#733

# The Preferred Temperature of Fish and their Midsummer Distribution in Temperate Lakes and Streams[1,2]

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## ABSTRACT

Laboratory studies of preferred temperature with yellow perch (*Perca flavescens*) are compared with results from 21 other species. These show that temperature, if acting alone, can determine the distribution of fish in laboratory apparatus. Factors such as light, conditioned responses related to feeding routines, and social behaviour can interfere with the expression of the response to temperature. Subdued lighting conditions were necessary in the experiments with *Oncorhynchus*, *Salvelinus* and *Coregonus*, whereas full daylight was required in experiments with *Perca flavescens*.

The level of thermal acclimation influences the range of temperature preferred. In general the preferred temperature is considerably higher than the acclimation temperature at low thermal acclimations, but this difference decreases up to the final preferendum, where both coincide. The final preferendum and the relation between acclimation and preferred temperature is characteristic for the species. The shape of the resulting curve may have some value in interpreting observations of fish mortalities and distribution in nature. The final preferendum of the yellow perch from the present work was 24.2°C., from other work using older fish it was 21.0°C.

Summer field observations of yellow perch in Lake Nipissing, Costello Lake and Opeongo Lake, in Ontario, showed average thermal distribution of 19.7°C., 21.0°C. and 21.2°C. respectively. This agrees well with 20.8°C. observed for four Wisconsin lakes. Oxygen depletion reported for Tennessee Valley reservoirs, distribution of primary prey species of lake trout in New York waters, and other factors, have been shown to modify the thermal distribution in nature. Differential sex response to temperature may be important in the perch. Field observations of thermal distributions for other species are also presented.

A comparison of the laboratory and field data shows good agreement with fish having colder final preferenda: *Salvelinus fontinalis*, *Salvelinus namaycush*, *Salvelinus* hybrid and *Coregonus clupeaformis*. Fish with warmer final preferenda, such as *Micropterus salmoides*, *Micropterus dolomieu* and *Lota lota lacustris*, showed higher temperatures in the laboratory than was shown by field observations. Young *Perca flavescens* showed similar results, but experiments with older perch showed excellent agreement between laboratory results and field observations. The lack of agreement between laboratory results and field observations is attributed to age differences; laboratory experiments being performed with young fish and field observations being made on older fish.

## INTRODUCTION

It is my purpose to discuss the influence of temperature on fish distribution, drawing on laboratory evidence and field examples. The characteristic of animals to move into specific thermal conditions when a range of temperatures is available to them has been termed thermal preference or selection; here the term preference

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will be used. Fry (1947) has defined the preferred temperature as the "region, in an infinite range of temperature, at which a given population will congregate with more or less precision", and the final preferendum as "a temperature around which all individuals will ultimately congregate, regardless of their thermal experience before being placed in the gradient".

There have been two approaches taken to study the preferred temperatures of fish; the description of the mechanism, and the classification of the various species in terms of their response to temperature. We are concerned with the latter here.

The preferred temperature studies in the laboratory will be reviewed and some examples of field observations will be presented to help establish the relation of preferred temperature to midsummer distribution. Experiments in the laboratory with yellow perch (*Perca flavescens*) will provide the basis for the laboratory discussions. Analysis of Lake Nipissing yellow perch data from the records of the Ontario Fisheries Research Laboratory, and similar data from Lake Opeongo and Costello Lake made available through the kindness of Drs. R. R. Langford and W. R. Martin, will provide the basis for the discussion of the field examples.

## LABORATORY STUDIES OF PREFERRED TEMPERATURE

### GENERAL LABORATORY PROCEDURE

The test chamber used for the yellow perch experiments was a tank 36 by 20 by 36 inches (94 × 57 × 94 cm.) and utilized a vertical gradient (see Brett, 1952, for a photograph and description). This tank was used in most of the studies reported herewith. Test chambers utilizing horizontal gradients have been of various dimensions and construction (see Doudoroff, 1938; Fisher and Elson, 1950; Tompkins and Fraser, 1950; and Sullivan and Fisher, 1952). The thermal gradients employed in the various experiments have varied with the experiment and the acclimation level of the population; in general the gradients approximated 0.5°C. per inch (0.2° per cm.), and included the acclimation temperature. Nearly all the experiments have been conducted under subdued light, especially those involving salmonids or coregonids; the yellow perch were tested in full daylight, some workers employed cameras and synchronized lights for observations in total darkness.

In general the fish have been introduced from their acclimation tanks at least 24 hours, and fed at least 8 hours, previous to the experiment. The operators have taken special pains not to disturb the fish during the experiment; in some cases special baffles were constructed to screen the observer from the fish. The gradient has been recorded at the beginning and end of each experiment. The distribution of the fish in the various segments of the gradient has been observed, and replication of the observations made to obtain sufficient data for reliability. Generally there have been consecutive series of experiments for each acclimation, with alterations in the gradient throughout the series, and a number of control observations without any gradient.

## LIMITATIONS IN LABORATORY STUDIES

Laboratory studies of preferred temperatures have some limitations which must be taken into account if their value is to be properly judged. Space and possibly time limitations in the laboratory are probably the most important deviations from natural conditions. Space limitations result in more interference from physical boundaries, more contact with other individuals, and compressed thermal gradients. Space and other considerations limit the number of individuals and the size of the individuals to the extent that most laboratory studies are of fish in the fry or fingerling stage. Fish behaviour under laboratory conditions must also be taken into account in the analysis; territorial behaviour and peck-order were observed in the experiments of Pearson (1952) with hybrid *Salvelinus* and some schooling was observed in the experiments with yellow perch. Conditioned responses related to laboratory feeding procedures were also mentioned by Brett (1952) for *Oncorhynchus* and by Pearson (1952) for *Salvelinus* hybrids. Yellow perch (*Perca flavescens*) were inactive in the dark and settled to the bottom, whereas speckled trout (Sullivan and Fisher, 1954; Graham, 1948), *Salvelinus* hybrids (Pearson, 1952), *Oncorhynchus* (Brett, 1952) and *Coregonus* (Tompkins and Fraser, 1950) were more precise in their temperature responses in subdued light.

## VERTICAL AND HORIZONTAL GRADIENTS

Both vertical (Brett, 1952; and others) and horizontal (Doudoroff, 1938; Tompkins and Fraser, 1950; Sullivan and Fisher, 1953) thermal gradients have been employed in laboratory experiments to determine thermal preferenda. The former presumably simulate thermal gradients as they occur in lakes, and the latter, stream conditions. A tactile factor would appear to be a major consideration when dealing with fish that normally keep contact with the bottom in their natural habitat.

Experiments on yellow perch are described below to illustrate the laboratory procedure and results.

## PREFERRED TEMPERATURE OF THE YELLOW PERCH

The apparatus and procedure as described by Brett (1952) were found suitable for experiments with the yellow perch (*Perca flavescens*), with slight modifications. All experiments were conducted in light corresponding to conditions in a well-lighted room. Modification of the observation technique (observation of one level at a time and replication through all levels) was made necessary by the rapid swimming activity of the perch when a thermal gradient was introduced. This rapid swimming throughout the experimental tank decreased if the fish remained three to four hours in the thermal gradient. In general initial observations were made three hours after the initiation of the gradient; subsequent observations were made approximately one hour apart.

