A Field Information-based System for Estimating Fish Temperature Tolerances

By J. G. Eaton, J. H. McCormick, B. E. Goodno, D. G. O'Brien, H. G. Stefany, M. Hondzo, and R. M. Scheller

ABSTRACT

In 1979, Biesinger et al. described a technique for spatial and temporal matching of records of stream temperatures and fish sampling events to obtain estimates of yearly temperature regimes for freshwater fishes of the United States. This article describes the state of this Fish and Temperature Database Matching System (FTDMS), its usage to estimate thermal requirements for fishes, some proposed maximum temperature tolerances for several freshwater fish species, and the way these FTDMS-derived values relate to various laboratory test results. Although applicable to all species for which collection records exist, initial development and refinement of FTDMS has focused on estimating the maximum weekly mean temperature tolerance for 30 common fishes of the United States. The method involves extensive use of automated data processing during data incorporation, quality assurance checks, data matching, and endpoint calculation. Maximum weekly mean temperatures derived from FTDMS were always less than laboratory-determined lethal temperatures and were similar to temperature criteria obtained from laboratory data through Environmental Protection Agency (EPA) interpolation procedures. The technique is a cost-effective means of generating temperature tolerance estimates for many U.S. fish species (i.e., more than 100).

A 1983 report on carbon dioxide and climate by the U.S. National Research Council concluded that a doubling of the ambient CO_2 concentration could take place within the next half-century and that, as a consequence, global mean air temperatures might increase as much as 1.5°C–4.5°C. The scale of this projection has been corroborated recently by further large-scale climate change modeling in the United States and abroad (IPCC 1992). Our investigation was largely stimulated by a need for information about thermal requirements that could be used to predict responses of freshwater fishes to global warming.

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The importance of environmental temperature to poikilothermic organisms has long been recognized and may well have been first studied with the invention of the thermometer (Rose 1967). From the 1940s through the 1970s, F. E. J. Fry at the University of Toronto and others contributed to a particularly dynamic period of research on the effects of temperature on freshwater fishes (Fry 1947, 1971). Many of these studies addressed the effects of acclimation temperature on the temperature that killed various species within specific time intervals (Fry et al. 1942; Hart 1947; Brett 1960), and the determination of preferred temperatures with respect to acclimation (Brett 1952). Collectively, these studies now serve as the foundation for today's understanding of fish thermal biology. However, Fry's influence on the topic did not end there since his students—principally R. J. Brett and his associates—continued this research into the 1960s and 1970s. The young colleagues expanded on and applied the products of earlier work to include studies about interactions among elements of a fish's environment and about feeding and subsequent growth (Brett and Sutherland 1970; Beamish 1974). Of particular relevance to this paper are Brett's studies of Pacific salmon diurnal movements with respect to thermal environment, feeding activity and metabolism (1971), and the relationships among ration size, growth rate, and food use efficiency (Brett et al. 1969), or some of the more subtle interactions in the adaptation of fishes to their environment.

A new appreciation of this fundamental knowledge of fish thermal biology arose in the late 1960s and early 1970s as North America's electric power industry increased its steam-driven, power-generating capacity. Coutant studied effects of thermal discharges on salmon in the Columbia River (Coutant 1970; Becker et al. 1971; Coutant 1973) and began to compile an annual review of the rapidly expanding literature on the effects of temperature on aquatic life for the *Journal of the Water Pollution Control Federation* (Coutant 1968–1980). In 1973, the National Academies of Sciences and Engineering published a comprehensive synthesis of most of the pertinent fish thermal effects literature as it applies to the need for and regulation of thermal discharges. This synthesis—which appeared as the chapter "Heat and Temperature" in "Section III, Freshwater Aquatic Life and Wildlife" of the NAS/NAE publication, *Water Quality Criteria 1972*, more commonly known as the *Blue Book*—provided a scientifically defensible foundation for protecting aquatic ecosystems, with emphasis on limiting harm to fishes. Additional investigations, both laboratory and field, helped establish general principles of how fishes at different life stages respond to elevated temperatures and determined the lethal limits for several species at specific life stages (Hokanson et al.1973b; Jones et al. 1977; McCormick and Wegner 1981). Other studies dealt with sublethal effects such as behavioral responses of fish to thermal discharges (Major and Mighell 1967; Munson et al. 1980; Ross and Siniff 1980) and the effects of chronic exposure to elevated temperatures on growth, mortality, and net biomass change (McCormick and Kleiner 1976; Hokanson et al. 1977; McCormick et al. 1977).

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Efforts to establish temperature requirements diminished in the late 1970s as power-generating plants and other facilities applied technologies such as cooling towers to control discharges of heated water. However, Biesinger et al. (1979) continued to gather existing field data from throughout the United States that related fish presence to temperature at the same sites as a means of estimating thermal tolerance limits. The temperature that fish have been experiencing when they are collected from lakes is usually not known because lakes stratify thermally, so it was necessary to restrict the matching of fish and temperature datasets to records from running waters, which are usually well mixed. This "national compendium" or database was used to construct yearly temperature-of-occurrence curves or regimes from weekly mean temperature records for several fish species in the database (Biesinger et al. 1979). The 95th percentile of the weekly mean temperatures was used to estimate the maximum temperatures tolerated by a particular species in nature. The technique was subsequently dubbed the "Fish and Temperature Database Matching System" (FTDMS) and contained data for more than 300 fish species collected at 574 field sites that were obtained from 1,905 source documents.

FTDMS was not available in time to be used in setting temperature water quality criteria for fish. However, the opportunity for using the field data approach occurred again in the mid-1980s when concern about global warming revived the interest of fisheries biologists in the thermal requirements of aquatic organisms. Computer technologies were advancing rapidly, making storage and manipulation of information in the database easier, more efficient, and more productive. State and federal agencies were also computerizing their fish and temperature data records, which could be more easily incorporated into FTDMS. To facilitate modern computerization of FTDMS, the original database gathered by Biesinger et al. (1979) was converted from 7-track to 9-track tape, arranged into a new file structure to more efficiently manipulate and analyze the original and new data, and rigorously reviewed to assure completeness, conversion integrity, and indications of original database errors that were corrected or eliminated.

