age 0 bluegill from the outfall area relative to fish with the same length from reference areas. Values are mean ranks (see text) ranging between 1 and 2. A mean rank greater than 1.5 indicated that outfall fish were heavier than reference fish of same length*

Length (mm)	Mean rank						
	1968				1969		
	8 August	21 August	20 September	30 November	4 August	11 August	21 August
15–19	1.8	—	—	—	1.7	1.6	1.3
20–24	1.9	2.0	1.8	—	1.4	1.6	1.9
25–29	2.0	1.9	1.2	—	2.0	1.0	1.4
30–34	1.6	1.3	1.0	—	—	—	1.6
35–39	1.2	1.4	1.2	1.0	—	—	—
40–44	—	—	1.2	1.3	—	—	—
45–49	—	—	—	1.3	—	—	—

recorded to the nearest 0.01 g and 1 mm, respectively.

Median weights of fish in each 1-mm length class were determined for each of the three areas on each date. Medians for the two reference areas were averaged at each length, and the average was compared to the median for fish of the same length from the outfall area. If no fish of a particular length was caught from one reference area, the median from the other reference area was used as the basis for comparison. The reference and outfall-area values were ranked within each 1-mm length class, the larger value being assigned rank 2 and the smaller 1 (both 1.5 if tied). Ranks were then summed for each of several 5-mm intervals of length and an average rank within each interval was computed for the outfall area. Under an hypothesis of no difference between weights of outfall and reference-area fish of the same length, expected average ranks of outfall-area fish were 1.5 for all 5-mm length intervals on each date.

In both years, about half (7 of 17 in 1968; 6 of 10 in 1969) the averages exceeded the expected value (Table 2). However, in 1968, average rank and fish length were significantly associated (chi-square one-sample test; $p < 0.01$). Outfall fish smaller than about 30 mm were heavier than their counterparts from the reference areas; at greater lengths reference-area fish were heavier than those from the outfall area. The transitional length may have decreased through time from August to November. No consistent trend was evident in 1969; relative condition of outfall fish fluctuated erratically with fish length and date (Table 2).

Although condition of OA fish relative to those from the reference areas varied systematically in 1968, the difference between smallest and largest of OA, RI, and RII median weights at each length amounted to only about 6% of the smallest median weight. Differences of this magnitude must have resulted partly from systematic variation in tissue mass of fish with equal length and not totally from differences in gut content of fish having identical tissue mass. Stomach contents of age 0 bluegill from an adjacent lake constituted only 2% of whole fish weight (J. F. Kitchell, Laboratory of Limnology, University of Wisconsin, personal communication). In any event, condition of outfall age 0 bluegill was never very different from that of reference-area fish.

Strawn (1969) and Trembley (1965) noted that fishes (species and sizes not specified) living in heated discharge areas seemed to be in good condition. However, brown bullhead and white catfish (*Ictalurus catus*) living in an effluent discharge canal on the Connecticut River had significant losses of condition during winter (Merriman 1970).

TEMPERATURE DISTRIBUTIONS OF FISHES IN THE OUTFALL AREA DURING SUMMER

Catch/Effort with Respect to Water Temperature

To generally relate fish distributions within the outfall area to temperature, the catch/effort data collected during August 1968 and July–August 1969 were examined for association with water temperature. Catch from each electrofishing run in the outfall area was

TABLE 3.—*Number of electrofishing runs made in the outfall area during summer by temperature, year, and time of day*

Median run temperature (C)	Number of runs			
	August 1968		July–August 1969	
	Day	Night	Day	Night
33.5	1	1	—	1
33.0	1	—	—	—
32.5	2	1	1	—
32.0	—	4	2	3
31.5	4	1	8	4
31.0	4	1	7	4
30.5	—	—	2	6
30.0	3	3	7	6
29.5	3	4	4	7
29.0	3	2	5	3
28.5	5	2	1	4
28.0	—	3	3	2
27.5	1	5	2	1
27.0	—	1	3	2
26.5	3	1	2	1
26.0	—	1	—	2
25.5	—	—	1	1
25.0	—	—	—	1
All	30	30	48	48

assigned the median temperature recorded during the run (Table 3). The catch was then categorized by species, length-class, year, and time of day. For each category of catch, catch/effort at each 0.5 C increment of temperature was computed. The resulting temperature distributions of catch/effort were analyzed for nonuniformity by application of the Kolmogorov-Smirnov one-sample test, $p \leqslant 0.05$. This analysis enabled identification of those fishes that tended to be more abundant at some than at other temperatures.

Fishes occurred at virtually all available temperatures, but in several cases the distribution of catch/effort was significantly nonuniform with respect to median run temperature (Table 4). Among fishes inferred to be not equally abundant at all temperatures, only longnose gar and medium-sized yellow bass were biased toward temperatures higher than expected under the hypothesis of uniform distribution: The expected interquartile range of catch/effort at night in 1969 was 26.5–31.0 C, but interquartile ranges for longnose gar and medium-sized yellow bass were 30.0–32.0 C and 28.5–31.0 C, respectively. Small rock bass, large pumpkinseed, small bluegill, largemouth bass, small black crappie, and small yellow perch were distributed at temperatures lower than expected; the same pattern held for large carp during the day in 1968 and for large and medium-sized bluegill at night in 1969. Small carp were concentrated at temperatures near 29 C during both day and night in 1969.

Gammon (1971) and Proffitt (1969) investigated near-outfall distributions of fishes belonging to faunas similar to that of Lake Monona. Although neither worker estimated the relative abundances of fishes at various temperatures, both concluded that most fishes avoided temperatures exceeding 33–34 C. On sampling dates in 1968 and 1969, only water in the jets and very near the outfalls of Lake Monona consistently reached 33 C. But several fishes, particularly smaller individuals, were relatively scarce above 30 C. Lowered abundance at higher temperatures may have resulted partly from avoidance of strong currents near the jets where higher temperatures occurred.

Fine-scale features of the temperature distributions of OA fishes were obscured by the large scale of sampling. Variation of temperature within a run limited resolution of capture temperatures to about 4 C. Fish caught at all points along a transect were assigned the median run temperature, but a fish caught near an end of some transects (Op, for example) may have been at temperatures 2–4 C lower or higher than the median. Median run temperatures overestimated temperatures experienced by fish that stayed near the bottom, because bottom temperatures were usually lower than at 0.5 m where temperature was recorded.

Most studies of heated discharge sites have generally yielded inadequate data on the temperature distributions of fishes (Coutant 1970). This has largely resulted from inability to measure, reliably and simultaneously, (1) water temperatures where fishes actually live, and (2) relative abundances of fishes within an area reasonably homogeneous except for variation in temperature. Allen, Boydstun, and Garcia (1970), for example, caught marine fishes by hook and line in the discharge area of a power plant at Buhne Point, California. Because it was impractical to measure temperatures at the points where

TABLE 4.—*Temperatures below which were obtained—and temperatures below which were expected—25%, 50%, and 75% of catch/effort from the outfall area during summer (see text). Each observed distribution of catch/effort that differed significantly from the expected distribution (uniform) is indicated by underlined quartile temperatures. Number of fish (N) contributing to each observed distribution appears to the right of the third quartile temperature*

		August 1968								July–August 1969							
		Day				Night				Day				Night			
		Quartile temperature (C)				Quartile temperature (C)				Quartile temperature (C)				Quartile temperature (C)			
Species	Length (mm)	1st	2nd	3rd	N	1st	2nd	3rd	N	1st	2nd	3rd	N	1st	2nd	3rd	N
Longnose gar	>350	—	—	—	—	—	—	—	—	—	—	—	—	30.0	31.0	32.0	25
Carp	⩽150	—	—	—	—	—	—	—	—	29.0	29.5	30.0	14	28.5	29.0	30.0	17
	>150	26.5	29.5	30.0	11	28.0	29.5	31.5	23	—	—	—	—	27.0	30.0	31.0	14
Yellow bass	51–100	—	—	—	—	—	—	—	—	—	—	—	—	28.5	30.5	31.0	14
	>100	—	—	—	—	27.5	30.0	31.5	13	28.0	29.5	31.5	10	26.0	30.0	31.0	29
Rock bass	⩽50	—	—	—	—	—	—	—	—	27.5	29.0	29.0	44	26.0	28.5	28.5	14
Pumpkinseed	⩽75	28.5	30.0	32.0	31	28.5	29.5	32.0	15	—	—	—	—	—	—	—	—
	>75	—	—	—	—	—	—	—	—	—	—	—	—	25.0	29.5	30.0	20
Bluegill	<75	27.0	29.0	31.0	3,681	27.0	29.0	30.5	1,940	26.5	28.5	29.0	838	26.0	28.5	29.5	634
	76–100	28.0	31.0	33.0	11	27.0	28.5	30.5	15	28.5	29.0	30.0	25	26.5	27.0	30.0	22
	>100	29.0	29.5	33.5	17	27.0	30.0	32.5	37	—	—	—	—	26.0	27.0	29.5	82
Largemouth bass	>50	—	—	—	—	—	—	—	—	25.5	28.0	29.5	24	—	—	—	—
Black crappie	⩽75	26.5	29.0	30.0	24	—	—	—	—	26.5	27.0	28.5	76	26.0	27.5	29.5	55
Yellow perch	26–100	—	—	—	—	—	—	—	—	25.5	27.5	30.5	11	—	—	—	—
Expected distribution (uniform)		28.5	30.0	32.5		27.5	29.3	31.5		27.5	29.3	31.0		26.5	28.8	31.0	

fishes were taken, catches could only be classified as coming from water warmer or cooler than 10.5 C.

Body Temperatures of Fishes with Respect to Water Temperature

The analysis of catch/effort provided a coarse measure of the temperatures experienced by fishes in the outfall area. During summer 1970, body temperatures of just-caught specimens were measured to obtain more accurate definition of fish distributions with respect to temperature. Sampling effort was expended during afternoon and evening on 11, 13, 17, 19, and 21 August 1970 throughout the outfall area.

Fishes were caught by the electrofishing technique described above, except that stunned individuals were removed from the water by hand-held dip net. After each specimen was lifted from the water, its body temperature was measured within 40 sec (median time, 12 sec) and recorded along with total length of the fish, central standard time, 0.5-m water temperature, and water depth.

Body temperatures were measured with a thermistor-bridge circuit. The thermistor, fixed in the tip of a 16-gauge hypodermic needle, was inserted into the epaxial musculature beneath the dorsal fin of the fish to a point near the interneural spines. The temperature measuring system reached thermal equilibrium within 3 sec.

Body temperatures of most fishes tended to increase with water temperature (Fig. 12). However, the slope of the relationship between fish and capture temperature was generally less than unity, i.e., fish temperatures tended to vary less than water temperatures. Body temperatures of yellow bass, rock bass, and yellow perch were virtually independent of capture temperatures.