The vertical distributions of a sample of yellow perch acclimated to 15°C. are shown for various thermal gradients in Figure 1. It is clear that these fish

were more often associated with the thermal conditions in the 20–25°C. range than any other physical feature of their environment; with alteration in the depth of these thermal conditions there was a corresponding shift in the distribution of the fish.
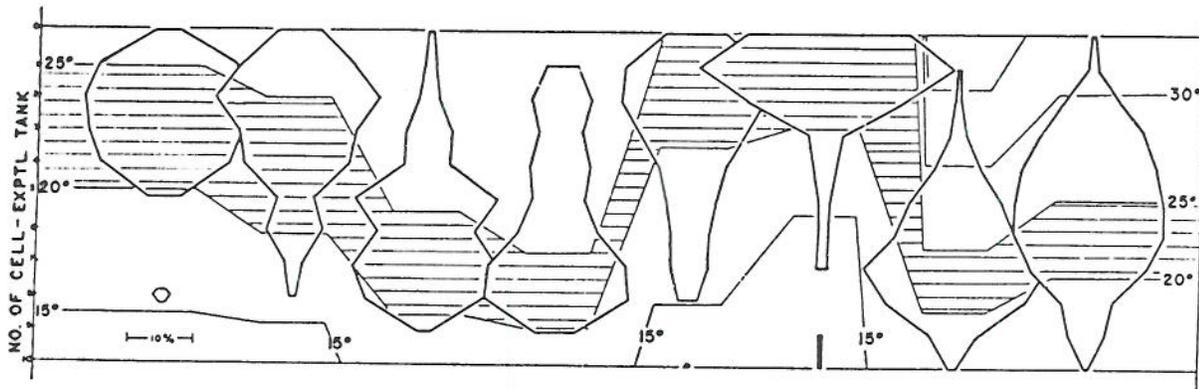


FIG. 1. The vertical distribution of yellow perch (*Perca flavescens*) and temperature isotherms (°C.) in a laboratory experiment. The distribution of fish is expressed as a percentage in each cell. Fish were acclimated to 15°C. Time between observations was approximately one hour, with two to three hours initially between start of gradient and first observation.

This figure also serves to illustrate a number of other points about laboratory preferred temperature experiments. Refractory individuals (see 1st, 5th and 6th distribution, Fig. 1) which did not respond to the gradient and remained near the bottom, and the effects of limited space (6th distribution, Fig. 1) where the fish were crowded into the upper strata by thermal conditions, were not included in the calculation of the mean temperature distribution. It should also be noted (7th distribution, Fig. 1) that yellow perch will continue to invade temperatures in excess of their upper lethal temperature (29.7°C. in winter, 32.3° in summer: Hart, 1952) and if the experiment is prolonged under these conditions the fish accumulate a lethal dose.

The preferred temperatures of the yellow perch at six different acclimations are shown in Table I; these results are compared with the unpublished results of

TABLE I. The mean or modal preferred temperature of the yellow perch at different acclimation temperatures. A—present experiments; B—McCracken and Starkman (1948). All temperatures are in degrees Centigrade.

| Acclimation temperature | Preferred temperature | | |
| | A | | B |
| | Mean | Mode | Mode |
|---|---|---|---|
| 5 | . . . | . . . | 11.0 |
| 8 | 18.6 | (17.5) | . . . |
| 10 | 19.3 | (20.6) | 17.0 |
| 15 | 23.0 | (24.5) | 20.0 |
| 20 | 23.1 | (21.5) | 20.5 |
| 25 | 24.5 | (24.0) | 21.5 |
| 30 | 26.7 | (26.5) | 27.5 |
| Final preferendum | 24.2 | . . . | 21.0 |
| Number of fish | 10–12 | | 3–4 |
| Age of fish | fingerling | | 2 yrs. old or older |
| Experimental period | Apr., May, Aug. | | Feb., Mar. |

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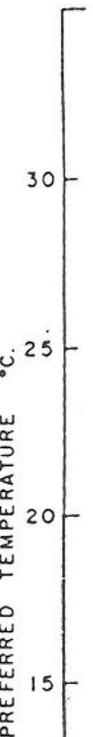were
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McCracken and Starkman (1948). It will be noted that although the apparatus and routine were similar, there were differences in the numbers of fish tested, the size of fish, and the season of experimentation. Any one of these factors could account for the discrepancy in the results of the two sets of experiments. Age may have a significant effect here, as it did with the cisco as shown by Fry (1937) in field studies. The season of experimentation may also have influenced the results as was shown for the speckled trout by Sullivan and Fisher (1952).

## COMPARISON OF LABORATORY RESULTS

The relation between preferred and acclimation temperatures for the present data in comparison with selected published results are shown in Figure 2. The line at 45° represents all points where the acclimation temperature coincides with the preferred temperature. The point at which the preferred temperature crosses this line is the final preferendum. The species presented were chosen to show the range of the temperatures preferred by fish, and the relation between the acclimation and preferred temperatures.
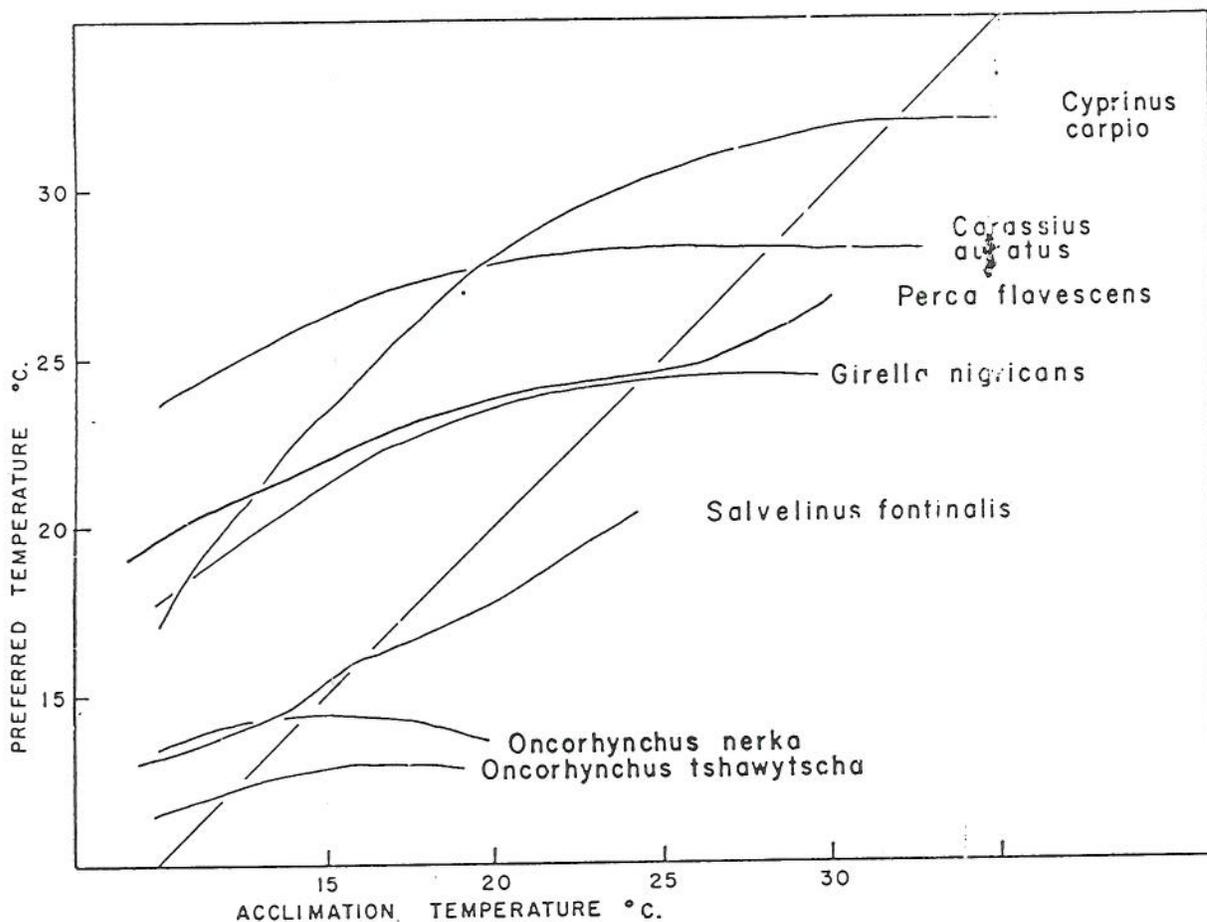