This paper describes the nature of the component databases, how the data in them are used to calculate maximum temperature tolerance estimates, and what these values are for 30 common fish species. To help the reader put these FTDMS values in perspective in relation to the state of knowledge on thermal tolerances, we have compared them with several additional types of fish temperature response information obtained from the literature.

Methods

Expansion of the FTDMS Database

Data Acquisition

Use of the FTDMS to estimate thermal tolerance limits for a species requires that temperature information throughout a wide range of thermal habitat conditions be included in the database. Therefore, new fish and temperature information are continually being sought and incorporated. The addition of private and state-owned fish location databases has more than doubled the size of the original FTDMS data files. Recent data collection efforts have focused on states adjacent to the Mississippi River from Canada to the Gulf of Mexico, although several data files from elsewhere in the United States also have been added (e.g., Oregon, Colorado, Texas).

For data to be acceptable for inclusion into the FTDMS, several criteria must be met. Most importantly, the data must be from discrete sampling events with precise date and location records. We have particularly sought data in computerized form, preferably in disk operating system (DOS) format to ease the data translation efforts. Ideally, the latitude and longitude of the station will have been

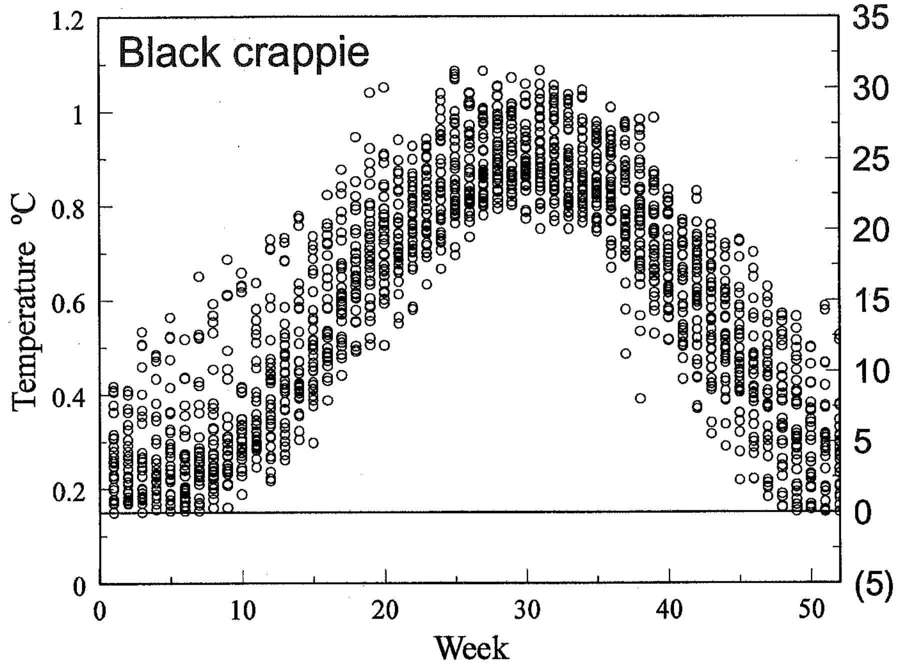

Figure 1. Black crappie F/T datasets (weekly mean temperatures) for all of the United States, plotted by weeks of the year.

determined using a Global Positioning System at the time fish were collected. However, frequently only a text description or the township and range of the station will be reported, so the latitude and longitude must be calculated and digitized into a Geographic Information System (GIS). Although data are available for nearly all North American freshwater fishes, in some cases the data files are so large that only a subset pertaining to the 30 species of concern here has been requested.

Incorporation of Fish Sampling Data

The fish sampling data in FTDMS reside on an IBM-compatible personal computer (PC), and all data manipulations are performed using Microsoft FoxPro, a database management system and programming language. Data have been received in a variety of formats, from DOS-compressed files to a 9-track tape using the EBCDIC character set. Data also have been obtained through electronic mail over the Internet system or using the Internet's File Transfer Protocol (FTP). All data received must be converted to DOS format and read into the FoxPro database, where they are analyzed for structure and completeness. File structures are frequently modified to remove extraneous data and enhance performance of the system. Latitude and longitude are converted to a decimal format; station indexes are quality assured to be unique; species codes and sample dates are formatted consistently; and a source field is added to the data file, providing a link to the original source. The fish sampling data are then ready to be matched with surface water temperatures.

Surface Water Temperature Data

The FTDMS uses records primarily from the U.S. Geological Survey (USGS) National Water Data Storage and Retrieval (WATSTORE) Daily Values File (Showen 1980). Water temperatures are obtained as daily means or calculated by averaging daily maxima and minima for states from which suitable fish collection records are acquired. Rarely will fish sample and water temperature records be taken concurrently by the same agency, but in cases where they have been, the temperature records usually consist of a single, instantaneous measurement taken sometime during the day. The original FTDMS database contained 40,000 instantaneous water temperature measurements (20% of all fish and temperature associations) that were used in constructing thermal regimes. These instantaneous values were excluded from the array used in the current analysis to eliminate temperatures that may have been diurnal extremes (Sinokrot and Stefan 1993; Stefan and Preudhomme 1993). Therefore, the smallest amount of temperature measurement data used now consists of at least two daily values employed in calculating a daily average. If a daily mean is provided by the USGS, all other values are disregarded.

The method for converting these water temperature data files is much like that for the fish sampling files—data are received on 9-track tape, downloaded to the PC, and read into FoxPro. From this point, the data are checked using a program that performs tests such as finding values obviously beyond normal temperature extremes, values recorded in differing units, or missing data. All records found to be flawed are flagged and ignored in subsequent manipulations.