Some fishes had body temperatures consistently higher than those of others caught during the same diel period (Fig. 13). Bluegill longer than 100 mm, largemouth bass longer than 100 mm, carp, and pumpkinseed had median body temperatures above 30 C during the afternoon; in contrast, afternoon medians for yellow bass, black crappie, rock bass, and yellow perch were below 29 C. Ex-

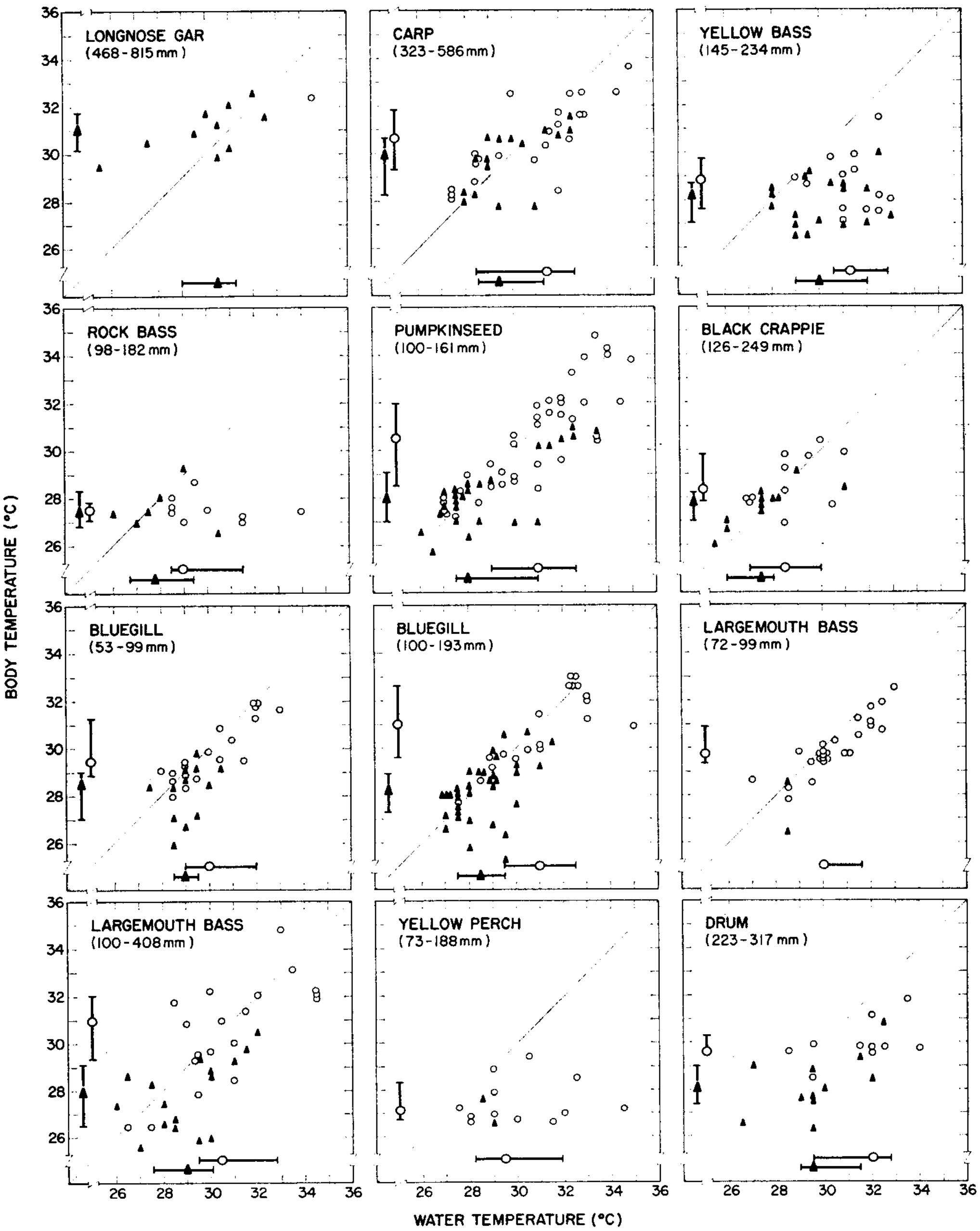


FIGURE 12.—Body temperature of fish and water temperature (0.5 m depth) at the place of capture for each fish caught in the outfall area during afternoon (open circle) and at night (filled triangle), August 1970. Distributions of body and water temperature are summarized near the respective axes by medians (large open circles and filled triangles for afternoon and night, respectively) and interquartile ranges (lines extending from medians).

cept for longnose gar and carp, with median body temperatures of 31.0 and 29.8 C, respectively, median fish temperatures at night were between 28.4 and 27.8 C, being highest for smaller bluegill and lowest for rock bass.

At night, both fish and 0.5-m temperatures were lower than in the afternoon; in fact, sample medians were lower at night in every case. Comparison of 95% confidence intervals for the medians indicated that body temperatures of five species at night were significantly lower than during the afternoon—bluegill, largemouth bass, pumpkinseed, black crappie, and freshwater drum. However, median water temperatures at points of capture decreased significantly from afternoon to night only for larger bluegill and for pumpkinseed.

Intramuscular temperatures depended primarily on the environmental temperatures a fish experienced during some short time interval (probably less than 30 min), ending at the moment of capture. Two other sources of variation may have influenced body temperatures: metabolic heat production and thermal exchange with the environment after capture. Because of muscular thermogenesis, core temperatures of fishes can exceed the temperature of the water in which they live (Barrett and Hester 1964; Carey and Teal 1969a, 1969b; Stevens and Fry 1970). Only active large fishes such as tunas and pelagic sharks maintain body temperatures several degrees warmer than their environment, but even *Tilapia mossambica* weighing only 40 to 200 g were about 0.5 C warmer than the 22–24 C water bath in which Stevens and Fry (1970) kept them. Larger fishes we caught, such as 5- to 8-kg carp, probably had body temperatures no more than 1 C above ambient temperature. Change in body temperature from the time a fish was stunned until its temperature was measured probably amounted to less than 0.5 C, even for smaller specimens. Despite the two sorts of potential error, intramuscular temperatures probably estimated within 1 C the exponentially smoothed average of each specimen's "recent" thermal experience.

Body temperatures were a better measure than capture temperature of where in the thermal environment fish actually lived. Variation of water temperature with depth rendered capture temperature a poor estimator of the temperatures experienced by some fishes, particularly those that lived near the bottom—yellow bass, rock bass, yellow perch, and freshwater drum (Fig. 13). Yellow bass, which concentrated near the discharge jets, actually lived in relatively cool water near the bottom. In contrast, longnose gar spent much of their time near the surface at temperatures higher than those recorded at 0.5 m. Several individual longnose gar, carp, and largemouth bass were 1–3 C warmer than the water from which they were caught (Fig. 12); these fishes must have moved horizontally from warm water into cooler water just prior to capture. Similarly, relatively low body temperatures of some specimens taken in the outfall area (particularly at night) suggested recent emigration from cool, deep water outside the outfall area.

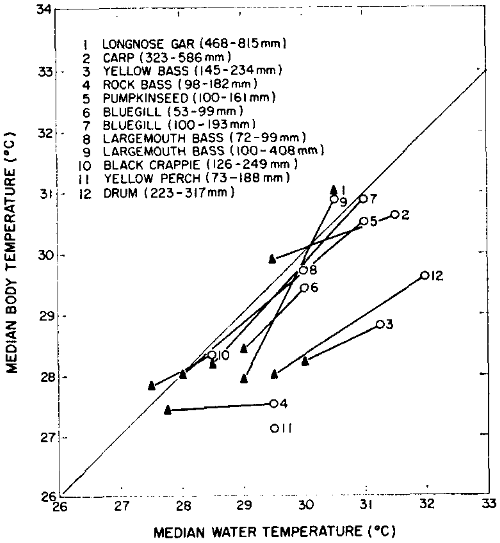


FIGURE 13.—Median body temperature of fish and median water temperature (0.5 m depth) at the places of capture for each of 10 species of fishes caught in the outfall area during afternoon (open circle) and at night (filled triangle), August 1970. This figure summarizes data from Figure 12.

The nocturnal decrease in both body temperatures of fish and water temperatures where they were caught was attributable to several causes:

(1) The outfall area in general was about 1.5 C cooler at night than in the afternoon.

Thus, had the fish simply maintained the same spatial distributions at night as during the day, they would have been cooler at night. However, median body temperatures of large bluegill, large largemouth bass, and pumpkinseed were more than 2.5 C lower at night than during afternoon, differences too large to have been produced wholly by nocturnal cooling of the outfall area without changes in fish distribution.

(2) Some fishes moved away from the jets into cooler water at night; large bluegill exhibited this distributional pattern. Young largemouth bass were abundant near the jets, particularly Js, during the afternoon, but they were rarely encountered anywhere in the outfall area at night.

(3) Some fishes may have stayed nearer the bottom at night than during the day. Adult largemouth bass and pumpkinseed were occasionally seen resting inactively on or just above the bottom at night; both species swam at mid-depths during afternoon. Even in water only 1 m deep, a fish that descended from 0.5 m to the bottom could have encountered temperatures as much as 3 C lower (Fig. 4).

(4) Decreased body temperatures at night could have resulted from a nocturnal increase in the rates at which fish swam into and out of the outfall area. Fishes swimming into warmer water of the outfall area would have warmed gradually at rates inversely proportional to body size. If results obtained by Stevens and Fry (1970) for *Tilapia* are applicable to the similarly proportioned bluegill, a 150-g fish (about 190 mm long) would have warmed to only 29 C six min after it had moved from 25 C water into 30 C water. In theory, then, recent immigrants would have had lower muscle temperatures than fish that had lived at the same elevated temperatures for a longer time. It is unlikely, however, that any nocturnal increase in fish movements could have been so drastic as to have shortened average residence times to the requisite level, ca. 10 min or less.

Therefore, that fish and capture temperatures were lower at night than during the day is attributed primarily to (1) a general decrease in temperature of the outfall area at night, (2) movements of fishes away from the jets at night, and (3) a tendency for fishes to stay nearer the bottom at night. Whereas processes (1) and (2) would have lowered both fish and capture temperatures, process (3) would have caused reduction in fish temperatures but not capture temperatures.

With the exception of Trembley (1960), other students of temperature distributions of freshwater fishes have not measured body temperatures but have relied instead on water temperatures measured where fishes were caught. Trembley measured gut temperatures of fishes caught in the outfall area of a power plant on the Delaware River, Pennsylvania. Fishes were caught by seining or hook and line; then, a mercury thermometer was inserted into the stomach by way of the mouth or anus. Although few data were presented for fishes living in the discharge lagoon, gut temperatures were graphed for about 50 fishes caught during June by hook and line approximately 500 m downriver from the discharge point. Brown bullhead and smallmouth bass were about 21–23 C (normal river temperature) during early morning before the power plant came on load, but gut temperatures of brown bullhead, smallmouth bass, and white catfish caught during midafternoon were 27–32 C. No river temperatures were given for the fishing location, but the effluent temperature was 39 C.

Temperature Acclimation Levels of Age 0 Bluegill

Age 0 bluegill were by far the most abundant group of fishes in the littoral zone during summer. However, no data on their temperature distribution were provided by the survey of body temperatures because small body sizes precluded effectual measurement of internal temperatures. Therefore, to evaluate the temperatures experienced in the outfall area by age 0 bluegill, we estimated their levels of temperature acclimation by heat resistance tests.

Young bluegill, 20–70 mm long, were caught by 10- to 20-m-long runs with the push net (no electroshock) from locations at both sides of both jets. One sample of 50–60 fish was obtained from each of the four locations during early afternoon on each of five successive dates, 31 August–4 September 1970.

The fish were transported to the laboratory and held overnight in styrofoam containers filled with Lake Monona water from outside the outfall area. During this time, the water temperature in the containers changed from 23–26.5 C to ambient temperature in the laboratory, 21.5–24.0 C. The thermal experience of the fish after capture was always at or below the minimum temperature recorded at capture.

On the day following capture, about 20 fish from each sample were transferred to a lethal temperature bath at 36.5 ± 0.05 C. Each bath contained 25 liters of continuously aerated water from Lake Mendota (which discharges into Lake Monona through a 1.3-km segment of the Yahara River). Resistance time, i.e., the time between entry into the bath and death (cessation of gill movement), was recorded for each specimen.