FIG. 2. Laboratory studies of preferred temperature: the yellow perch (*Perca flavescens*) compared with various other fish. The line at 45° joins all points where preferred and acclimation temperatures coincide. Data from various sources: *Cyprinus*—Pitt, Garside and Hepburn (1956); *Carassius*—Fry (1947); *Girella*—Doudoroff (1938); *Salvelinus*—Graham (1948); *Oncorhynchus*—Brett (1952).

There has been a gradual accumulation of information on the preferred temperatures of various fish, mostly at the University of Toronto; some of which have been published, but many are manuscripts in preparation. Table II presents the final preferenda for a number of species for which data are available. These results are self-explanatory in most cases with the exception of the three instances where a range of temperature is shown rather than a single point. The preferred temperature curves for *Micropterus salmoides* and *Salvelinus fontinalis* tended to follow the preferred-acclimation line closely over this range. The results for *Salmo trutta* represent the range of preferred temperatures for fish living continuously in a thermal gradient for a period of two years. Tait (MS), whose work this is, considers the study preliminary at this stage and the manuscript is in preparation at the moment.

TABLE II. The final temperature preferenda for various species of fish as determined by laboratory experiments, in degrees Centigrade. Young of the year or yearling fish were used, except as noted.

| Species | Final preferendum | Authority |
|---|---|---|
| Lepomis macrochirus | 32.3 | Fry and Pearson (MS, 1952) |
| Micropterus salmoides | 30.0–32.0 | Fry (MS, 1950) |
| Cyprinus carpio | 32.0 | Pitt, Garside and Hepburn (1956) |
| Lepomis gibbosus | 31.5 | Anderson (MS, 1951) |
| Carassius auratus | 28.1 | Fry (1947) |
| Micropterus dolomieu | 28.0 | Fry (MS, 1950) |
| Esox vermiculatus | 26.0 | Berst and Lapworth (MS, 1950) |
| Perca flavescens | 24.2 | Present work |
| Esox masquinongy | 24.0 | Jackson and Price (MS, 1949) |
| Girella nigricans[a] | 23.5 | Doudoroff (1938) |
| Lota lota lacustris | 21.2 | Crossman, Irizawa and Peacock (MS, 1953) |
| Perca flavescens | 21.0 | McCracken and Starkman (MS, 1948) |
| Salmo trutta[b] | 12.4–17.6 | Tait (MS, 1958) |
| Salvelinus fontinalis | 14.0–16.0 | Graham (1948); Fisher and Elson (1950) |
| Oncorhynchus nerka | 14.5 | Brett (1951) |
| Oncorhynchus keta | 14.1 | Brett (1951) |
| Salmo gairdnerii | 13.6 | Garside and Tait (MS, 1958) |
| Coregonus clupeaformis[c] | 12.7 | Tompkins and Fraser (MS, 1950) |
| Salvelinus hybrid[d] | 12.0 | Pearson (MS, 1952) |
| Salvelinus namaycush | 12.0 | McCauley and Tait (MS, 1956) |
| Oncorhynchus tshawytscha | 11.7 | Brett (1951) |
| Oncorhynchus gorbuscha | 11.7 | Brett (1951) |

[a]*Girella*—a marine species.
[b]*Salmo trutta*—two years old or older.
[c]*Coregonus*—two-year-olds.
[d]*fontinalis* × *namaycush*.

## FIELD OBSERVATIONS OF FISH DISTRIBUTION WITH ASSOCIATED TEMPERATURES

There are few field studies directly concerned with distribution of fish and the influence of temperature. The following data derived from published material, was in nearly every case from papers not concerned with thermal conditions and fish distributions *per se*. In order to derive thermal distribution from these papers it was necessary to take some liberties with the authors' data. In many cases the author's presentation did not lend itself to the derivation of average distributions and associated average temperatures at the pertinent depths; in these instances a range of temperatures was extracted.

## LIMITATIONS IN FIELD STUDIES

The study of the influence of temperature on field distributions of fish has limitations other than those found for laboratory studies. Some of these are inherent, and may not be adequately accounted for in the treatment of the data. These limitations include problems in capture where it is difficult to randomly and completely search all portions of the environment with equal intensity. Possibly the most serious limitation is in the collection and analysis of associated pertinent data and observations. Indeed, it is difficult to assess the multitude of factors posed. In the present analysis factors other than temperature will be ignored unless their influence is definitely suggested.

## YELLOW PERCH FIELD DISTRIBUTION AND THERMAL PREFERENCE

Netting studies in Lake Nipissing and routine limnological observations including a special cisco study (Fry, 1937), combined extensive netting with complete temperature records. This netting revealed the following seasonal distribution for perch. During the first half of May, before the warm-up period, perch were netted in small numbers from 60 to 150 feet (18–46 m.). In late May and early June perch were caught in small numbers from 20 to 30 feet (6–9 m.), but there was not adequate netting in deeper water. During the period of thermal stratification perch were only netted in the epilimnion, and in the vicinity of the 20° isotherm; they tended to move from their shallow distribution in mid-June to follow the 20° isotherm to its greatest depth in early August. In late August and early September there was not adequate netting in water less than 30 feet deep, but the indications are that perch were not present in numbers deeper than 30 feet. Netting in the fall did not allow assessment of their distribution. The same seasonal distribution for the European perch (*Perca fluviatilis*) was demonstrated by Worthington (1950) and Allen (1935) in Lake Windermere, but they did not present temperature data.