Since the size of the temperature data files is approaching 100 Mb, the limited computing power of the PC makes it impractical to perform file maintenance and processing. Therefore, the temperature files are uploaded to the EPA Cray C94 supercomputer after the quality-assurance phase. This system can perform multiple operations simultaneously, resulting in a tremendous improvement in performance over a personal computer. A program has been written in the C programming language and optimized for the supercomputer to calculate mean temperatures for every USGS sampling station for every week on record. The output files are then transferred back to the PC for further manipulation.

Calculating the Thermal Tolerance of Fish

Matching Fish and Temperature Stations

After fish sampling and weekly mean temperature data are entered into FTDMS, the fish presence data are matched temporally and spatially with weekly mean temperatures to create a "Fish/Temperature (F/T) matched pairs" file. First, fish sampling locations within 7.5 km of a USGS temperature recording station are identified using a program that calculates the distance between the two locations. If fish sampling data meet this criteria, the location information is converted from its native state in the FoxPro database to a GIS file so both stations can be examined visually. To be accepted for creating an F/T dataset, each selected fish collection station must (1) be on the same branch of a river as the temperature station, (2) have no tributaries joining the river branch between the two stations, and (3) not be located on or near a lake shore. All of these are determined by the GIS coverage of major rivers and streams in the area (1:2,000,000 USGS Digital Line Graphs—hydrology layer). The resulting file of station matches is used as an input file by the F/T dataset creation program.

Fish thermal experience records were created from the original FTDMS database by using the following method described in Biesinger et al. (1979): "An F/T dataset is created, for a given species, at a specified station, if a fish occurrence and a temperature reading are recorded during the same year of record." Using this criterion, the F/T dataset files are computed using FoxPro on the PC for each source; a master F/T dataset file is created by merging the output from all sources.

Extracting Fish Thermal Regime Information

The temperatures in the master F/T file can be tabulated or plotted by weeks of the year for each species, with the resulting temperatures describing a species' composite thermal regime (Figure 1). Examination of this data plot provides an additional quality assurance check in which any potentially erroneous values or outliers can be identified and carefully reviewed before including them in subsequent analyses. Because of the possibility of undetected invalid data points in the source data, a 95th percentile rather than a maximum weekly mean temperature was thought to be a better, more conservative estimate of the upper thermal tolerance in the original method description (Biesinger et al. 1979) and has been adopted for subsequent analyses. Several procedures have been examined for obtaining estimates of maximum temperatures tolerated (Eaton et al. in press), and the method used here calculates them from a subset of the F/T datasets for each species that consists of the 5% of the highest weekly mean temperatures. Maximum tolerance estimates are only generated for species for which 1,000 or more F/T datasets are available. Therefore, the 95th percentile is calculated from a minimum of 50 warmest weekly mean temperature values, and at least two of the highest of these are automatically discarded. This method considers and rejects the same proportion of F/T values for each species, regardless of the total number of values available.

A confidence measure (SE) for the estimated maximum tolerance temperature related to F/T set variability and the total number of F/T sets in the highest 5% subset, was calculated using a nonparametric "bootstrap" technique (Efron 1983). The technique iteratively (1,000 times) samples randomly (n–1) F/T datasets, calculates a 95th percentile, and determines the SE of the resulting 1,000 percentile values.

Results and Discussion

A total of 207,846 weekly mean F/T datasets from 29 states have been generated for all species and entered into the master file. Table 1 presents maximum temperature estimates for 30 species of freshwater fishes and standard errors for these values. In general, relatively high SEs were obtained for species with the fewest datasets, but only one SE exceeded 1°C. The accuracy of the maximum tolerance estimate is dependent on the geographic distribution of F/T datasets in relation to the range limits of a species. Imperative is that the database contain F/T values near the "real" upper thermal tolerance limit for each species. The strategy employed to include this information in the database was to search for and incorporate as much fish and temperature data along a north-south axis (the Mississippi corridor) as possible. The influence of this relationship on FTDMS tolerance estimates was examined by dividing the master F/T file into datasets for each species from above and below the 40th parallel (roughly across the middle of the United States) and calculating tolerances for each region. Values for the south then were compared with those for all of the United States for coolwater and warmwater fish and found to be

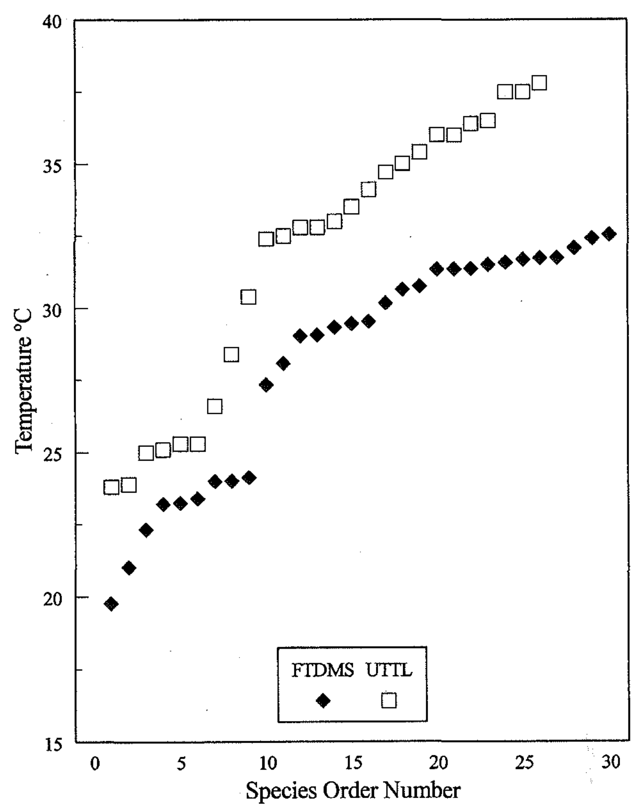

Figure 2. Pattern plot of lowest to highest 95th percentile FTDMS temperatures (solid diamonds) and laboratory-derived upper thermal tolerance limits (UTTLs, hollow squares) for the 30 fish species investigated.