To relate resistance times of fish from the outfall area to their level of temperature acclimation, the resistance time distributions for age 0 bluegill of known temperature acclimation were required. For this calibration, about 400 age 0 bluegill were collected from RII with several short runs of the push net (no electroshock) on the afternoon of 16 September 1970. Water temperature 0.5 m beneath the surface was 20 C. The fish were transported in styrofoam containers to the laboratory where half were put into each of two acclimation tanks; each tank contained 100 liters of continuously aerated and filtered Lake Mendota water at 22 C. Fifteen hours later the temperature of each tank was reset for 26.0 C. After 30 hr at 26.0 C, one tank was raised to 30.0 C; the other tank remained at 26.0 C. After 3 additional days, fish in the two tanks were assumed to be fully acclimated to temperatures at least as high as 26.0 and 30.0 C. Fish were randomly withdrawn from each tank for determination of their distributions of resistance time. As soon as the samples had been removed, the temperature of each acclimation tank was increased 1.0 C. On subsequent days, the temperature of each tank was increased a maximum of 1.0 C per day. Fish acclimated to 26.0, 27.0, 28.0, 29.0, 29.5, 30.5, and 31.0 C were tested from one tank; fish acclimated to 30.0, 31.0, 32.0, and 33.0 C were tested from the other. Temperatures in each acclimation tank varied less than 0.1 C about the set points.

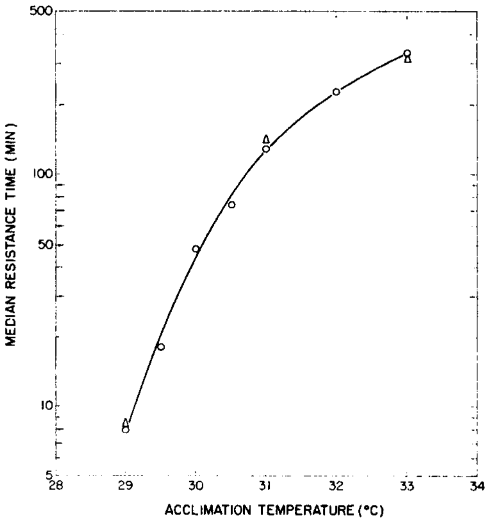


FIGURE 14.—Relationship of acclimation temperature and median time to death at a lethal temperature (36.5 C) for samples of 20 age 0 bluegill acclimated in the laboratory. Circles indicate samples held overnight at room temperature before resistance tests; triangles indicate samples tested immediately after removal from the acclimation temperature. The curve, fitted by eye to the circles, was used to estimate acclimation temperatures of fish from the outfall area (Fig. 15).

During acclimation, the fish experienced a 14-hr light period each day (0600–2000 CST) followed by 10 hr of darkness. Light was supplied by a 15-watt incandescent bulb centered about 15 cm above the surface of each tank. Photoperiod control circuitry provided "dawn" and "dusk" periods of about 1 hr (see p. 692).

The fish were fed at least once daily with living zooplankton, primarily *Daphnia* sp. from Lake Monona or Lake Mendota.

Fish were removed from the acclimation tanks about 0.5 hr after feeding, held overnight in styrofoam containers at ambient temperature (21–23 C), and then tested in the same manner as the fish of unknown acclimation. To determine whether substantial loss of acclimation occurred during overnight holding at ambient temperature, additional

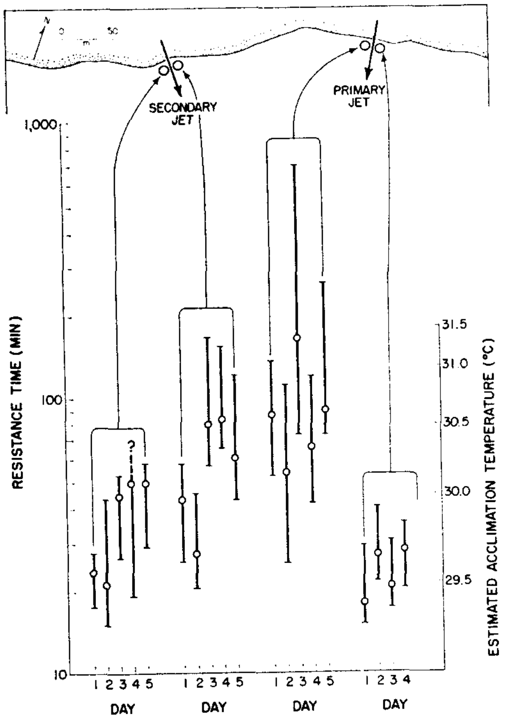


FIGURE 15.—Median (circle) and interquartile range (vertical line) of times to death at a lethal temperature (36.5 C) and estimated median acclimation temperature (circle) for each sample of about 10 age 0 bluegill from the outfall area, 31 August–4 September 1970. The data from each sample are grouped by location of sample collection and ordered within each group by date of sample collection (day 1 = 31 August, . . . , day 5 = 4 September).

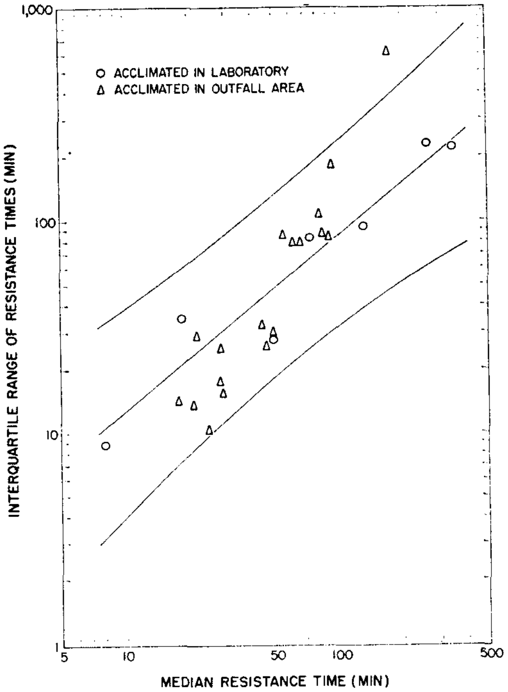


FIGURE 16.—Interquartile range of resistance time related to median resistance time for samples of age 0 bluegill acclimated to constant temperatures in the laboratory or collected from the outfall area. The middle line indicates the least-squares linear regression of log interquartile range on log median resistance time for laboratory-acclimated fish; the upper and lower lines bound the 95% parametric confidence interval about the regression line.

samples were tested immediately after removal from the acclimation tanks.

With the relationship between acclimation temperature and resistance time established (Fig. 14), we could proceed with evaluation of heat resistance data on age 0 bluegill tested directly from the outfall area.

Median times of heat resistance, ranked within dates, varied significantly among locations within the outfall area (Friedman two-way AOV; $p < 0.02$). Young bluegill collected between the two jets had longer resistance times than their counterparts caught on the same date from outside the respective jets (Fig. 15). Fish from each side of the primary jet differed more in heat resistance than those from each side of the secondary jet. Data from all locations and dates indicated that median heat resistance times were positively correlated (Kendall's $\tau = 0.44$; $p < 0.01$) with water temperature at the sites of fish collection. Water temperature within locations differed significantly among dates (Friedman two-way AOV; $p = 0.05$); median resistance times did not (Friedman two-way AOV; $p = 0.25$).

All samples of fish from the outfall area had median resistance times corresponding to those of fish acclimated between 29.4 and 31.3 C in the laboratory (cf. Figs. 14 and 15). Water temperatures at fish-collecting sites ranged from 25 to 36 C. Thus, age 0 bluegill at different locations in the outfall area were acclimated to temperatures constituting a narrow interval in the range of available habitat temperatures. Moreover, individual fish within each location were apparently acclimated to virtually the same temperature, because variation of resistance times within samples of fish from the outfall area did not differ greatly from variation within samples of homogeneously acclimated fish having corresponding median resistance times (Fig. 16).

Although all samples of bluegill from the outfall area had estimated acclimation temperatures within a 1.9 C interval, the four locations nevertheless yielded differently acclimated fish. The difference in acclimation between fish from the two sides of each jet implied that age 0 bluegill did not freely mingle across the jets, particularly the primary jet. The continuous, high velocity discharge from the primary outfall probably constituted a more effective barrier to alongshore movements of young bluegill than did the intermittent, diffuse flow from the secondary outfall.

Heat resistance of young bluegill from the outfall area was assumed to vary only with the time-temperature distribution they experienced up to the time of capture. Precise inferences about the distributions were not permitted by the heat resistance data because a given level of heat resistance could have resulted from any number of sequential combinations of temperature and exposure time.

However, evidence from the literature suggested that most thermal experience accumulated by the fish during the several days prior to capture occurred at or below the estimated acclimation temperature. Acclimation levels of brown bullhead in a small Ontario lake during summer were more similar to maximum (25–26 C) than to average (18–22 C) water temperatures (Brett 1944). Cutthroat trout (*Salmo clarki*) kept constantly at 20 C and at temperatures that cycled (square wave) from 10 to 20 C every 6 to 48 hr were almost equally heat tolerant (Heath 1963). Female mosquitofish (*Gambusia affinis*) in an experimental temperature gradient spent most of their time between 25.5 and 29 C, and the mean temperature of their distribution was about 27 C (Bacon, Neill, and Kilambi 1968). Even so, they were more heat resistant than fish acclimated to 28 C and probably had an average acclimation level of about 29 C (cf. Hart 1952).

If young bluegill in the outfall area behaved like the mosquitofish in their heterothermal environment, they probably spent most of the time at temperatures lower than their estimated acclimation temperatures. Periodic decreases in temperature within the outfall area (Fig. 3) would not have resulted in greatly decreased heat resistance levels because acclimation to a lower temperature occurs slowly (Brett 1944, 1946). Median resistance times of acclimated bluegill held overnight at temperatures 10 C below the acclimation temperature differed little from those of fish tested immediately after removal from the acclimation tank (Fig. 14).

Proximity of fishes' acclimation levels during summer to maximum habitat temperatures (and the persistence of attained levels despite drops in environmental temperature) Brett (1944) attributed to "a 'summation' in temperature adaptation in a field of varying temperatures." Summation, in Brett's usage, occurs because fishes' loss of tolerance to high temperatures proceeds slowly compared with rates of upward acclimation (Loeb and Wasteneys 1912; Brett 1944, 1946; Heath 1963). In habitats having upper or lower temperatures so extreme that fish avoid them, summation occurs only over the range of temperatures actually encountered and results in eventual acclimation to the temperature demarcating the limit of upper avoidance temperatures. Our data indicated that the upper limit for young bluegill in the outfall area was no higher than about 31.5 C.

BEHAVIORAL REGULATION OF TEMPERATURE BY FISHES IN THE LABORATORY

Introduction

To evaluate the extent to which temperature might govern distributions of fishes in the outfall area of Lake Monona, thermoregulatory behavior of representative species was investigated in the laboratory.

Temperatures preferred by fishes were determined by allowing specimens to behaviorally regulate the temperatures of tanks in which they lived; the experimental approach has been described by Neill, Magnuson, and

Chipman (1972). Temperature preference data were collected from young fish representing six species that differed among themselves in the temperatures at which they occurred during summer in the outfall area.

With additional experiments on two of the six species, we explored the behavior of fish in environments with food available at only one of two temperatures. The object of these experiments was to determine the extent to which fish might invade water warmer or cooler than the preferred temperature to get food.

General Equipment and Procedures

Each of 10 test tanks was a 50-liter fiber glass aquarium with one glass side; inside dimensions were 60 cm long × 30 cm wide × 30 cm deep. A double-walled partition of black (opaque) Plexiglas divided each tank into halves. A tube (40 mm inside diameter) of black polyethylene penetrated the center of the partition to form a 6-cm-long tunnel through which a fish could swim from one half of the tank into the other.