Records of intensive netting studies in two different lakes in Algonquin Park, Ontario, are available, coupled with extensive temperature data. They show the same summer perch distribution as was found in Lake Nipissing, but in sharper detail. The results of this work are presented in Figure 3A. The thermocline is similarly constituted in both these lakes with Costello tending to have a steeper gradient, and because of its sheltered nature, a shallower one. The top of the thermocline in both lakes closely corresponds to the position of the 20° isotherm. In neither of these lakes were oxygen conditions poor in the hypolimnion.

Netting studies of hybrid trout (*Salvelinus fontinalis* × *namaycush*) by Martin and Baldwin (1958) are shown in conjunction with the thermal conditions in Figure 3B and 3C. In these two Algonquin Park lakes thermal stratification varied considerably in depth and constitution in the different years, but the thermal position of the hybrid trout remained similar.

Fry's (1937) work on the cisco (*Leucichthys artedi*) is the most thorough treatment of field distribution of a fish that has come to our attention. He concludes that temperature is the principal factor influencing the vertical migrations

of these fish. He further demonstrates that age plays an important role in this
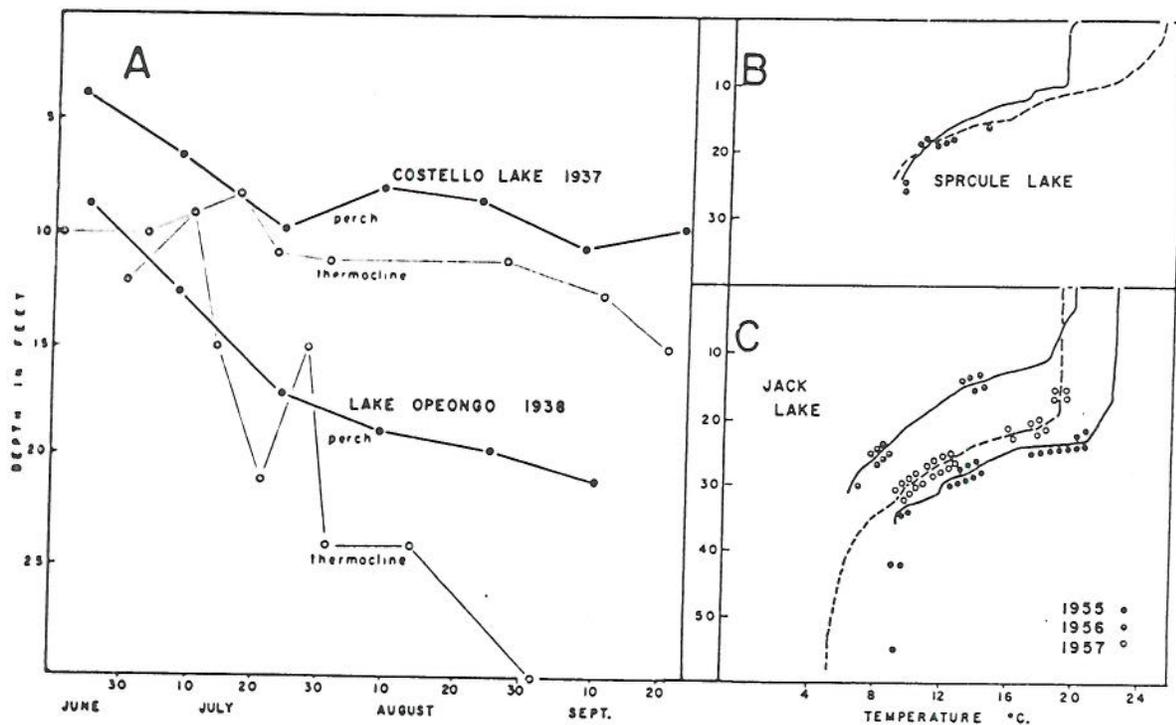fish's reaction to temperature. Figure 4 is a reproduction of Fry's figure showing



FIG. 3. *Panel A.* Mean distribution of yellow perch in relation to the top of the thermocline.
Solid dots—perch mean depth; open dots—top of the thermocline.
*Panels B and C.* Depth distribution of hybrid trout (*Salvelinus fontinalis* × *namaycush*) in
relation to thermal conditions. Each dot represents one fish. (Adapted from Martin and
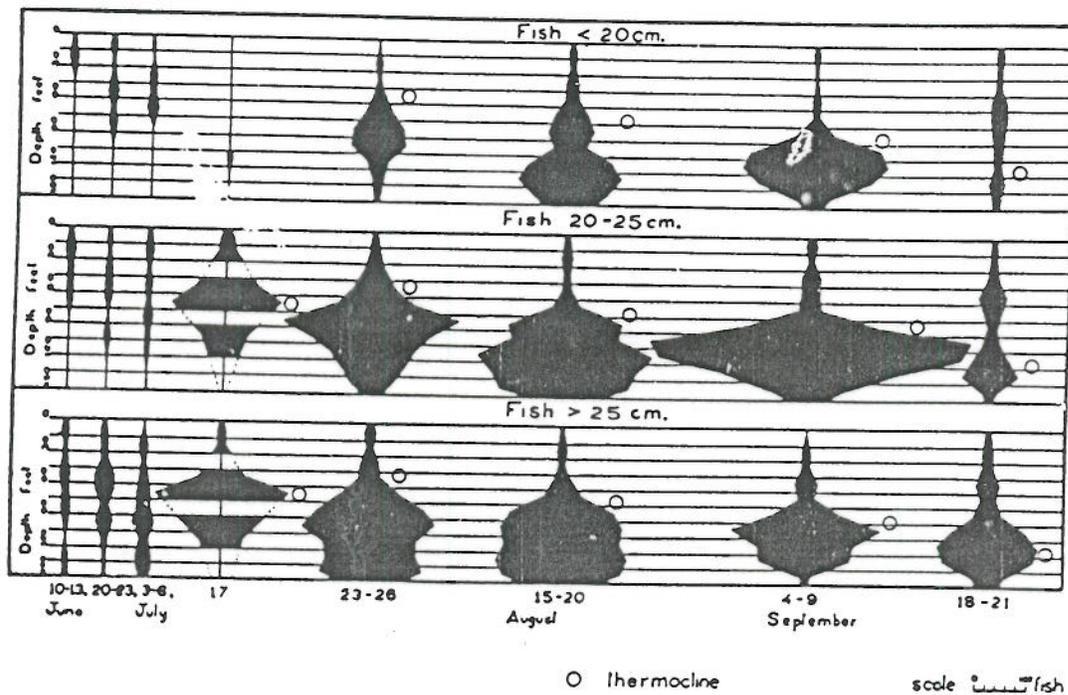Baldwin, 1958.)