Table 1. The 95th percentile weekly mean temperatures and standard errors calculated for the highest 5% of F/T dataset values (N) for each species

Species		95th percentile	Standard error	N
Black crappie	*Pomoxis nigromaculatus*	30.6	SE 0.31	146
Bluegill	*Lepomis macrochirus*	31.7	SE 0.08	495
Brook trout	*Salvelinus fontinalis*	22.3	SE 0.34	180
Brown bullhead	*Ictalurus nebulosus*	29.5	SE 0.78	85
Brown trout	*Salmo trutta*	24.1	SE 0.40	53
Carp	*Cyprinus carpio*	31.4	SE 0.06	714
Channel catfish	*Ictalurus punctatus*	31.6	SE 0.17	393
Chinook salmon	*Oncorhynchus tshawytscha*	24.0	SE 0.12	282
Chum salmon	*Oncorhynchus keta*	19.8	SE 0.18	70
Coho salmon	*Oncorhynchus kisutch*	23.4	SE 0.23	193
Cutthroat trout	*Oncorhynchus clarki*	23.2	SE 0.43	109
Flathead catfish	*Pylodictis olivaris*	32.5	SE 0.14	122
Freshwater drum	*Aplodinotus grunniens*	32.4	SE 0.25	213
Gizzard shad	*Dorosoma cepedianum*	31.5	SE 0.12	502
Golden shiner	*Notemigonus crysoleucas*	30.8	SE 0.27	134
Green sunfish	*Lepomus cyanellus*	31.7	SE 0.11	390
Largemouth bass	*Micropterus salmoides*	31.7	SE 0.11	391
Mountain whitefish	*Prosopium williamsoni*	23.2	SE 0.66	83
Northern pike	*Esox lucius*	28.0	SE 0.58	72
Pink salmon	*Oncorhynchus gorbuscha*	21.0	SE 1.01	76
Rainbow trout	*Oncorhynchus mykiss*	24.0	SE 0.14	442
Rock bass	*Ambloplites rupestris*	29.3	SE 0.40	121
Sauger	*Stizostedion canadense*	30.1	SE 0.33	106
Smallmouth bass	*Micropterus dolomieui*	29.5	SE 0.21	209
Smallmouth buffalo	*Ictiobus bubalus*	32.1	SE 0.16	236
Walleye	*Stizostedion vitreum*	29.0	SE 0.15	102
White bass	*Morone chrysops*	31.4	SE 0.06	249
White crappie	*Pomoxis annularis*	31.3	SE 0.09	215
White sucker	*Catostomus commersoni*	27.3	SE 0.37	433
Yellow perch	*Perca flavescens*	29.1	SE 0.74	64

higher (14 species) or the same (2 species) for the 16 cases where 1,000 or more F/T sets were available. This result strongly indicates that a potential exists for improving tolerance estimates by deriving them from dataset sub-groups corresponding spatially with species' southern-range limits. With two exceptions, the increases ranged from 0.1°C to 0.5°C and averaged 0.23°C. However, south values increased more for smallmouth bass and white sucker, being 0.9°C and 2.6°C higher, respectively. In both cases the number of F/T sets available for calculating tolerances for the south were much (four to eight times) smaller than the number of datasets for all of the United States. Tolerance estimates for coldwater fish were not consistently higher for either the north or south. Currently, the increase in standard errors associated with splitting the master F/T file to calculate regional tolerances approximately offsets the potential improvement in tolerance estimates gained by this geographic focusing technique, so the values in Table 1 are derived from F/T sets for all of the United States. However, as the database expands, it may be useful in the future to calculate tolerances from regional subsets of F/T datasets.

Further insights can be gained by comparing FTDMS highest 95th percentile temperatures to other kinds of temperature tolerance information found in the literature (Table 2). In regard to spatial relationships, it is likely that the highest 95th percentile temperatures in Table 1 are underestimates of upper tolerance levels for some warmwater fishes. It seems reasonable that if these species can tolerate temperatures found in streams to the southern border of the United States, which was the geographic limit for the data used in this analysis, then they could tolerate even higher temperatures in streams they might inhabit south of the U.S. border. A scatter plot of lowest to highest 95th percentile temperatures from Table 1 and of lowest to highest laboratory-derived thermal tolerance limits from Table 2 (Figure 2) indicates a relative flattening of the FTDMS data curve for warmwater fishes, probably reflecting extremes of surface water heating capacity for U.S. streams.

Most of the literature data have been generated through acute mortality tests or long-term growth studies conducted in the laboratory. Those listed in Table 2 were chosen based on their representativeness and on an availability of information about exposure conditions. Maximum weekly mean temperatures derived from FTDMS were always lower than the laboratory-determined lethal temperature (UTTL) values (Table 2), as would be expected. However, the difference between the two kinds of values is generally greater for most warmwater fishes than for coldwater and coolwater species, again indicating that the true field temperature tolerance might be greater than the FTDMS 95th percentile temperatures. Our assignment of species to coldwater, coolwater, or warmwater guilds is somewhat arbitrary but mostly follows established convention, which is based on laboratory mortality test data (Hokanson 1977). The trout-salmon-whitefish (coldwater) species, comprising the nine lowest FTDMS data points in Figure 2, are found at distinctly lower temperatures than the others, but no obvious separation point that might indicate a guild boundary is observed for the 21 other data points representing the tolerances of coolwater and warmwater fishes. Also, based on the FTDMS values in Table 2, some changes in guild membership might be appropriate, such as a transfer of white crappie to warmwater, and transfer of smallmouth bass and rock bass to coolwater (perhaps a moot point considering the preceding observation).

Another analysis consisted of dividing the master F/T dataset file on a temporal basis to see if lower tolerance values would be observed with a more restricted matching of fish and temperature sample dates, indicating that fish might not have been at a site when the water was at its warmest. The original F/T definition assumes that, since a fish record can be matched with 52 weekly mean temperatures, the particular species of fish

Table 2. A comparison of upper thermal tolerance limits (UTTL, C) as determined by laboratory mortality tests; of the highest 95th percentiles from the present analysis; of final preferendums, literature maximum growth temperatures, or calculated maximum growth temperatures obtained by fitting a curve to literature growth data; and of U.S. EPA (1976) water quality criteria for growth and survival.