An electronic monitoring system sensed and recorded the time and direction of each pass of a fish through a tunnel. Sensing elements of each test unit were a pair of photocells in waterproof glass tubes. The photocells received light passing horizontally across the tunnel from a pair of light sources (red, about 6,500 Å) mounted in tubes that penetrated the tunnel's opposite wall. Interruption of a light beam by a fish caused a voltage drop through the photoelectric cell which, when amplified by transistors, produced a change in state of a bistable multivibrator. State of the multivibrator and its signal to an event recorder were determined by which light beam (right or left member of the pair) was last interrupted. Whether a fish passed completely through the tunnel or only entered the tunnel to then back out into the same side of the tank, the result of the action was correctly interpreted: After the move, the fish was in that half of the tank adjacent to the light beam last broken. A second channel of the event recorder was activated whenever either or both light beams were blocked, whether or not a change occurred in state of the multivibrator. The two channels together provided a continuous, unambiguous, and permanent record of a single fish's movements between the halves of each tank through time.

Each half of each test tank was supplied with the following basic equipment: (1) a compressed air diffuser for aerating and mixing the water; (2) one or more submersible aquarium heaters switched by a mercury contact thermometer through a solid state relay to precisely maintain above-ambient temperatures; (3) a coil of acrylic-coated copper tubing through which cold water could circulate to decrease ambient temperature; (4) a 0.5-liter polyethylene bottle (with holes, and the top half removed) which contained the cooling coil, heaters and air diffuser—an arrangement that increased the efficiency and precision of temperature control; (5) a truncated tetrahedron of clear, 3-mm-thick Plexiglas panes that formed a "funnel," the smaller end of which surrounded the mouth of the tunnel to facilitate location of the tunnel by the fish, especially during darkness; and (6) a 0.5-liter glass jar covered with black polyethylene film and laid on its side at the bottom of the tank to provide cover for the fish.

Except during tests, experimental fishes lived in 30- to 200-liter holding tanks. Submersible heaters switched by contact thermometers through solid state relays enabled precise (±0.1 C) control of temperature in some holding tanks. Other tanks had no temperature control equipment and fluctuated with ambient temperature (18–23 C). Cooling coils were not used in holding tanks.

The test and holding tanks were in a chamber fabricated from a wooden frame covered with black polyethylene film to exclude extraneous light. Each tank was illuminated by an incandescent bulb centered 15 cm above the water. The test tanks and 30- and 50-liter holding tanks were lighted by 15-watt bulbs; a 25-watt bulb lighted the single 200-liter holding tank. Illumination was controlled by capacitor-dimmer circuitry coupled to a 24-hr timer to provide a 14:10 photoperiod (the 1 August photoperiod at Madison) with "dawn" between 0600 and 0700 and "dusk" between 2000 and 2100 CST.

Only filtered (otherwise untreated) Lake

Mendota water was used in all tanks. Water in each tank was continuously aerated. Some water from each tank was exchanged for fresh water at least once every week for holding tanks, or once every 3 days for test tanks.

Maintenance of Environmental Temperature by Behavioral Thermoregulation

Experimental Technique and Procedures.—Eight of the 10 test tanks were modified to evaluate thermoregulatory performances of young fishes through the technique described by Neill, Magnuson, and Chipman (1972). The left-right signal from the monitor unit of each tank controlled heat transfer so that a fish could regulate temperature by dividing its time between halves of the tank. Passage of the fish into one side (e.g., right) of the tank caused that side to begin warming at 3 to 5 C an hour. Warming of the right side ceased only when the fish swam to the other side; then the right side began cooling at 3 to 5 C an hour. Temperature of the left side was kept 2 C lower than that of the right side by a comparator-relay circuit. Accordingly, the fish always had available alternative temperatures 2 C apart within the range 18–40 C. Sequential testing and choosing of one temperature over the other resulted in thermoregulation; thus, the fish served as its own thermostat.

In these experiments, a fish could maintain tank temperature in a "band" no narrower than 2 C, the differential between the two sides of the tank. A differential of 2 C was chosen for several reasons. In preliminary experiments in which the sides of a tank were set at constant temperatures 1 or 2 C apart, selection of one side over the other by bluegill and black crappie was more consistent when the difference was 2 C. This result was congruous with the observation by Moss (1970) that juvenile American shad (*Alosa sapidissima*) responded consistently to rapid temperature changes of 4 C but not to 1 C changes. A differential of 2 C was also more compatible with intrinsic comparator limitations than were smaller or larger differentials. Finally, larger differentials were difficult to manage because of heat flux problems.

Most young fishes placed in the tanks learned to swim through the tunnel within a few hours. During a training period of 3 to 7 days, maximum attainable temperature of the warmer side was limited to 22 C. On the last day of training, maximum attainable temperature of the warmer side was advanced to 30 C and then, 24 hr later, to 40 C. During all experiments, temperature of each side of each test tank was recorded from a thermistor once every 6 min by a multi-channel analog recorder.

The thermoregulatory performance of each subject was assessed from data collected on the second, third, and fourth days after maximum attainable temperature was set at 40 C. The temperature record for each fish was divided into day (0700–2000) and night (2100–0600) categories. For each diel period, upper and lower turnaround temperatures were tabulated for the 3-day trial. Upper turnaround temperatures were local temperature maxima recorded from the warmer side of the tank; lower turnaround temperatures were the local minima recorded from the cooler side of the tank (Neill, Magnuson, and Chipman 1972). If a subject made fewer than three passes through the tunnel during a day or night period, turnaround temperatures for that period were excluded from analysis.

Species tested were carp, rock bass, bluegill, largemouth bass, black crappie, and yellow perch. Carp were seined in October 1969 from an oxbow of the Wisconsin River, 20 km below Prairie du Sac-Sauk City, Wisconsin. Black crappie and largemouth bass were seined from Lake Mendota on 21 April and 23 August 1970, respectively. All other specimens were caught by seine or push net from Lake Monona between 15 August and 15 September 1970. All specimens were less than 1 year old when they were collected.

Thermoregulatory tests began on 6 August 1970 and ended 20 November 1970. Largemouth bass were placed in the test tanks the day after capture. All other specimens lived in the holding tanks at ambient temperature (20–22 C) for at least 15 days prior to tests. Carp and black crappie, both kept under uncontrolled light conditions for several months after capture, lived in the experimental light environment for more than 30 days before they were tested. Total lengths of specimens at the end of tests were carp, 81–97 mm; rock bass, 48–59 mm; bluegill, 53–83 mm; largemouth bass, 65–75 mm; black crappie, 75–88 mm; and yellow perch, 82–118 mm. The numbers of fish tested were 5 carp, 6 rock bass, 13 bluegill, 8 largemouth bass, 8 black crappie, and 17 yellow perch.

Fishes were fed once daily during holding and training and twice daily during thermoregulatory tests. Carp, bluegill, and yellow perch were fed pelleted food; black crappie were fed mealworms (*Tribolium* spp.); largemouth bass were fed small fishes. Rock bass ate pellets and mealworms in the holding tanks but received only pellets in the test tanks. Food was put into that side of each test tank in which the fish occurred at the moment of feeding.

Results.—Regulatory performance varied with species, individual specimen, and time of day. Sample records have been presented by Neill, Magnuson, and Chipman (1972). In terms of amount of temperature fluctuation allowed by individual fish, bluegill were the best regulators, yellow perch poorest, and the others intermediate. The specimen that kept its environmental temperature most nearly constant was a bluegill: On the first day of the trial, it kept the warmer side of the tank between 31.5 and 32.0 C from 0600 to 1400, between 31.7 and 33.0 C from 1400 to 1700, and between 32.2 and 32.5 C from 1700 to 2000.

Each species maintained its environmental temperature between limits different from those observed for one or more of the other five species (Fig. 17). Carp and bluegill performed similarly; both species maintained temperatures between 28.5 and 33.5 C. Largemouth bass regulated at temperatures lower than carp and bluegill but somewhat higher than rock bass and black crappie, both of which avoided temperatures lower than 25.5 C or higher than 30.0 C. Yellow perch avoided temperatures higher than 26.5 C; they kept their environment decidedly cooler than did any other species.

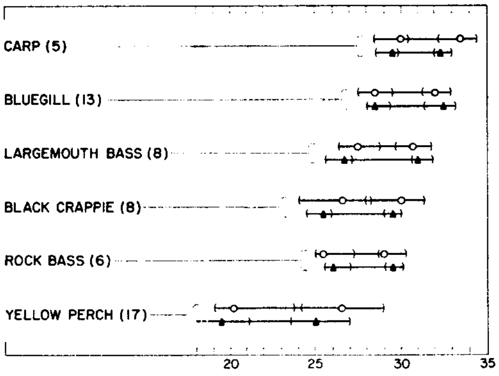


FIGURE 17.—Upper and lower turnaround temperatures for thermoregulating carp, bluegill, largemouth bass, black crappie, rock bass, and yellow perch. Medians during day and night are indicated by open circles and filled triangles, respectively. Parentheses about medians indicate the interquartile range of turnaround temperature. The number of fish tested is given in parentheses to the right of each species' name.

Whether or not yellow perch entered into the analysis, the species differed significantly among themselves in both upper and lower turnaround temperatures (Kruskal-Wallis one-way AOV; $p < 0.01$). Differences in regulatory performance among species were also supported by consideration of 95% confidence intervals constructed for median upper and lower turnaround temperatures (Neill 1971). Considering both day and night data and ignoring overlaps that were "small," a multiple-comparison test of confidence regions indicated the following groupings of the six species (in descending order from those regulating at highest temperatures):

1. carp ≅ bluegill ≅ largemouth bass;
2. largemouth bass ≅ rock bass ≅ black crappie;
3. yellow perch.

The exact probability level (Type I error) associated with the test could not be determined; it was probably somewhat greater than 0.05. (Problems relevant to multiple-comparison tests are discussed by Steel and Torrie 1960.)

A preferred temperature range could be defined for each species: the region of temperature bounded by the median upper and lower turnaround temperatures. The preferred temperature range for yellow perch was about 6 C wide. For the other five species, it was almost constant in width, about 3.5 C.

For no species was there a significant difference between day and night medians of either upper or lower turnaround temperature. However, the *variation* among regulatory performances of conspecific individuals did change from day to night; in each species, upper as well as lower turnaround temperatures were less variable at night than during the day (Fig. 17).

Activity, as measured by the frequency of tunnel passes, varied among species and, within species, between day and night (Table 5). Species maintaining highest temperatures were also most active. Never did any carp or largemouth bass, and only once did a bluegill or a rock bass, make fewer than 10 tunnel passes during 1 day or night; usually, each fish passed through the tunnel more than 10 times during each hour. The event records indicated that rock bass were more active than black crappie; however, the two species differed less in the proportion of cases in which fewer than 10 passes were made per period (Table 5). Yellow perch were less active than any other species. In several cases, yellow perch made few or no passes through the tunnel during the night (Table 5). Individuals of the other species made frequent tunnel passes after dark, although activity was reduced at night.

Discussion.—Activity level and thermoregulatory performance were not independent of each other. More active fish, for example bluegill, kept their environment warmer than did less active fish like yellow perch. Whether activity and thermoregulation were related as cause and effect, or effect and cause, could not be determined. However, lowered nighttime activity did not result in significant decreases in the median turnaround temperatures, even though the frequency distribution of temperature between the turnaround points probably shifted toward lower temperatures. (Lack of synchronization between event and temperature records often made it impossible to determine which temperature of a pair the fish experienced at any instant; therefore, frequency distributions of temperature could not be constructed.)

That median turnaround temperatures at night were less variable than those during the day could be attributed to decreased intensities of nonthermal stimuli at night or decreased tendency for fish to respond to nonthermal stimuli at night. In any case, position effects apparently decreased at night so that individuals of each species responded to temperature more homogeneously at night than during the day.