FIG. 4. Seasonal changes in vertical distribution in ciscoes of different
lengths at station 4, Lake Nipissing, Ontario, 1935. (A reproduction of
figure 15 of Fry, 1937, with the author's permission.)

the relative depth distributions of three different size groups of cisco and the relation of the thermocline to the distributions. In essence the younger fish remained longer in the upper, warmer water during the warm-up period; the return to the epilimnion in the fall was more complicated.

Dendy (1948) concluded from his work in three Tennessee reservoirs that accurate prediction of fish depth distribution could be made on the basis of knowing the thermal structure, due allowance being made for unfavourable oxygen conditions. Dendy's figure showing the thermal distributions of largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion vitreum*) and sauger (*Stizostedion canadense*) is reproduced in Figure 5. This figure clearly demonstrates how these three species continue to increase their thermal experience up to a certain point, then each "levels off" at a particular thermal level, and does not radically depart from it unless that temperature stratum becomes deficient in oxygen.
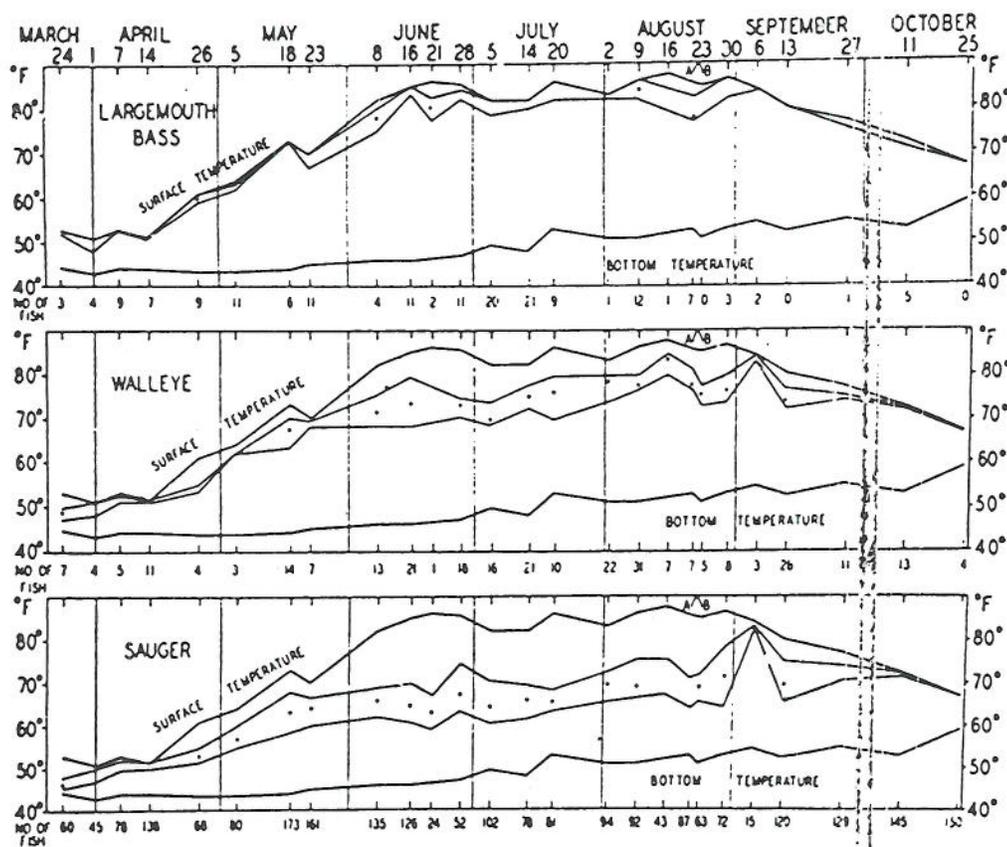


FIG. 5. Distribution of the middle 50% of largemouth bass, walleye, and sauger in relation to temperature, Norris Reservoir, 1943. The two middle lines show that temperature range of the middle 50% of the fish caught. When the range was wide, the temperature where the median fish was caught is indicated by dot. Presence of walleye in unusually warm water on August 16 and September 6, and of sauger in the same zone on September 6, resulted from oxygen shortages in the strata formerly occupied by these species. For further explanation see Dendy (1945, fig. 13, p. 428). (A reproduction of figure 2 of Dendy, 1948, with the permission of the author and the American Fisheries Society.)

The depth distribution of lake trout (*Salvelinus namaycush*) in Algonquin Park lakes (Martin, 1952) and in Cayuga Lake (Galligan, 1951) are in close agreement in the temperatures where these fish are located during the summer. Galligan (1951) makes the interesting observation that the July distribution of the lake trout was in much shallower water than would be expected, and this observation was correlated with the occurrence of alewives in shallow water during their spawning season.

The results presented above are summarized in terms of temperature in Table III. In addition to the above results, additional observations are included

TABLE III. Field observations of various species of fish and associated temperatures. Some temperatures are estimates derived from the author's tabled or figured data. August distributions and temperatures were used wherever possible.

| Species | Temp., °C. | Water | Location | Author |
|---|---|---|---|---|
| *Micropterus salmoides* | 26.6–27.7 | Norris Reservoir | Tenn. | Dendy, 1948 |
| *Micropterus punctatus* | 23.5–24.4 | " | " | " |
| *Stizostedion v. vitreum* | 20.6 | Trout Lake | Wis. | Hile & Juday, 1941 |
| " | 22.7–23.2 | Norris Reservoir | Tenn. | Dendy, 1948 |
| *Dorosoma cepedianum* | 22.5–23.0 | " | " | " |
| *Aplodinotus grunniens* | 21.6–22.2 | " | " | " |
| *Ambloplites rupestris* | 14.7–21.3 | Lakes | Wis. | Hile & Juday, 1941 |
| " | 20.7 | Streams | S. Ont. | Hallam, 1958 |
| *Perca flavescens* | 21.2 | Lake Opeongo | Ontario | Present work |
| " | 21.0 | Costello Lake | " | " |
| *Perca flavescens* (small) | 12.2 | Muskellunge Lake | Wis. | Hile & Juday, 1941 |
| *Perca flavescens* (larger) | 20.2 | " | " | " |
| *Perca flavescens* | 20.2 | Silver Lake | " | " |
| " | 21.0 | Nebish Lake | " | " |
| " | 20.8 | Trout Lake | " | " |
| " | 19.7 | Lake Nipissing | Ontario | Present work |
| *Micropterus dolomieu* | 20.3–21.3 | Nebish Lake | Wis. | Hile & Juday, 1941 |
| " | 21.4 | Streams | S. Ont. | Hallam, 1958 |
| *Stizostedion canadense* | 18.6–19.2 | Norris Reservoir | Tenn. | Dendy, 1948 |
| *Salvelinus fontinalis* | 14.2–20.3 | Moosehead Lake | Maine | Cooper & Fuller, 1945 |
| " | 15.7 | Streams | S. Ont. | Hallam, 1958 |
| " | 12.0–20.0 | Redrock Lake | Ontario | Baldwin, 1948 |
| *Cottus bairdii* | 16.5 | Streams | S. Ont. | Hallam, 1958 |
| *Salvelinus* hybrid[a] | 13.1 | Jack L., Sproule L. | Ontario | Martin & Baldwin, 1958 |
| *Catostomus commersonnii* | 11.8–20.6 | Musk., Trout, Silver L. | Wis. | Hile & Juday, 1941 |
| *Catostomus c. commersonnii* | 14.1–18.3 | Moosehead Lake | Maine | Cooper & Fuller, 1945 |
| *Prosopium cylindraceum* | 13.9–17.5 | " | " | " |
| *Pomolobus pseudoharengus* | 4.4– 8.8 | Cayuga Lake | N.Y. | Galligan, 1951 |
| *Salmo salar sebago* | 13.6–16.2 | Moosehead Lake | Maine | Cooper & Fuller, 1945 |
| *Salvelinus namaycush* | 10.0–15.5 | Cayuga Lake | N.Y. | Galligan, 1951 |
| " | 14.0 | White Lake | Ontario | Kennedy, 1941 |
| " | 11.0–11.5 | Moosehead Lake | Maine | Cooper & Fuller, 1945 |
| " | 8.0–10.0 | Louisa, Redrock L. | Ontario | Martin, 1952 |
| *Osmerus mordax* | 12.8 | Lake Champlain | N.Y. | Greene, 1930 |
| " | 6.6– 8.3 | Cayuga Lake | N.Y. | Galligan, 1951 |
| *Coregonus clupeaformis* | 11.4–11.9 | Moosehead Lake | Maine | Cooper & Fuller, 1945 |
| *Catostomus catostomus* | 11.0–11.6 | " | " | " |
| *Lota lota maculosa* | 10.8–11.4 | " | " | " |
| *Leucichthys artedi* | 8.0–10.0 | Lake Nipissing | Ontario | Fry, 1937 |
| " | 5.5–7.2 | Cayuga Lake | N.Y. | Galligan, 1951 |
| *Oncorhynchus nerka* | 10.6±0.44 | Cultus Lake | B.C. | Foerster, 1937 |