	UTTL[a] (acclimation temperature) test duration, lifestage	FTDMS max. 95th percentile	Max. growth temp., lifestage	EPA max. wkly. mean temp.
COLDWATER SPECIES				
Brook trout	25.3(24) 3.5d, J[b] Fry et al. 1946	22.3	14.4 CMGT[c], L–J McCormick et al. 1972	19/24
Brown trout	25.3(23) 7d, J Frost and Brown 1967	24.1	18 CMGT, J Brown 1946	NA
Chinook salmon	25.1[d] 8.5d, J Brett 1952	24.0	20.2 CMGT, J Brett 1952	NA
Chum salmon	23.8[d] 6.3d, J Brett 1952	19.8	NA[e]	NA
Coho salmon	25.0[d] 6.3d, J Brett 1952	23.4	15 P[f], J USDI 1970	18/24
Cutthroat trout	NA	23.2	NA	NA
Mountain whitefish	NA	23.9	NA	NA
Pink salmon	23.9[d] 4.3d, J Brett 1952	21.0	NA	NA
Rainbow trout	26.6(24) 1d, J Charlon et al. 1970	24.0	18.1 CMGT, J Hokanson et al. 1977	19/24
COOL WATER SPECIES				
Black crappie	32.5 (NA) 4d, J Brungs and Jones 1977	30.6	28.3 P, NA Neill and Magnuson 1974	27/NA
Northern pike	28.4(18) 7d, L Hokanson et al. 1973a	28.0	23.9 CMGT, L Hokanson et al. 1973a	28/30
Sauger	30.4(25.8)4d, J Smith and Koenst 1975	30.1	22.0 MGT, J Smith and Koenst 1975	25/NA
Walleye	31.6(24.1) 4d, J Koenst and Smith 1976	29.0	22.0 MGT, J Koenst and Smith 1976	NA
White crappie	32.8 (25.6) 4d, J Peterson et al. 1974	31.3	27–28.5 P, A Gammon 1973	28/NA
White sucker	30.5(24.1) 4d, J Koenst and Smith 1982	27.3	26 CMGT, L–J McCormick et al. 1977	28/NA
Yellow perch	33(∅ 30) 7d, J McCormick 1976	29.1	26.8 CMGT, J McCormick 1976	29/NA
WARM WATER SPECIES				
Bluegill	37.3(33) 4d, J J. Banner and Van Arman 1973	29.5	30 CMGT, J Lemke 1977	32/35
Brown bullhead	37.5[d] 0.5d, J Brett 1944	29.5	27.8 CMGT, J Keast 1985	NA
Carp	36(34) 2d, J Meuwis and Heuts 1957	31.4	31.2 P, NA Neill and Magnuson 1974	NA
Channel catfish	37.8(34) 5d, J Allen and Strawn 1968	31.6	30 P, J Andrews and Stickney 1972	32/35
Flathead catfish	NA	32.5	31.5-33.5 P, A Gammon 1973	NA
Freshwater drum	32.8(25-31)2d, J Cvancara et al. 1977	32.4	31.3 P, J Reutter and Herdendorf 1976	NA
Gizzard shad	36.5[d] 1d, J Hart 1952	31.5	28.5–31.0 P, A Gammon 1973	NA
Golden shiner	34.7[d] 1d, U Hart 1952	30.8	23.8 P, M Cincotta and Stauffer 1984	NA
Green sunfish	35.4[d] 2d, J Boswell 1967	31.7	30.6 P, NA Cherry et al. 1977	NA
Largemouth bass	36.4(30) 1d, J Hart 1952	31.7	29 CMGT, J McCormick and Wegner 1981	32/34
Rock bass	36(36) 7d, J Cherry et al 1977	29.3	27.4 P, NA Neill and Magnuson 1974	NA
Smallmouth bass	35(35) 7d, J Cherry et al. 1977	29.5	28.2 CMGT, J Horning and Pearson 1973	29/NA
Smallmouth buffalo	NA	32.1	31–34 P, A Gammon 1973	NA
White bass	33.5(25–31)2d, J Cvancara 1977	31.4	NA	NA

was at that location for the whole year. Development of datasets in accordance with this "yearly matching" definition produces the greatest number of F/T datasets with the widest geographic coverage. A "seasonal matching" group of F/T datasets is created when fish occurrence and temperature records for the same seasons of a year are combined. For the current analysis, the year was separated into two seasons, cold and warm. The warm season was defined as week 14 through week 42 (mid-March through mid-October); any fish sample taken in the cold season was matched with temperatures from week 14 through week 42. A fish sample taken later than week 42 was matched with temperature readings from weeks 43 through 52 and with temperatures from the first 13 weeks of the following year. Likewise, a fish sample taken earlier than week 14 was matched with temperatures from weeks 43–52 of the previous year and weeks 1–13 of the current year. The results showed a mean difference of only 0.40°C between yearly and warm season tolerance values for the 24 species with sufficient F/T datasets. Warm season values were higher for eight of the 24 species and were the same as yearly for five species. Among coldwater fish, warm-season

[a]UTTL: Upper Thermal Tolerance Limit. This value is acclimation and time-of-exposure dependent, thus UTTL values are followed by acclimation temperature (in parenthesis) and time in days to 50% mortality.

[b]L, J, A, M, U: Larval, Juvenile, Adult, Mixed, Unknown. Lifestage of test organism is included because age also affects thermal response.

[c]CMGT: Calculated Maximum Growth Temperature. This temperature is calculated by fitting a curve to experimental temperature-growth rate data with a second degree polynomial equation.

[d]Ultimate Upper Incipient Lethal Temperature (Fry et al. 1946). This is the upper lethal temperature which is achieved at maximum acclimation temperatures, i.e. it cannot be increased by raising the acclimation temperature. The UUILT is also a time-of-exposure dependent 50% mortality value.