TABLE 5.—*Frequency distribution of tunnel passes by thermoregulating fish. Total of the cases in each row equals the number of specimens multiplied by 3, the number of test days*

Species	Diel period	Number of tunnel passes per diel period										
		0	1	2	3	4	5	6	7	8	9	⩾10
Carp	day	—	—	—	—	—	—	—	—	—	—	15
	night	—	—	—	—	—	—	—	—	—	—	15
Bluegill	day	—	—	—	—	—	—	—	—	—	—	39
	night	—	—	—	—	—	—	—	—	1	—	38
Largemouth bass	day	—	—	—	—	—	—	—	—	—	—	24
	night	—	—	—	—	—	—	—	—	—	—	24
Black crappie	day	—	—	—	1	—	—	—	—	1	—	22
	night	3	1	—	1	—	—	—	—		—	19
Rock bass	day	—	—	—	—	—	—	—	—	—	—	18
	night	1	—	—	—	—	—	—	—	—	—	17
Yellow perch	day	3	—	2	—	—	—	—	—	1	—	45
	night	16	2	5	2	1	—	—	—	2	—	23

The minimum possible width of the preferred temperature range was intimately related to activity of fish and to rate of heat exchange in the experimental system. The following equation approximated the relationship:

$$W = (r/f) + 2\,C$$

where, W = minimum width of range in degrees Celsius;
r = rate of temperature change;
f = frequency of tunnel passes.

Thus, to maintain a range width of 6 C in a tank whose temperature changed 4 C/hr, yellow perch must have moved at least once per hour. The other species, to maintain range widths of about 3.5 C, had to move at least 2.7 times per hour. Because many fish moved more frequently than 10 times per hour, temperatures could have been regulated more precisely than they were.

Turnaround temperatures were probably species-specific and independent of initial acclimation temperature. Each fish except largemouth bass was held at temperatures between 20 and 23 C before tests; yet, turnaround temperatures varied greatly among species. Acclimation probably increased rapidly during the 2 days preceding data collection. Within a few hours after we relinquished control of maximum tank temperature, most fish raised their environmental temperatures to the level maintained for the duration of the experiment. Investigations by Loeb and Wasteneys (1912), Sumner and Doudoroff (1938), Doudoroff (1942), Brett (1944, 1946), and Allanson and Noble (1964) suggested that our specimens should have been completely acclimated to their new thermal regimes within 1–3 days. So, after access to temperatures up to 30 C for 1 day and 40 C for an additional day, thermoregulatory behavior was presumably dictated by self-imposed acclimation levels which remained constant during the succeeding 3-day trial. There was no indication of consistent drift in thermoregulation toward either higher or lower temperatures during the trials.

Thermoregulatory performances of our fish were generally consistent with available information on their final temperature preferenda.[3] Published data are available for two of the six species; carp and yellow perch have final preferenda of 32.0 C (Pitt, Garside, and Hepburn 1956) and 24.2 C (Ferguson 1958), respectively. Ferguson (1958) cited unpublished manuscript values of 32.3 C for bluegill and 30–32 C for largemouth bass. All four species have final temperature preferenda somewhat nearer the upper than lower turnaround temperatures we recorded. Such asymmetry of turnaround temperatures relative to the final preferendum was not unexpected, because fishes typically prefer temperatures much nearer the upper than lower lethal levels (see data compiled by Fry 1964).

Effect of Food Availability on Behavioral Thermoregulation

When availability of food was independent of temperature, Lake Monona fishes of six species kept themselves within narrow intervals of environmental temperature. Further experiments with two of the species, bluegill and yellow perch, explored the extent to which behavioral thermoregulation might be altered by temperature-dependence of food availability.

Experimental procedures.—The 10 test tanks were modified so that fish gained access to food by spending time in one half of a tank but not in the other. Each tank was equipped with an automatic pellet feeder described by Neill and Byles (1972). The feeders dispensed food into one half (food side) of each tank about 25 cm from the tunnel mouth. Each 3-mm-long × 3-mm-diameter pellet fell into a small funnel, the tip of which was 3 cm beneath the surface of the water. When the pellet was wetted sufficiently to sink, it passed through the funnel tip and, unless intercepted by the fish, fell into a second small funnel. The latter funnel formed a throat into a 0.2-liter glass jar on the floor of the tank. Each pellet was available to the fish for about 2 sec while it sank through 15 cm of water between the funnels. Pellets not intercepted accumulated in the glass jar.

Each feeder was activated only while the fish was in the food side of its tank between 0700 and 1830 CST. A timer triggered a switch to supply power to all feeders potentially between 0700 and 1830. However, each feeder was energized during this 11.5-hr interval only while the fish was in the food side of the tank, the monitoring system only then closing the contacts of a relay to complete the circuit to the feeder motor. One pellet was dispensed for every 5 min the fish accumulated in the food side of its tank during the feeding period.

Three experiments were performed. In each experiment, temperature in the right side of each tank was the midpoint (Tp) of the preferred range determined from thermoregulatory tests described above. The left side of each tank was also maintained at Tp for a training period of 4 days; thereafter, the left side was either cooler or warmer than the right side.

In the first experiment, fish were offered food at temperatures above or below Tp (food

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[3] The final temperature preferendum (Fry 1947) is the temperature about which fish living in a temperature gradient will ultimately congregate, regardless of their previous thermal experience. Fry and others (see Fry 1964) have considered the final preferendum to be species-specific.

side = varied-temperature side). One fish acclimated to Tp was put into each test tank, both sides of which were maintained by contact thermometer at Tp for 4 days. During this period, the fish received only food dispensed by the feeder into the left side of the tank. After the last day of the training period, between 1830 and 2000, temperature of the left side was increased 2 C in five tanks and decreased 2 C in the other five tanks. The right side of all tanks remained at Tp. Thereafter, left-side temperature was progressively increased or decreased 2 C between 1830 and 2000 on each successive day.

The second experiment repeated the first, except that the feeders dispensed food into the right side of each tank (food side = preferred-temperature side). Thus, food was available at Tp between 0700 and 1830 each day but never at temperatures above or below Tp.

A final experiment allowed fish to choose on several consecutive days between Tp without food and a single temperature above Tp with food; the object of this experiment was to determine if the fraction of time fish spent in the food side might change after the first day at a varied temperature. One fish was put into each of five test tanks, both sides at Tp, with food dispensed on the left side (food side = varied-temperature side). At the end of the training period, temperature of the left side was increased to Tp + 4 C (bluegill) or Tp + 6 C (yellow perch). This regime was then maintained 6 days with no further changes in temperature.

Bluegill (63–93 mm long) and yellow perch (105–129 mm long) were used in these experiments because of their divergent preferred range midpoints—30 and 23 C, respectively. The same specimens served in all three experiments, except that (1) the five bluegill that had experienced temperatures above Tp in the first experiment were replaced, and (2) three yellow perch that died during the first experiment were replaced. During the 16 to 18 days between experiments, the fish lived in holding tanks at Tp. Fish were individually marked with fin clips after the first experiment to ensure that each specimen encountered the same sequence of thermal environments during the second experiment as during the first. Only those specimens that had not been exposed to temperatures exceeding Tp were used in the final experiment; this was accomplished by using fish that had, during the first and second experiments, been in test tanks whose left-side temperatures were decreased.

Experiment 1. Food available at nonpreferred temperatures.—When both sides of all tanks were at temperature Tp on the final day of training, the median bluegill and yellow perch spent about 73% and 43%, respectively, of the feeding period in the side whose temperature was to be varied (Fig. 18). Then, as temperature diverged from Tp, both species progressively spent less time in the side with varied temperature. Median time spent by bluegill in the side with varied temperature dropped to 50% of the initial level at about 26 and 33 C and to 5% at about 20 and 35 C (by interpolation, Fig. 18a). Thus, the rate of decrease for bluegill was somewhat steeper as temperature increased than as it decreased. For yellow perch, time in the side with varied temperature was more symmetric about Tp and decreased less abruptly than in the case of bluegill. At about 19 and 29 C, 50% reduction occurred; at about 14 and 33 C, 95% reduction occurred (by interpolation, Fig. 18b). Data were more variable among yellow perch than among bluegill.

Most bluegill and yellow perch reduced time spent at the varied temperatures by reducing both the frequency and duration of forays into the varied-temperature side of the tanks (Neill 1971). The number of forays per feeding period was highly variable among individuals within each species. Among yellow perch, inter-individual variation in number of forays tended to increase as temperature decreased or increased from Tp. But among bluegill, variation in the number of forays decreased at temperatures above Tp. Bluegill decreased duration of forays more abruptly at high temperatures than at low temperatures. In the 8 C interval, 30 to 22 C, forays briefer than 0.5 min increased from 8% to 50% of the total number, but in the 8 C interval above Tp, 30 to 38 C, forays less than 0.5 min long increased from 7% to 95% of the total. Yellow perch may have actually increased foray duration at moderate departures from Tp (–2,

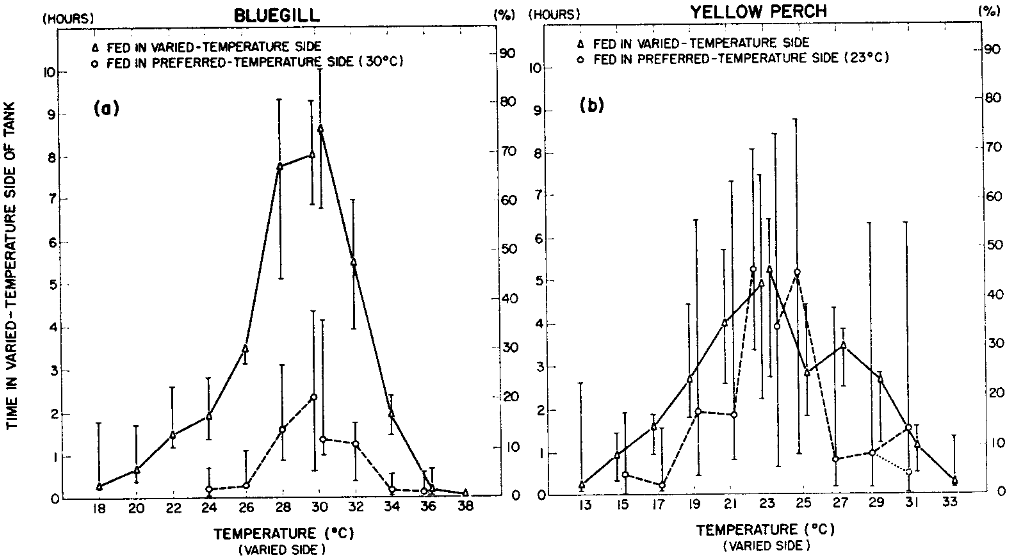

FIGURE 18.—Time spent in the varied-temperature side of tanks by bluegill (a) and yellow perch (b) fed in the side with varied temperature or in the side with the preferred temperature, Tp. Medians are given by point symbols; vertical lines about medians indicate interquartile ranges for samples of three to five fish.

+6 C), but at more extreme temperatures they made increasing proportions of very brief forays. The few yellow perch that increased the number of forays at extreme temperatures (causing increased inter-individual variation in number of forays) did so by making forays of short duration, i.e., less than 0.5 min.

Three yellow perch died during the experiment; all were in tanks with increasing temperature in the varied side. One jumped out of the 23 C side of its tank when the varied-temperature side was 31 C. The other two were found dead in the varied-temperature side of their tanks; tank temperatures were 35–23 C in each case. Both fish last entered the 35 C side during darkness (2021 and 2235 hr). They presumably died because of overexposure to 35 C, a temperature above the upper lethal limit for yellow perch (Fry 1964).