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from other papers, the range or average temperature presented being subject to the limitations mentioned earlier. In each case the data were derived from depth distributions transposed to temperatures at this depth, from the author's tabled or figured data, with the following exceptions. In some cases the author derived and mentioned the temperature at the average depth distribution. The temperature for *Salvelinus namaycush* in White Lake (Kennedy, 1941) is the temperature of White Lake at the time of peak migration from this lake into a deeper lake. The temperature for *Oncorhynchus nerka* is the 8-year average temperature at the time of cessation of the downstream migration for this species (Foerster, 1937). The temperature for *Osmerus mordax* in Lake Champlain is the temperature recorded by Greene (1930) which is avoided by this species. These latter three examples, while admittedly different from the remainder, are close to the defined final preferendum. The temperatures recorded for stream fish by Hallam (1958) are average stream temperatures where these species were found.

Wherever possible August distributions and temperatures were used since these would best represent conditions where the maximum range of temperatures were available, and it also represents a period when spawning activities do not interfere with the behaviour of the fish.

Graphical presentation of the data in Table III allows easier appreciation of the thermal position of each of the species; this has been presented in Figure 6. Wherever information from several sources are available and overlapping, the range or average for the different waters are presented (except in the case of the perch where there is close agreement in all average temperatures). It should be emphasized that the range presented for the species does not necessarily represent the species' preferred temperature, but is primarily a function of the ease or difficulty experienced in handling the author's data.

## DISCUSSION

### LABORATORY STUDIES

Laboratory studies are of value in the interpretation of field observations, but the limitations of each must be kept in mind. Laboratory results have clearly demonstrated that temperature acting alone can control the distribution of fish in laboratory apparatus. Aggregations of fish have been induced in specific temperature ranges in both horizontal gradients (Doudoroff, 1948; Sullivan and Fisher, 1953; Fisher and Elson, 1950; Sullivan and Fisher, 1952; and others) and vertical gradients (Fry, 1947; Brett, 1952; Pitt, Garside and Hepburn, 1956; and others). Various authors have found that light (Sullivan and Fisher, 1954; Brett, 1952; Pearson, 1952; and others), feeding activity (Brett, 1952; Pearson, 1952; and others), and social behaviour (Pearson, 1952) interfered with precise temperature selection in fish.

It has been demonstrated that thermal acclimation has a significant effect on the preferred temperature, by Fry (1947), Pitt, Garside and Hepburn (1956), and others. Doudoroff (1938) considered the influence of acclimation as temporary since *Girella*, when acclimated to 10°C., would always move into, and
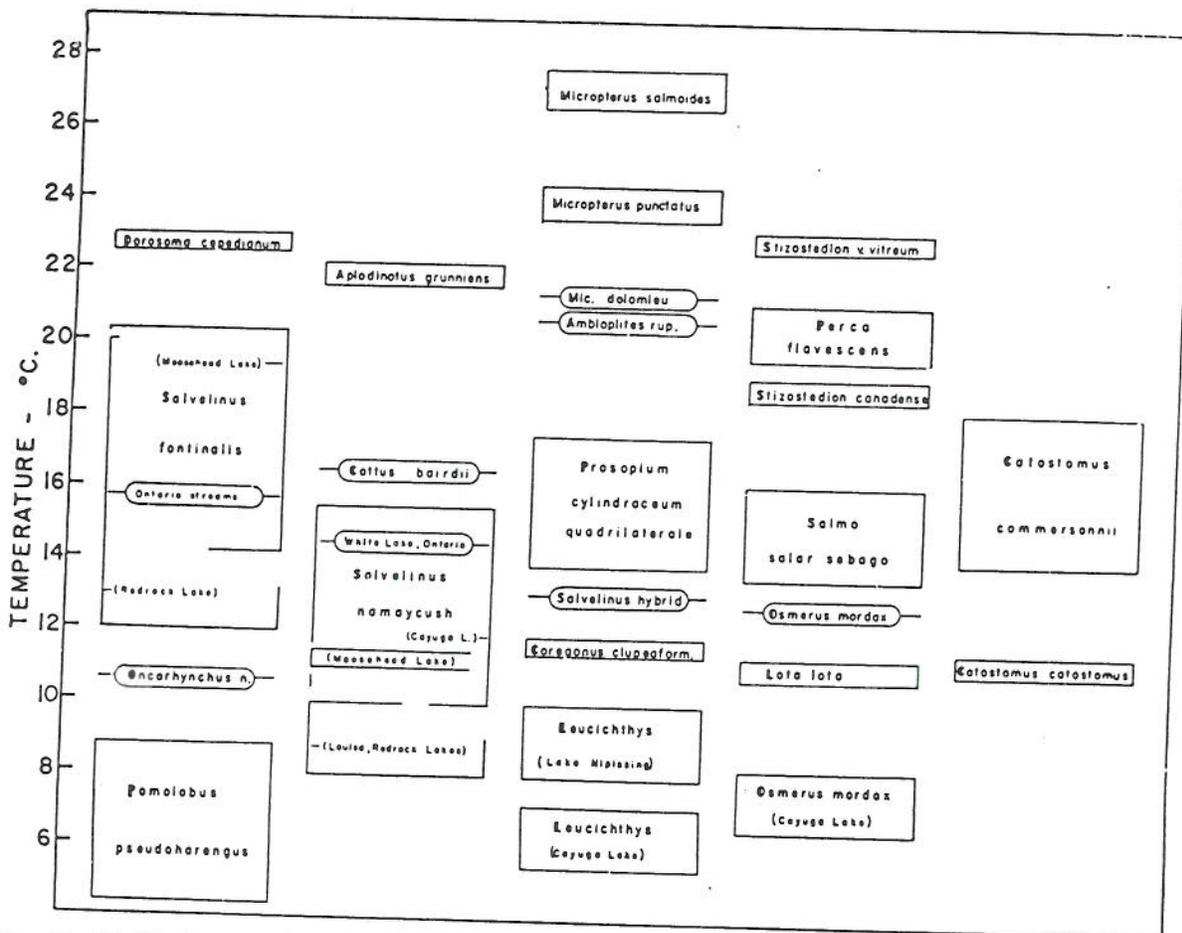
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Fig. 6. Field observations of fish and associated temperatures during midsummer (August mostly). The depth of each rectangle corresponds to the temperature range. Pointers on laterally rounded figures represent a derived average. Vertical relations only are important. (Data from various sources; see also Table III.)