[e]NA: Data not available.

[f]P: Final Temperature Preferendum. This temperature has been observed to agree closely with maximum growth temperatures (Magnuson et al. 1990).

values were lower only for brook trout, which was reduced by 0.6°C (to 21.7°C). The largest difference, and the only one of more than 1.0°C, was a 1.5°C reduction for freshwater drum. The magnitude of the differences, the lack of a consistent direction of change, and the increase in SEs because of the smaller number of F/T sets indicate that the yearly values are the best tolerance estimates at this time. Semiannual or quarterly associations of temperature recording and fish collection dates may be more appropriate, especially for coldwater and coolwater species, after database expansion.

A potential source of error in the FTDMS system is the possibility of fish inhabiting isolated refuges or cool spots in streams and therefore having been collected at stream temperatures different from those being recorded at the corresponding USGS monitoring station. Freshwater fish are known to be able to detect small differences in water temperature (Bardach and Bjorklund 1957) and to seek cooler water if it is available under conditions of heat stress (Kaya et al. 1977; Headrick and Carline 1993). This is most likely to be a factor with coldwater and coolwater fish populations that are continually being thermally challenged by temperatures at the southern limits of their U.S. range. Numerous instances of such "behavioral thermoregulation" have been observed, especially among fish in lakes (Neill and Magnuson 1974; Spigarelli et al. 1974; Coutant 1985). Berman and Quinn (1991) used surgically implanted radio transmitters to show that chinook salmon maintained a mean internal body temperature 2.5°C below the ambient temperature in the Yakima River during the four months prior to spawning. In this case the function of the behavior was postulated to be for energy conservation at sublethal temperatures and not survival. However, in other instances, fish either will not or cannot avoid lethal temperatures and will be killed. McMichael and Kaya (1991) cite an observation of trout and mountain whitefish in the Madison River, Montana, dying at high temperature (27°C) while those still alive in the same stream reach continued to feed; similar behavior has been observed in different U.S. regions. The extent to which the thermal refuge factor might be influencing the estimated tolerances for coldwater and coolwater fishes is obviously unknown, but the consistency of the FTDMS values with the other lethal and sublethal temperatures from the various sources given in Table 2 suggest that the influence, if any, is minor. It might be noted in particular that the FTDMS values are similar to, but in no cases greater than, the EPA temperature criteria values for total survival for a week's exposure. Therefore, we do not propose any reduction or correction factor at this time to compensate for a refugia effect.

In summary, we consider the current method an important addition to the criteria generation techniques that use laboratory data because the method is based directly on the temperatures at which fish populations exist in nature. Use of the 95th percentile of weekly mean F/T datasets rather than the 100th percentile appears to be an adequate factor to protect against the possible mechanical (e.g., inaccuracies in temperature records) or biological (e.g., fish in thermal refuges) problems that might be buried in the database. Much additional useful information is contained in the FTDMS database. F/T sets at the 5th percentile level will provide information about the sensitivity of warmwater fish to low winter temperatures. As demonstrated for smallmouth bass (Shuter et al. 1989) and largemouth bass (McCormick and Jensen 1992), cold (winter) temperatures and their duration will be important in determining the northern range distribution of some warmer-water fishes. Weekly means, as were used in calculating the current set of tolerance estimates, are only one possible expression of the temperature regimes experienced by fishes in nature. It would be interesting to examine species' tolerances in terms of daily means, or of daily or weekly maxima, which are also contained in the database. There are sufficient data in FTDMS for generating tolerances for many additional fish species, and more will become obtainable as the database expands. In conclusion, this system is a cost-effective way to generate a wide range of temperature tolerance information for a large number (100+) of freshwater fish species.

Acknowledgments

The authors thank K. E. F. Hokanson for important contributions to the conceptualization and development of FTDMS that were facilitated by an extensive knowledge of the thermal effects literature and a career of work in the field of thermal biology. We also thank J. A. Westman for GIS data manipulations and computer programming; D. J. Fairchild for fish and temperature field data acquisition; J. A. Wisniewski and D. J. Grunwald for thermal literature database development; and R. L. Spehar, J. D. Yount, E. P. Hunt, G. A. Chapman, C. A. Frissell, and J. J. Magnuson for critical review of the manuscript.

References

Allen, K. O., and **K. Strawn**. 1968. Heat tolerance of channel catfish (*Ictalurus punctatus*). Proc. Annu. Conf. Southeast Assoc. Game and Fish Commissioners 21:399–410.

Andrews, J. W., and **R. R. Stickney**. 1972. Interactions of feeding rates and environmental temperature on growth, food conversion, and body composition of channel catfish. Trans. Am. Fish. Soc. 101:94–99.

Banner, A., and **J. A. Van Arman**. 1973. Thermal effects of eggs, larvae, and juveniles of bluegill sunfish. EPA, Report R3-73-041, Duluth, MN.

Bardach, J. E., and **R. G. Bjorklund**. 1957. The temperature sensitivity of some American freshwater fishes. Am. Nat. 91:233–251.

Beamish, F. W. H. 1974. Apparent specific dynamic action of largemouth bass (*Micropterus salmoides*) Lacepede. Can. J. Zool. 50:153–164.

Becker, C. D., **C. C. Coutant**, and **E. F. Prentice**. 1971. Experimental drifts of juvenile salmonids through effluent discharges at Hanford. Part II. 1969 drifts and conclusions. Report 1527, Battelle Northwest Laboratories, Richland, WA.

Berman, C. H., and **T. P. Quinn**. 1991. Behavioral thermoregulation and homing by spring chinook salmon (*Onchorynchus tshawytscha* Walbaum) in the Yakima River. J. Fish Biol. 39:301–312.

Biesinger, K. E., R. P. Brown, C. R. Bernick, G. A. Flittner, and **K. E. F. Hokanson**. 1979. A national compendium of freshwater fish and water temperature data. Volume 1. Data management techniques, output examples and limitations. EPA, Report 600/3-79-056, Duluth, MN.