Experiment 2. Food available at the preferred temperature.—When both sides of each tank were at temperature Tp, the median bluegill and yellow perch spent about 16% and 40%, respectively, of the feeding period in the side whose temperature was to be varied (Fig. 18). If allocation of time under initial temperature conditions in this experiment was the same as in the first, the median bluegill spent 73% of the feeding period in the side with food and 16% in the side without food, whereas the median yellow perch spent almost equal time in the sides with and without food—43% and 40%, respectively. The remainder, 11% for the bluegill and 17% for the yellow perch, could be attributed to time the fish spent resting in the tunnels; these percentages were consistent with tunnel time estimated from the event-chart records.

As in the first experiment, time spent by fish at the varied temperature decreased as it decreased or increased from Tp (Fig. 18). As the varied temperature diverged from Tp, time spent by bluegill in the varied side remained dramatically below that during the first experiment. Although the difference between experiments was less marked with yellow perch than with bluegill, median times of yellow perch at temperatures above and below Tp were also significantly lower during this experiment than in the first (one-tailed Wilcoxon test; $p = 0.05$).

Responses of yellow perch were generally more varied during this experiment than in the first, and medians of time in the side with varied temperature fluctuated about the trend relating time to temperature (Fig. 18b). Among yellow perch in tanks with increasing temperature was one fish that consistently spent more than 75% of its time in the warmer side. The aberrant response of this fish affected median time most on the final day of the experiment (varied side at 31 C); on that day, another fish had to be excluded from analysis because the preferred-temperature side of its tank was potentially 3 C too warm during the first 3.5 hr of the feeding period. If data from the excluded fish were considered acceptable, median time at 31 C was reduced from 13% to 4% of total time (dotted circle, Fig. 18b).

In neither species was there a substantial change during this experiment, as compared with the first, in the *rate* at which time at the varied temperature decreased as that temperature diverged from Tp (Fig. 18). However, bluegill and yellow perch did spend more time at nonpreferred temperatures when food was available only at those temperatures than when food was available only at the preferred temperatures. When fed at the preferred temperatures, bluegill and yellow perch spent less than 5% of their time at temperatures outside the ranges 26 to 34 C and 17 to 31(?) C, respectively. These ranges were greater, 18–36 C for bluegill and 13–33 C for yellow perch, when food was not available at preferred temperatures.

As in the first experiment, each species generally reduced both number and duration of forays into the varied-temperature side as its temperature diverged from Tp (Neill 1971). In this experiment, however, differences between the experimental groups under initial temperature conditions prevented further interpretation of the foray data. Those bluegill and yellow perch destined to experience decreased varied-side temperatures made fewer and longer forays than the other experimental group during the final day at Tp. Perhaps the difference between groups was due to their different histories. All fish to be exposed to decreasing temperatures had been used in the first experiments, but all the bluegill and three of five yellow perch which were to experience increasing temperatures were naive in that they had not previously encountered food in any but the preferred-temperature side of the tank, nor had they experienced a temperature differential between sides.

Initial differences in foray behavior during the second experiment did not result in substantially different distributions of total time between tank halves. Time in the side whose temperature was to be varied did not differ significantly between experimental groups under initial temperature conditions in either of the two experiments with either species (Mann-Whitney U-test; $p > 0.6$ in each case). Similar allocations of total time were possible despite differences in foray behavior, because an inverse relationship existed between foray frequency and duration. Thus, two fish under identical conditions of temperature and food distribution tended to accumulate similar amounts of time in the varied-temperature side of the tank even though one made many short forays whereas the other made fewer but longer forays.

Experiment 3. Food available for six consecutive days at a nonpreferred temperature.—Time in the side whose temperature was to be varied did not differ significantly under initial temperature conditions from that observed in the first experiment (Mann-Whitney U-test; $p > 0.8$ for each species); median percentages of time were 76% for bluegill and 41% for yellow perch (Fig. 19). On the second day after varied-side temperature was increased to 34 C for bluegill and 29 C for yellow perch, time at the varied temperature decreased to levels similar to those observed in the first experiment (Mann-Whitney U-test; $p > 0.3$ for each species). (A decrease occurred on the first day, but difficulties with temperature control made the data unreliable.) Median times of neither species changed significantly during the remainder of the experiment (Kruskal-Wallis one-way AOV; $p > 0.9$ for each species). However, variability of time allocation among yellow perch may have increased toward the end of the experiment.

Lack of change in time spent at the varied temperature during the final 5 days of the experiment suggested that all potential adjustment to temperature heterogeneity may have been effected by the second day after varied-side temperature was raised from Tp. Al-

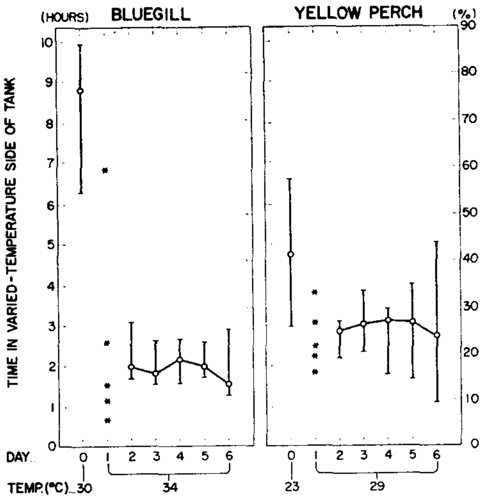

FIGURE 19.—Time spent in the varied-temperature side of tanks, at the preferred temperature (Tp) for 1 day and at a temperature higher than Tp for 5 subsequent days, by bluegill and yellow perch fed in the varied-temperature side when the other side was continuously at Tp. Sample size was three to five fish in each case; medians are indicated by circles and interquartile ranges by vertical lines. Data during the first day (day 1) at temperatures higher than Tp were considered unreliable because of temperature-control problems; the amounts of time each bluegill and yellow perch spent in the varied-temperature side of the tanks during day 1 are indicated by asterisks.

though temperature-acclimation levels of fish at the end of the experiment must have been higher than at the beginning, the data did not offer evidence for or against dependency of time at the nonpreferred temperature on acclimation level. If time allocation did depend on level of temperature acclimation, complete acclimation to 34 C in bluegill and 29 C in yellow perch may have occurred during the first day after these temperatures became available.

Discussion.—Bluegill and yellow perch responded similarly when allowed to partition their time in an environment of two parts—one with temperature Tp and the other with a temperature which increased or decreased from Tp at 2 C/day. Each species decreased the proportion of time spent at the alternative temperature as it diverged from Tp. This response occurred whether food was available at Tp or at the alternative temperature.

However, a larger proportion of time was spent at any alternative temperature when food was available only at that temperature than when food was available only at Tp. Conversely, temperatures of the alternative environment diverged farther from Tp before fish which were fed there reduced occupancy to the same proportion of time as fish fed at Tp. Alternative temperatures at which bluegill and yellow perch spent at least 5% of the feeding period spanned 8 and 14 C when food was available at Tp but 18 and 20 C when food was available at the alternative temperatures.

Although availability of food clearly biased the distribution of each species at extreme temperatures, only bluegill elected to spend a disproportionately large fraction of time in the compartment with food when both halves of the tank were at temperature Tp. The time so spent—about 70% of the feeding period—was much more than necessary to keep the stomach filled with food, even if the efficiency of pellet interception was only 50%. (Bluegill fasted for 24 hr intercepted and ate as many as 12 consecutively dispensed pellets; so, the efficiency of "hungry" fish may have been considerably greater than 50%.) A fish of median weight (10 g bluegill; 12 g yellow perch) gained potential access to its maximum daily meal[4] by spending only about 15% of the feeding period in that half of the tank with food.

Temperature did eventually limit each species' acquisition of a maximum daily meal. Bluegill did not obtain a maximum daily meal at temperatures below 24 C or above 34 C; temperatures limiting acquisition of a maximum daily meal for yellow perch were 17 C and about 30 C.

Acclimation of fishes to an increase in temperature occurs much more rapidly than acclimation to a decrease of equal magnitude (Loeb and Wasteneys 1912; Brett 1944, 1946;

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[4] Maximum daily meal, as used here, was the largest quantity of pellets a fish could consume during 11.5 hr, given that most of the food was digested at or near Tp. The maximum daily meal of both species was assumed to be about 4% of body weight. On occasions when individual fish consumed all pellets dispensed during a feeding period, the maximum amounts eaten by a bluegill and a yellow perch were 4.2% and 4.0%, respectively, of body weight.

Heath 1963). Moreover, upward acclimation over a temperature interval of given length proceeds more rapidly the higher the end-point temperature (Brett 1946). Therefore, acclimation levels of fish that experienced increasing temperatures in these experiments may have kept pace with the 2 C/day temperature rise. In contrast, acclimation levels of fish in tanks with decreasing temperature probably remained near Tp throughout the experiments because the time spent at low temperatures was unlikely to have been sufficient for much downward acclimation.

If acclimation states were as supposed, thermal stresses governing time spent in food environments with increasing and decreasing temperature were of different types. Time spent at temperatures increasing from Tp became much reduced when those temperatures approached the ultimate incipient upper lethal limits, 35 C for bluegill and 32 C for yellow perch (Fry 1964); above these temperatures, each species spent less than 5% of time. But, both bluegill and yellow perch curtailed time to less than 5% when decreasing temperatures were still several degrees above the lower lethals for Tp-acclimated fish—about 12 C for bluegill (Hart 1952) and probably less than 4 C for yellow perch (Fry 1964). Thus, bluegill and yellow perch were practically excluded from environments with food when temperatures exceeded the ultimate upper lethals or when temperature dropped about 10 C below the acclimation temperature, Tp. In the case of increasing temperature, exclusion was apparently caused by the fishes' absolute inability to acclimate to temperatures above the lethal limits. At decreasing temperatures, however, the limits were apparently set by fishes' unwillingness to endure nonlethal stresses imposed by temperatures several degrees below the acclimation levels.

Although neither species spent much time at temperatures above the upper lethal limits, the median bluegill and yellow perch that were fed at increasing temperatures did make about 20 and 40 forays, respectively, into water 3 C above the upper lethal temperature. These fishes would have died within a few hours had passage back into the Tp environment been prevented during a foray. Perhaps the two yellow perch that died at 35 C during the first experiment were prevented from returning to 23 C by their decreased ability, in darkness, to find the tunnel.

Midpoint of the preferred temperature range, 30 C for bluegill and 23 C for yellow perch, was confirmed as a reasonably accurate estimate of the preferred temperature. Had a temperature 2 C above or below Tp been preferred over Tp, the fraction of time spent in the alternative environment at that temperature should have increased over that when both environments were at Tp. No substantial increase was observed in any of the experiments. That is, relative to an environment at Tp but without food, no combination of temperature and food was preferred over Tp with food. Also, relative to an environment at Tp with food, no temperature without food was preferred over Tp without food.

Only bluegill spent more time at some temperatures if food was offered there than at Tp without food. If 11% of each feeding period was spent in the tunnel, then the fraction of time spent in the compartment with food was not reduced to equal that spent at Tp without food (44.5%) until the temperature of the food compartment decreased to about 27 C or increased to 32 C. In this sense, the environment preferred by bluegill was shifted 3 C downward and 2 C upward from the preferred temperature by the availability of food in that environment when no food was available at the preferred temperature.

INTEGRATION AND CONCLUSIONS

Distribution of Lake Monona Fishes Relative to the Outfall Area

Lake Monona fishes were diversely distributed within the littoral zone. Some fishes regularly avoided the outfall area; these were yellow perch, mottled sculpin, subadult yellow bass, and subadult black bullhead. Others were occasionally or usually concentrated in the outfall area relative to reference areas—longnose gar, large carp, large yellow bass, young rock bass, young pumpkinseed, bluegill, and largemouth bass. Still other fishes, even though some were caught in relatively large numbers, could not be placed with conviction in either group. Among these were subadult carp, large pumpkinseed, black crappie, Iowa darter, and logperch. Thus, distributions varied not only among species but also among size classes within some species.