would eventually become acclimated to, higher temperatures. Doudoroff's conclusion is not in contradiction to the other studies, but serves to emphasize that laboratory studies illustrate specific points at various acclimation levels, a process that would be continuous in nature during spring and summer.

The final preferendum in the laboratory, as defined by Fry (1947), is that temperature where the temperature preference is the same as the acclimation level. In nature this would be manifest as the temperature where the fish would eventually congregate.

## PREFERRED TEMPERATURE CURVES

Preferred temperature curves (Fig. 2) have not received detailed attention primarily because there have been too few for comparison. There appears a basic similarity in the portion representing acclimations lower than the final preferendum (to the left). Presumably this portion of the curve gives some indication of the relative rate at which a given species may move into progressively warmer water. Thus at low acclimation temperatures fish have a strong tendency for moving into warmer water. There are a number of recorded cases in the literature where fish acclimated to low temperatures invade warm water in large numbers

in spite of a lethal effect. These cases are recorded or noticed more readily because an extensive mortality ensues, likely because the temperatures are lethal for fish at low acclimation temperatures. Gizzard shad (*Dorosoma cepedianum*) from Lake Erie in the vicinity of the Port of Erie, Pennsylvania, during recent winters have moved into the warm water effluent of power plants where they die in large numbers (Hancock, 1954; and personal communication from A. Larsen). Alewives (*Pomolobus pseudoharengus*), according to Graham (1956), move into shallow warm water in late spring where they suffer extensive mortalities. Hancock (1954) also reports large aggregations of fish (mostly white crappie) in mid-winter in the presence of a local temperature gradient of 1-2 degrees.

Higher acclimations closer to the final preferendum presumably would be reflected in nature by a more gradual move into water at the temperature of the final preferendum. A comparison of the thermal experience of the surface waters and the perch in Lakes Nipissing, Opeongo and Costello would indicate this. The figure (Fig. 5) of Dendy (1948) also tends to show this, where two species experience the surface water warm-up until late spring, then sound to deeper water, but they then still increase their thermal experience at a slower rate. The largemouth bass which continually inhabited surface waters presumably might have invaded still warmer water had it been available.

Temperatures higher than the final preferendum would presumably move the fish out of surface waters. This would appear to be illustrated by the observations of Foerster (1937) who found young *Oncorhynchus nerka* left surface waters when the temperature rose to 10.6°C., and the observations of Kennedy (1941) who records *Salvelinus namaycush* moving into a cold lake from a warming lake when the latter reached 14°C.

FIELD OBSERVATIONS

One of the most decisive examples of the directive action of temperature in the field is reported by Hancock (1954). He showed that local large aggregations of fish (principally white crappie) were induced by a temperature gradient of 1–2°C. This was in the winter under ice cover.

YELLOW PERCH

Yellow perch in Lake Nipissing were scattered throughout the lake to depths of 150 feet (46 m.) in the spring, but after the initial spring warm-up period they were only found in the surface waters, later, in mid- and late summer, they frequented the vicinity of the 20°C. isotherm. The Lake Opeongo and Costello Lake data show a similar distribution picture. This appears comparable with the yellow perch distribution in the Wisconsin lakes studied by Hile and Juday (1941). The average thermal distribution in August as derived from this paper was 20.8°C. Their record of smaller perch in deeper water (11 meters—12.2°C.) in Muskellunge Lake cannot be accounted for on present evidence. The differential depth distribution of the two sexes of perch reported by Eschmeyer (1938) may account for it. If this is the case, then sex should be considered in the thermal distribution of perch.

Worthington (1950) and Allen (1935) working with the European perch (*Perca fluviatilis*) in Lake Windermere, England, describe the same distribution as has been found for the yellow perch in Lakes Nipissing, Costello and Opeongo. Allen (1935) discusses this distribution and remarks on the coincidence of the distribution and thermal conditions, but does not credit temperature as being the factor triggering the movement into shallow water in the spring prior to spawning. He felt that sexual development must control this movement from deep water into shallow water. Neither author prese:  1 temperature data for Lake Windermere.

### CISCO

Fry's (1937) study of the summer migration of the cisco is the most comprehensive treatment of the summer distribution of a fish, and of the causal factors, that has come to our attention. These fish move into shallow water in the spring and remain there for varying periods depending on their age and sex (Fig. 4). Fry related their movement from shallow water to deep water in late spring and early summer to rising temperatures in the epilimnion. They descended to the bottom in their initial sounding, but ascended to the lower thermocline in late summer. The decrease in oxygen and the increase in carbon dioxide in the bottom water was held responsible for concentrating the cisco below the thermocline. Fry considered the late summer piercing of the thermocline, and return to the epilimnion to be the resultant of the balance of intolerance to carbon dioxide and to high temperatures.

### OTHER SPECIES OF FISH

Dendy (1946, 1948) has presented evidence in detail related to the thermal distributions of fish in various Tennessee Valley reservoirs. He also recorded the influence of dissolved oxygen on these distributions. Figure 5 is a reproduction of Dendy's figure showing the thermal distribution for largemouth bass (*Micropterus salmoides*), walleye (*Stizostedion v. vitreum*) and sauger (*Stizostedion canadense*) through March to October. Here he illustrates the influence of temperature in its control of the general distribution of these fish, and the modification of this distribution caused by low concentrations of oxygen. Poor oxygen conditions on August 16 moved walleye into warmer water, and similar conditions on September 6 moved both walleye and sauger into warmer water. Table III summarizes Dendy's observations for various species of fish.