Boswell, T. O. 1967. The effects of water hardness on the upper lethal temperature of the green sunfish (*Lepomis cyanellus*). Master's thesis. New Mexico State University, Las Cruces, NM.

Brett, J. R. 1944. Some lethal temperature relations of Algonquin Park fishes. University Toronto Studies, Biology Series No. 52. University of Toronto Press, Toronto.

———. 1952. Temperature tolerance in young pacific salmon (*Oncorhynchus*). J. Fish. Res. Board Can. 9:265–323.

———. 1960. Thermal requirements of fish—three decades of study. Pages 110–117 *in* C. M. Tarzwell, ed. Biological problems of water pollution. Department of Health, Education and Welfare, Robert A. Taft Sanitary Engineering Center, Cincinnati, OH.

———. 1971. Energetic response of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11:99–113.

Brett, J. R., J. E. Shelbourn, and **C. T. Shoop**. 1969. Growth rate and body composition of fingerling sockeye salmon (*Oncorhynchus nerka*) in relation to temperature and ration size. J. Fish. Res. Board Can. 26:2363–2394.

Brett, J. R., and **D. B. Sutherland**. 1970. Improvement in the artificial rearing of sockeye salmon by environmental control. Fish. Res. Board Can., Gen. Ser. Circ. 89.

Brown, M. E. 1946. The growth of brown trout (*Salmo trutta* Linn.). III. The effect of temperature on the growth of two-year-old trout. J. Exp. Biol. 22:145–155.

Brungs, W. A., and **B. R. Jones**. 1977. Temperature criteria for freshwater fish: protocol and procedures. EPA, Report 600/3-77-061, Duluth, MN.

Charlon, N., B. Barbier, and **L. Bonnet**. 1970. Thermal resistance of rainbow trout (*Salmo gairdneri* Richardson) to abrupt temperature variations. Ann. d'Hydrobiol. 1:73–89.

Cherry, D. S., K. L. Dickson, J. Cairns Jr., and **J. R. Stauffer**. 1977. Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. J. Fish. Res. Board Can. 34:239–246.

Cincotta, D. A., and **J. R. Stauffer Jr**. 1984. Temperature preference and avoidance studies of six North American freshwater fish species. Hydrobiol. 109:173–177.

Coutant, C. C. 1968–1980. Thermal pollution-biological effects: a review of the literature of 1967–1979. J. Water Pollut. Control Fed. 40–52.

———. 1970. Thermal resistance of adult coho (*Oncorhynchus kitsutch*) and jack chinook (*O. tschawytscha*) salmon, and the adult steelhead trout (*Salmo gairdnerii*) from the Columbia River. Report 1508, Battelle Northwest Laboratories, Richland, WA.

———. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Board Can. 30:965–973.

———. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. 114:31–61.

Cvancara, V. A., S. F. Stieber, and **B. A. Cvancara**. 1977. Summer temperature tolerance of selected species of Mississippi River-acclimated young-of-the-year fishes. Comp. Biochem. Physiol. 56A:81–85.

Eaton, J. G., H. McCormick, H. G. Stefan, and **M. Hondzo**. *In press.* Extreme value analysis of a fish/temperature field database. J. Ecol. Engineer.

Efron, B., and **G. Gong**. 1983. A leisurely look at the bootstrap, the jackknife, and the cross-validation. Am. Statistic. 37(1):36–48.

Frost, W. E., and **M. E. Brown**. 1967. The trout. New Naturalist Series, Collins, St. James Place, London.

Fry, F. E. J. 1947. Effects of the environment on animal activity. University of Toronto Biology Series No. 55. University of Toronto Press, Toronto.

———. 1971. The effect of environmental factors on the physiology of fish. Pages 1–98 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, volume 6. Academic Press, New York.

Fry, F. E. J., J. R. Brett, and **G. H. Clawson**. 1942. Lethal limits of temperature for young goldfish. Rev. Can. Biol. 1:50–56.

Fry, F. E. J., J. S. Hart, and **K. F. Walker**. 1946. Lethal temperature relations for a sample of young speckled trout (*Salvelinus fontinalis*). University of Toronto Biology Series No. 54. University of Toronto Press, Toronto.

Gammon, J. R. 1973. The effect of thermal effluents on the populations of fish and macroinvertebrates in the Wabash River. Technical Report 32, Purdue University Water Research Center.

Hart, J. S. 1947. Lethal temperature relations of certain fish in the Toronto Region. Trans. Royal Soc. Can. (Section 5) 41:57–71.

Hart, J. S. 1952. Geographical variations of some physiological and morphological characters in certain freshwater fish. University of Toronto Biology Series No. 60. University of Toronto Press, Toronto.

Headrick M. R., and **R. F. Carline**. 1993. Restricted summer habitat and growth of northern pike in two southern Ohio impoundments. Trans. Am. Fish. Soc. 122:228–236.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34:1524–1550.

Hokanson, K. E .F., C. F. Kleiner, and **T. W. Thorslund**. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 34:639–648.

Hokanson, K. E. F., J. H. McCormick, and **B. R. Jones**. 1973a. Temperature requirements for embryos and larvae of the northern pike (*Esox lucius* Linnaeus). Trans. Am. Fish. Soc. 102:89–100.

Hokanson, K. E. F., J. H. McCormick, B. R. Jones, and **J. H. Tucker**. 1973b. Thermal requirements for maturation, spawning, and embryo survival of the brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 30:975–984.

Horning II, W. B., and **R. E. Pearson**. 1973. Growth temperature requirements and lower lethal temperatures for juvenile smallmouth bass (*Micropterus dolomieui*). J. Fish. Res. Board Can. 30:1226–1230.

IPCC (Intergovernmental Panel on Climate Change). 1992. Climate change 1992: the supplementary report to the intergovernmental panel on climate change scientific assessment. Cambridge University Press, Cambridge, UK.