Distributions of fishes also differed among seasons and, within seasons, between day and night. Kinds, sizes, and numbers of fish fluctuated throughout the littoral zone. However, the abundance of most fishes in the outfall area approximated a constant ordinal relationship to their abundances in reference areas from season to season and from day to night. Although several fishes (e.g., yellow bass, bluegill, largemouth bass) tended to be more uniformly distributed at night than during afternoon, no size class of a species was significantly more abundant in one area during the afternoon but in another at night. In only two cases were there significant seasonal reversals in the ordinal relationship between areas. Small bluegill were more abundant in the reference areas during November 1968 but in the outfall area during most other seasons. Small black crappie were more abundant in the outfall area during summer 1968 but in the reference areas during summer 1969.

Fish Distribution, Temperature, and Behavioral Thermoregulation

Results of the different research phases argued jointly that the varied distributions of fishes among outfall and reference areas during summer primarily reflected different behavioral responses to temperature. The lines of evidence supporting this conclusion are listed and discussed below.

1. During summer, fishes in the outfall area were generally not uniformly distributed with respect to temperature, and different fishes tended to be most abundant within different ranges of available temperature.

Catch/effort from 50-m transects indicated that fishes were not equally abundant at all temperatures and that some fishes occurred at higher temperatures than others. More accurate description of temperatures experienced by outfall-area fishes was permitted by measurements of their body temperatures.

Measurement of body temperatures confirmed partial segregation among species with respect to temperature. During afternoon, median body temperatures of carp, pumpkinseed, bluegill, and largemouth bass were above 29 C, while those of yellow bass, rock bass, black crappie, and yellow perch were below 29 C. At night, only longnose gar and carp had median body temperatures above 29 C, whereas yellow bass, rock bass, pumpkinseed, bluegill, largemouth bass, and black crappie had median body temperatures below 29 C.

2. During late summer, young bluegill at different locations in the outfall area were acclimated to temperatures within a narrow interval of the available range.

Fish collected on five dates from four locations within the outfall area had estimated acclimation temperatures between 29.4 and 31.3 C even though water temperatures varied between 25 and 36 C at the collection sites. To have attained acclimations between 29.4 and 31.3 C, young bluegill must have spent a majority of time at or below these temperatures and almost no time above 31.5 C.

This conclusion was in substantial agreement with the distribution of body temperatures observed for slightly larger young bluegill. The highest body temperature among 31 specimens was 31.8 C; the interquartile range of body temperatures was 28.8 to 31.2 C during afternoon and 27.0 to 29.0 C at night.

3. The more abundant a species was in the outfall area relative to reference areas during summer, the higher were the temperatures in the outfall area at which representatives of that species occurred during summer.

During summer, median body temperatures of fishes in the outfall area were positively correlated (parametric $r = +0.75$) with concentration of those fishes in the outfall area relative to reference areas (Fig. 20). The correlation was highly significant ($p < 0.01$) despite probable variation introduced by measuring body temperatures in 1970 and abundances in 1968 and 1969.

Not only did fishes that were concentrated both day and night in the outfall area live there at higher temperatures than representatives of groups that were never concentrated in the outfall area (e.g., large carp vs. large rock bass), but also diel changes in the distribution of other fishes were accompanied by

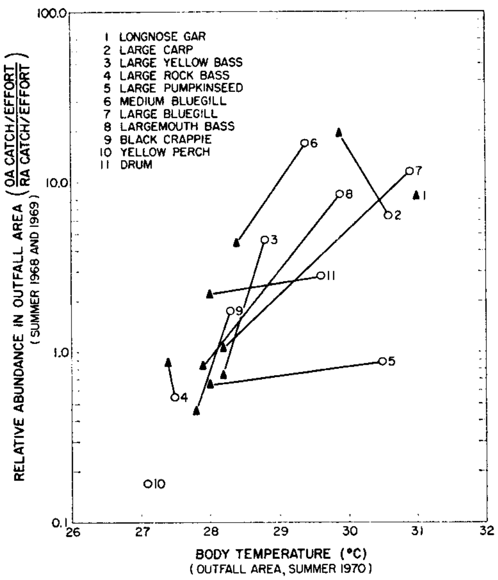

FIGURE 20.—Relative abundances of fishes in the outfall area during summer 1968 and 1969 compared with their median body temperatures in the outfall area during summer 1970. Data collected during afternoon and evening are indicated by open circles and filled triangles, respectively. The ordinate value of each point is the geometric mean of the values for 1968 and 1969 if data were obtained in both years (see Fig. 8).

changes in the temperatures they occupied in the outfall area (Fig. 20). Large yellow bass, medium and large bluegill, and largemouth bass were concentrated in the outfall area during afternoon but were more evenly distributed at night; within the outfall area, these fishes occurred at higher temperatures during afternoon than at night. There was little diel change in outfall-area temperatures occupied by large carp and large rock bass, whose interareal distributions remained similar from day to night.

Only large pumpkinseed during afternoon deviated markedly from the apparent relationship between body temperature and concentration in the outfall area (Fig. 20). During afternoon, large pumpkinseed occurred in water about 2.5 C warmer than was consistent with their position in the array of relative abundances. Many of these fish, including those with highest body temperatures, were caught in or near the discharge jets, to which they may have been attracted by factors other than temperature. At night, large pumpkinseed did not aggregate near the outfalls and had a median body temperature of 28 C, the same as other fishes in similar relative abundance.

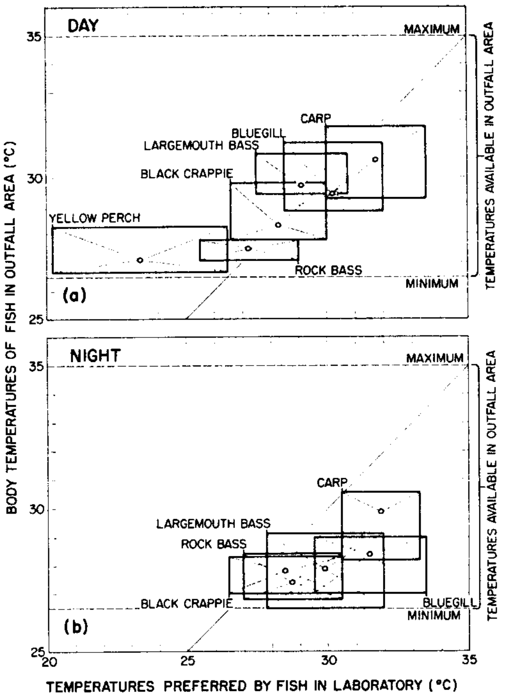

FIGURE 21.—Body temperatures of fishes in the outfall area in August 1970 compared with temperatures they maintained by behavioral thermoregulation in the laboratory; (a) day, (b) night. A circle indicates the median body temperature and midpoint (Tp) of the preferred range of temperature for each species. Rectangles indicate, vertically, interquartile ranges of body temperature and, horizontally, the preferred range of temperature. (The preferred range is limited by median upper and lower turnaround temperatures.)

4. Diurnal temperature distributions of six species in the outfall area during August conformed to the distributions of temperature they maintained by behavioral thermoregulation in the laboratory (Fig. 21a).

Those fishes that regulated at higher temperatures in the laboratory occurred at higher temperatures in the outfall area. Moreover, all species except yellow perch had median body temperatures in the outfall area within 1.2 C of the midpoint of the preferred range in the laboratory.

Yellow perch avoided the outfall area; they were never more than 0.15 times as abundant there as in the reference areas. The few individuals that did occur in the outfall area lived in water that was the coolest available but still warmer than the upper turnaround temperature, 26.5 C. There was little water anywhere in the littoral zone cooler than 26.5 C in August 1970.

Nocturnal temperature distributions of five species (only 2 yellow perch were caught at night) were correlated somewhat less well with thermoregulatory limits than were diurnal distributions (Fig. 21b). Some fishes in the outfall area, notably bluegill and largemouth bass, occurred at temperatures lower at night than during afternoon. While laboratory fish may have spent more time near the lower turnaround temperatures at night than during the day, turnaround temperatures remained the same from day to night and did not, therefore, reflect any downward shift in average temperatures the fish maintained.

Temperature distributions of fishes in the outfall area were assessed from specimens generally larger than those used in the thermoregulation experiment. Only the comparisons for bluegill, largemouth bass during the day, and yellow perch could be based on fish of similar size. In the other cases, few or no field data were collected from specimens as small as those convenient for use in experiments.

Considering that field and laboratory data were reasonably consistent despite variation in the sizes of fish compared, the following conclusion was suggested: The different temperature distributions of six species within the outfall area resulted from species-specific behavioral thermoregulation.

Coutant (1970), in a review of both published and unpublished literature on reactions of fishes to heated discharges, did not cite empirical evidence that fish distributions in outfall areas correspond with their thermoregulatory performances in experimental temperature gradients.

Ferguson (1958) has examined his and other data in what has been the only systematic attempt to test agreement between distributions of fishes in unheated waters and the temperatures they prefer in the laboratory. For species with lower preferenda (three salmonids, one coregonid), laboratory and field data were in substantial accordance; however, largemouth bass, smallmouth bass, and the burbot (*Lota lota*) preferred temperatures in the laboratory about 3, 6, and 10 C higher than the respective temperatures at which they occurred most frequently in lakes during midsummer. Fingerling and larger yellow perch had final preferenda of 24 and 21 C, respectively; field observations indicated that adult yellow perch live at about 21 C during summer. Largely on the basis of the data for yellow perch, Ferguson (1958) argued that fishes with higher preferenda—such as the two basses and the burbot—prefer the same temperatures in laboratory and field, but smaller individuals prefer temperatures higher than do adults; thus, the discrepancy between field and laboratory information reflected use of young fish in determination of preferenda, whereas field data were derived mainly from older fish.

Variation in preferenda of yellow perch, which Ferguson attributed to size or age, may instead have resulted from seasonal effects. Data from fingerlings were collected during summer, but older fish were tested in winter. Both the temperatures tolerated (Hoar 1955; Hoar and Robertson 1959; Neill 1967) and preferred (Sullivan and Fisher 1953; Neill 1967) by fishes may fluctuate seasonally, perhaps in correspondence with changing photoperiod. Temperature tolerances of some fishes also vary with size (Hart 1947; Hagen 1964; Neill, Strawn, and Dunn 1966; Coutant 1970), but an unequivocal effect of size, *per se*, on final temperature preferendum has not been demonstrated experimentally for any fish.

Explanations not based on a size effect may account for the discrepancies noted by Ferguson (1958) between final preferenda and fish distributions in nature. First, temperature preferenda of some fishes may exceed maximum temperatures available in unheated habitats. Second, field data reviewed by Ferguson (1958) were based partly on net catches at night, when, as present results have indicated, some fishes do occupy waters cooler than the final preferendum. Third, the final temperature preferendum may correspond more closely to the upper limit than to the lower limit of the preferred range of temperature.

In summary, major features of the littoral distributions of Lake Monona fishes during summer were consistent with the following explanation: Temperature was a major factor governing fish distribution, in that fish tended to be most abundant in that part of the habitat having temperatures within or nearest a species-specific preferred range of temperature determined in the laboratory. Disparate distributions of some conspecific fish of different size resulted from the influence of factors other than size-related differences in preferred temperature.