*Salvelinus* hybrids (*fontinalis* × *namaycush*) in two Algonquin Park lakes offer a clear-cut example of temperature influencing the distribution of fish. Martin and Baldwin (1958) show (Fig. 3B, 3C) that thermal conditions control the depth distribution of these fish. Thermal stratification in three consecutive years occurred at different depths during the observation period, and the hybrids showed similar differences in their distributions.

### EFFECT OF THE THERMOCLINE

Since the thermocline is the boundary between the warm and cold water it has come to be looked upon as a natural boundary in the distribution of fish, to
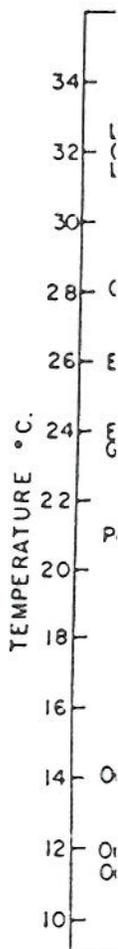
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FIG. 7.
*Right.* A

the extent that we speak of warm- and cold-water fish. The evidence at hand is not sufficient to reach a firm conclusion on the thermocline as a barrier. It may act as a thermal or density barrier. Fry (1939) points out that the sharpness of the thermocline in early summer in Lake Opeongo determines the availability of perch to lake trout. Bardach (1955) related oxygen conditions to perch distribution when he considered the effects of shallow and deep (early and late—Bardach's terms) thermoclines in Lake West Okoboji.

## COMPARISON OF LABORATORY RESULTS WITH FIELD OBSERVATIONS

Figure 7 compares the laboratory final preferenda on the left, and the available field observations with available laboratory results on the right. The authority for these data may be found in Tables II and III. Many of the laboratory studies have no counterpart in field observations. They are presented for reference. These studies appear to array themselves on the temperature scale in keeping with general field observations.
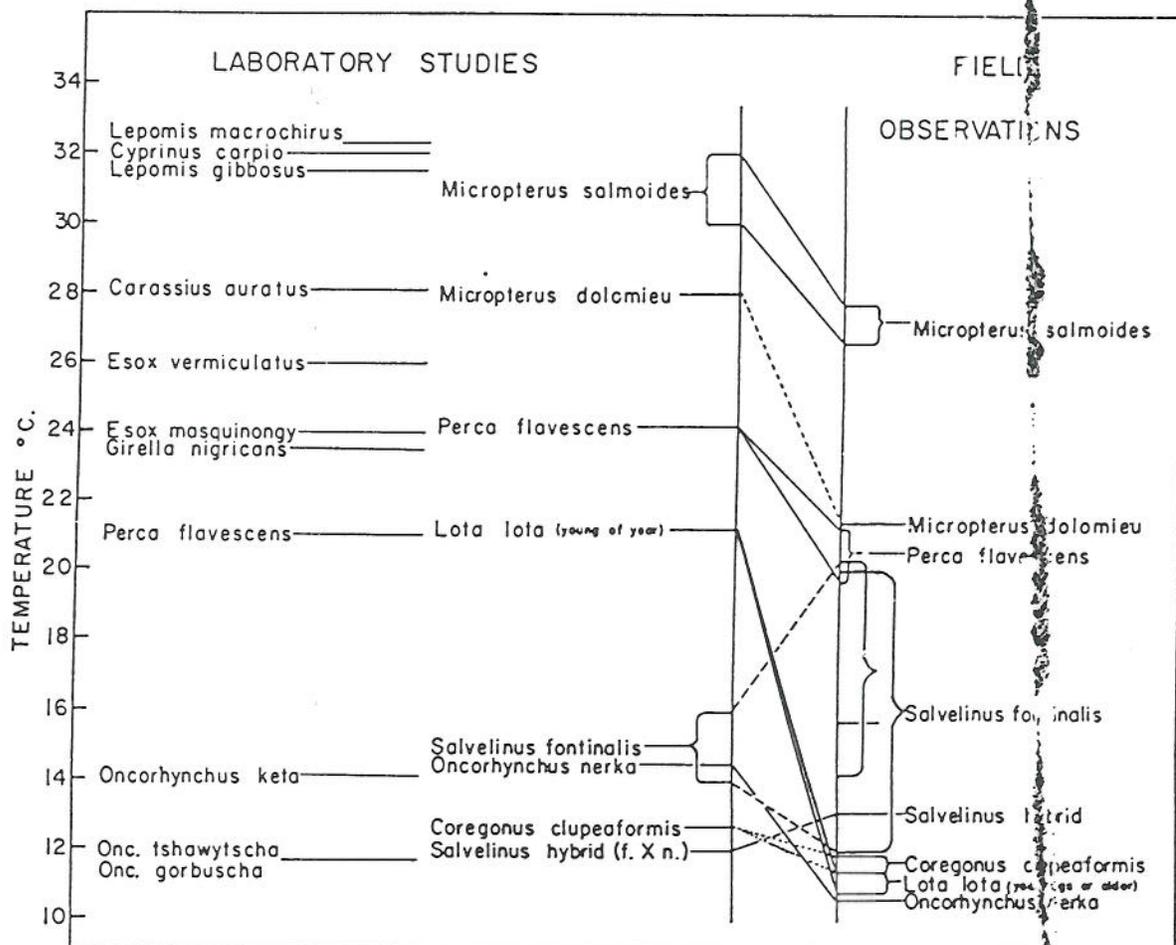


Fig. 7. *Left.* A comparison of various final preferenda as found by laboratory studies. *Right.* A comparison of field observations with laboratory results for a number of species. (See text for discussion and sources.)

Two laboratory final preferenda are presented as a range rather than a single temperature. In these two cases (*Micropterus salmoides* and *Salvelinus fontinalis*) the thermal preference curve paralleled the final preferendum line closely over this range, rather than crossing it cleanly.

The closest agreement between laboratory results and field observations lies within the lower temperature range. *Salvelinus fontinalis*, *Salvelinus namaycush* (not shown in Figure 7—see Tables II and III), *Salvelinus* hybrid and *Coregonus clupeaformis* are surprisingly close in view of the inherent limitations. All other species compared indicate the laboratory studies are consistently too high. Doudoroff (1938) also found this to be the case. The most plausible reason for this is that the laboratory studies are almost without exception of fry or fingerlings. Fry (1937) showed that young cisco tended to remain in warmer water while the older fish moved into colder water. General field observations also point to the fact that the young of *Micropterus*, *Perca* and *Lota* remain in water warmer than that inhabited by older individuals. Field observations of *Perca* (19.7–21.2°C.) when compared with the author's laboratory work (24.2°C.) show a discrepancy, but when compared with McCracken and Starkman's (1948: 21.0°C.) show good agreement. McCracken and Starkman conducted their experiments at a different season (winter), and with fewer fish that were older (two years old or older) than mine. The age differences between the fish used in these two experiments are considered the significant factor.

It is also possible that the discrepancy shown by *Micropterus salmoides* might have been decreased if there had been warmer water available (see Fig. 5) at the time of field observations (Dendy, 1948).

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