Jones, B. R., K. E. F. Hokanson, and **J. H. McCormick**. 1977. Winter temperature requirements for maturation and spawning of yellow perch (*Perca flavescens* Mitchill). Pages 189–192 *in* M. Marois, ed. Proceedings of the world conference towards a plan of action for mankind, Volume 3. Biological balance and thermal modifications. Pergamon Press, New York.

Kaya, C. M., L. R. Kaeding, and **D. E. Burkhalter**. 1977. Use of a cold-water refuge by rainbow and brown trout in a geothermally heated stream. Prog. Fish Cultur. 39:37–39.

Keast, A. 1985. Growth responses of the brown bullhead (*Ictalurus nebulosus*) to temperature. Can. J. Zool. 63:1510–1515.

Koenst, W. M., and **L. L. Smith Jr.** 1976. Thermal requirements of the early life history stages of walleye (*Stizostedion vitreum vitreum*) and sauger, (*Stizostedion canadense*). J. Fish. Res. Board Can. 33:1130–1138.

_____. 1982. Factors influencing growth and survival of white sucker (Catostomus commersoni). EPA, Project Summary EPA 600/S3-82-051. National Technical Information Service, Springfield, VA.

Lemke, A. E. 1977. Optimum temperature for growth of juvenile bluegills, *Lepomis macrochirus* Rafinesque. Prog. Fish Cultur. 39:55–57.

Magnuson, J. J., J. D. Meisner, and **D. K. Hill**. 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Trans. Am. Fish. Soc. 119:254-264.

Major R. L., and **J. L. Mighell**. 1967. Influence of the Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of sockeye salmon. U.S. Fish and Wildlife Service Fishery Bulletin 66:131–147.

McCormick, J. H. 1976. Temperature effects on young yellow perch (*Perca flavescens* Mitchill). EPA, Report 600/3-76-057, Duluth, MN.

McCormick, J. H., K. E. F. Hokanson, and **B. R. Jones**. 1972. Effects of temperature on growth and survival of young brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 29:1107–1112.

McCormick, J. H., and **K. M. Jensen**. 1992. Osmoregulatory failure and death of first-year largemouth bass (*Micropterus salmonoides*) exposed to low pH and elevated aluminum, at low temperatures in soft water. Can. J. Fish. and Aquat. Sci. 49:1189–1197.

McCormick, J. H., B. R. Jones, and **K. E. F. Hokanson**. 1977. White sucker (*Catastomus commersoni*) embryo development and early growth and survival at different temperatures. J. Fish. Res. Board Can. 34:1019–1025.

McCormick, J. H., and **C. F. Kleiner**. 1976. Growth and survival of young-of-the-year emerald shiners (*Notropis antherinoides*) at different temperatures. J. Fish. Res. Board Can .33:839–842.

McCormick, J. H., and **J. A. Wegner**. 1981. Responses of largemouth bass from different latitudes to elevated water temperatures. Trans. Am. Fish. Soc. 110:417–429.

McMichael, G. A., and **C. M. Kaya**. 1991. Relations among stream temperature, angling success for rainbow and brown trout, and fisherman satisfaction. N. Am. J. Fish. Manage. 11:190–199.

Meuwis, A. L., and **M. J. Heuts**. 1957. Temperature dependence of breathing rate in carp. Biol. Bull. 112:97–107.

Munson, B. H., J. H. McCormick, and **H. L. Collins**. 1980. Influence of thermal challenge on conditioned feeding forays of juvenile rainbow trout. Trans. Am. Fish. Soc.109:116–121.

NAS/NAE (National Academy of Sciences/National Academy of Engineering). 1973. Water Quality Criteria 1972. U.S. Government Printing Office, Washington, DC.

National Research Council. 1983. Changing climate: a report of the CO_2 assessment committee. National Academy Press, Washington, DC.

Neill, W. H., and **J. J. Magnuson**. 1974. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a power plant at Lake Monona, Wisconsin. Trans. Am. Fish. Soc. 103:663–710.

Peterson, S. E., R. M. Schutcky, and **S. E. Allison**. 1974. Temperature preference, avoidance, and shock experiments with freshwater fishes and crayfishes. Bulletin 10, Ichthyological Associates, Ithaca, NY.

Reutter, J. M., and **C. E. Herdendorf**. 1976. Thermal discharge from a nuclear power plant: predicted effects on Lake Erie fish. Ohio J. Sci. 76:39–45.

Rose, A. H. 1967. Pages 1–3 *in* A. H. Rose, ed. Thermobiology. Academic Press, New York.

Ross, M. J., and **D. B. Siniff**. 1980. Spatial distribution and temperature selection of fish near the thermal outfall of a power plant during fall, winter and spring. EPA, Report 600/3-80-009. Duluth, MN.

Shuter, B. J., P. E. Ihssen, D. L. Wales, and **E. J. Snucins**. 1989. The effects of temperature, pH and water hardness on winter starvation of young-of-the-year smallmouth bass (*Micropterus dolomieui* Lacepede). J. Fish Biol. 35:765–780.

Showen, C. R. 1980. Data formats for U.S. Geological survey compiler files containing daily values for water parameters. U.S. Geological Survey, Open-file Report 76-563 (revised).

Sinokrot, B. A., and **H. G. Stefan**. 1993. Stream temperature dynamics: measurements and modeling. Water Resour. Res. 29:2299–2312.

Spigarelli, S. A., G. P. Romberg, W. Prepejchal, and **M. M. Thommes**. 1974. Body temperature characteristics of fish at a thermal discharge on Lake Michigan. Pages 119–132 *in* J. W. Gibbons and R. R. Scharitz, eds. Thermal ecology. U.S. Atomic Energy Commission, Springfield, VA.

Stefan, H. G., and **E. B. Preud'homme**. 1993. Stream temperature estimation from air temperature. Water Resour. Bull. 29:27–45.

U.S. Department of the Interior. 1970. Physical and ecological effects of waste heat on Lake Michigan. U.S. Fish and Wildlife Service, Ann Arbor, MI.

U.S. Environmental Protection Agency. 1976. Quality criteria for water. U.S. EPA, Washington, DC.