Fish Distribution and Nonthermal Factors: Food, Predators, Currents

Temperature has been almost universally regarded as the primary factor governing the use of outfall areas by fishes (Dryer and Benson 1957; Trembley 1961; Alabaster 1964, 1969; Alabaster and Downing 1966; Mihursky 1967; de Sylva 1969; Mount 1969; Allen, Boydstun, and Garcia 1970; Gammon 1970). In general, distributions of Lake Monona fishes in conjunction with laboratory results supported the hypothesis of thermal primacy.

However, some aspects of the distributions of Lake Monona fishes indicated the influence of factors other than temperature. Spatial segregation of young and adults of two species, carp and yellow bass, probably did not reflect size differences in preferred temperature. Adult carp were concentrated in the outfall area during summer, but young carp were not. Thermoregulatory behavior of young carp indicated that they preferred temperatures between 30 and 33.5 C—temperatures available only in the outfall area. Young yellow bass avoided the outfall area, but larger fish were relatively abundant there and were particularly concentrated near the jets. Yet, large yellow bass stayed near the bottom in water not much warmer than the reference areas where the young lived. Young rock bass were concentrated in the outfall area but lived at essentially normal littoral temperatures by avoiding locations near and between the jets. Large pumpkinseed, although not concentrated in the outfall area as a whole, lived near the outfalls during afternoon at temperatures approaching the maximum effluent temperature. Finally, greater abundance of young black crappie in the outfall area during August 1968 but in the reference areas during July–August 1969 could not be attributed to a temperature difference between years.

Although solutions are not offered for all problems referenced in the previous paragraph, some insight into their probable complexity is suggested by consideration of nonthermal aspects of the outfall environment. Nonthermal agents may have operated either independently or synergistically with each other and temperature to influence use of the outfall area by fishes.

One nonthermal effect of the power plant's operation was to increase the abundance of zooplankton in the littoral zone. Samples of zooplankton and young bluegill from the study areas during summer 1969 showed that:

1. Limnetic zooplankters, primarily *Daphnia* spp. and copepods, were 4 to 10 times more abundant in the outfall area than in reference areas, where densities of 5 to 20 animals/liter normally occurred (Brauer, Neill, and Magnuson[5]);
2. Limnetic zooplankters were very concentrated near each outfall (densities up to 350 animals/liter) and sometimes eddied at the surface in floating "mats" several animals thick and as much as a few meters in diameter (Brauer et al.[5]); and,
3. Young bluegill in reference areas fed primarily on the littoral amphipod, *Hyalella azteca* (87% of the items in sampled stomachs), but young bluegill in the outfall area ate primarily limnetic zooplankton (93% of the items in stomachs) (T. C. Byles, Laboratory of Limnology, University of Wisconsin, personal communication).

Thus, the supply of food for fish in part of the normally zooplankton-poor littoral zone was enriched by the discharge of water con-

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[5] Unpublished manuscript, Garrett A. Brauer, W. H. Neill, and J. J. Magnuson: Effects of a power plant on the distribution and abundance of zooplankton near the plant's effluent outfalls. Laboratory of Limnology, University of Wisconsin, Madison, Wisconsin 53706.

taining limnetic zooplankton that had been pumped through the power plant's cooling system. Young bluegill and probably other planktivorous fishes were able to exploit this food resource.

The concentration of displaced zooplankton in the outfall area may have attracted such fishes as yellow bass, pumpkinseed, bluegill, and young largemouth bass. Fishes are known to aggregate in areas where planktonic food is relatively abundant (Lucas 1956; McNaught and Hasler 1961; Schaefer 1961).

Laboratory experiments with bluegill and yellow perch confirmed that fishes may be attracted to food-rich environments but suggested that attraction to food does not override behavioral thermoregulation. Provided that an environment with the preferred temperature is available, the fraction of time spent in a food-rich environment is likely to decrease abruptly as its temperature diverges from the preferred. Fishes may, however, briefly foray from an environment offering the preferred temperature, but not food, into cooler or warmer (even lethally warm) water where food is available.

Although planktonic food for fish was relatively concentrated in the outfall area, so too was the longnose gar, one of the major fish predators of Lake Monona. During summer 1968, longnose gar in the outfall area fed primarily on young bluegill (Haase 1969), which were very abundant. Low densities in the outfall area of young carp and young black bullhead may have resulted in part from predatory activities of longnose gar. Evidence from Lake Mendota suggests that young carp are more vulnerable to longnose gar than are young bluegill and other spiny-rayed fishes (Haase 1969).

The flow of water from the outfalls may have influenced the formation and maintenance of fish aggregations at the primary outfall during late winter and spring. Adult yellow bass, which dominated outfall aggregations, also concentrated during the same season in the swiftly flowing water below a navigation lock on the Yahara River between Lakes Mendota and Monona. The temperature of the river was about 8 C, while the heated effluent was 14–20 C. Strawn (1969) noted the similarity between aggregation of fishes at power plant outfalls and in reservoir spillways. Takayama et al. (1967) found that rainbow trout (*Salmo gairdneri*) gathered at an inlet discharging into the pond in which they were held. Concentration of fish occurred whether the inflow was warmer or cooler than the pond but was most marked when the influent was near acclimation temperature.

To close the discussion of nonthermal effects, we note parenthetically that low concentrations of dissolved oxygen were not observed in the outfall area. Water in the outfall area during summer 1968 was supersaturated (up to 115%) with oxygen. Other workers (Trembley 1965; Alabaster and Downing 1966) also observed little or no decrease in the oxygen content of effluent from power plants, although ". . . the spectre of loss of dissolved oxygen in power stations is continually raised by speculative articles for the layman" (Coutant 1970, p. 359).

Responses of Lake Monona Fishes to Power Plant Operation: Present Assessment and Some Unresolved Problems

Investigation of the distributional ecology of fishes in Lake Monona's littoral zone, laboratory experiments on behavioral thermoregulation of fishes, and information from the literature suggested the following major conclusions:

1. Distributions of fishes within the littoral zone of Lake Monona were markedly and differentially influenced by the discharge of heated effluent.

2. Major features of the distributions during summer resulted from fishes' different responses to elevated temperatures of the outfall area.

3. During summer, fishes avoided or concentrated in the outfall area and, within it, distributed themselves primarily in accordance with thermoregulatory behavior, whereby each individual tended to maximize its exposure to temperatures within the preferred range of the species.

4. Behavioral thermoregulation was not overridden, but in some cases may have been modified, by behavioral responses to the outfall area's peculiar nonthermal features—

abundant food, strong currents, concentrated predators.

Our work did not provide empirical evidence for or against the contention that Lake Monona fishes responded to operation of the power plant with ecological prudence, i.e., that fishes concentrated in that fraction of the habitat which was optimum for performance of their life processes. An attempt to assess one measure of young fishes' ecological success—growth rate—yielded results confounded by size-differential movements of the fish. Thus, information from other studies must constitute the basis for conjecture as to whether distribution of Lake Monona fishes reflected preference for optimum habitats.

It seems logical that fishes ought to prefer environments that are, in some sense, optimum. Experimental evidence from the literature confirms that preferred and optimum temperatures of fishes are highly correlated when other components of environment are not limiting. Among 12 physiological responses of sockeye salmon (*Oncorhynchus nerka*), only 2—food conversion efficiency and food intake—have thermal optima different from 15 C, the final temperature preferendum (Brett 1971). The final temperature preferendum, 25 C, of the guppy (*Poecilia reticulata*) corresponds to the optimum temperature for development of resistance to lethal temperatures and for maximum growth rate (Fry 1964). Young channel catfish grow fastest and convert food to flesh most efficiently at 29 C (Strawn 1969) or 30 C (Andrews and Stickney 1972); their final temperature preferendum is 29 C (Strawn 1969).

However, the optimum temperature for growth and perhaps other activities may vary with the availability of food, whereas the final temperature preferendum may not. When Brett, Shelbourn, and Shoop (1969) provided young sockeye salmon with excess food, growth was most rapid at temperatures near the final preferendum, 15 C. But when food was restricted to less than 6% of dry body weight per day, the optimum temperature for growth decreased and, at 1.5%, was only 5 C. In contrast, channel catfish fed 6%, 4%, or 2% of their weight per day grew fastest at 30 C on each ration (Andrews and Stickney 1972).

If, when food is limiting, the optimum temperature for growth does decrease and the correspondence between optimum and preferred temperatures is to be maintained, the final temperature preferendum must also decrease. Indirect evidence suggests, to the contrary, that the final temperature preferendum may not be greatly influenced by food supply. The relationship between preferred temperature and feeding level has not been systematically evaluated, but temperatures preferred by starved fishes have been reported. Opaleye (*Girella nigricans*) preferred the same temperatures whether or not they had been starved for 2 weeks (Doudoroff 1938). Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*), and rainbow trout—all starved 2 or 3 weeks—preferred respective temperatures 2 C higher, 2 C lower, and 4 C lower than did fed controls (Javaid and Anderson 1967). These data suggest that starved fishes prefer temperatures only slightly lower or even higher than those preferred by well-fed fish.

Both planktivorous and piscivorous fishes of Lake Monona had access to abundant food in the outfall area. Thus, fishes that during summer lived at preferred temperatures in the outfall area also encountered conditions that were presumably optimum for growth.

But if food had been deficient in the outfall area, we believe that distributional responses of fishes would have been little different from those we observed. Both temperature preferences of starved fishes (Doudoroff 1938; Javaid and Anderson 1967) and the behavior of bluegill and yellow perch offered food at extreme temperatures suggest that fishes tend to prefer certain species-specific temperatures regardless of whether or not food is available at those temperatures. Thus, a food-deficient outfall area might be expected to attract fishes that prefer high temperatures even though it would offer poorer conditions for their maintenance and growth than would be available in unheated parts of the habitat.

Whether significant advantages or disadvantages accrue to individual fish in outfall areas depends not only on "quality" of the outfall environment but also on the amount of time the fish lives there.

Although fish distributions in Lake Monona were treated as if static, dynamic features were recognized. The study areas certainly did not consist of closed systems, each with its own resident populations of fish. Rather, at any instant the assemblage of fishes in a part of the littoral zone consisted of individuals that had been there for different periods of time. That a very small fraction of marked fishes was recaptured suggested that larger fish resided in the study areas no longer than several days before they were replaced by new immigrants. Many larger fishes (adult bluegill, yellow bass) must have stayed in the littoral zone no more than 12 hr consecutively, because the individuals present in the study areas were obviously fewer during the day than at night. Presumably, smaller fishes moved about less than larger ones. However, diel changes in length-frequency distributions suggested that even small bluegill made onshore-offshore movements.

Further evaluation of the power plant's impact on fishes must await answers to the following questions pertaining to dynamic aspects of fish distribution:

1. How do fishes arrive in the outfall area?
2. How long do individual fish stay in the outfall area?
3. What factors cause fish to leave the outfall area?
4. Once a given fish has left the outfall area, is it likely to return and, if so, how soon?

ACKNOWLEDGMENTS

We thank the many persons who encouraged and helped us in this investigation. T. C. Byles, G. G. Chipman, B. L. Haase, R. M. Mullen, and B. K. Quirk gave particularly valuable assistance in execution of the research. W. C. Burns, C. C. Coutant, A. E. Dizon, A. D. Hasler, J. A. Hoopes, J. F. Kitchell, W. P. Porter, and R. K. Strawn made helpful comments on the manuscript. The final draft of the manuscript benefited from expert attention by L. Lembeck, typist, and T. Nakata, draftsman.

This work is based on a Ph.D. thesis submitted by W. H. Neill to the graduate faculty of the University of Wisconsin, Madison, in 1971. Financial support was provided in part by the Wisconsin Utilities Association and by the Office of Water Resources Research, Department of the Interior (MG OWRR B-028-Wis—WRC 70-010M).

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