

An Analysis of the Influence of Annual Thermal Variables on the Occurrence of Fifteen Warmwater Fishes

ROBERT M. SCHELLER*¹

*DynTel Corporation
6201 Congdon Boulevard, Duluth, Minnesota 55804, USA*

VIRGINIA M. SNARSKI AND JOHN G. EATON

*U.S. Environmental Protection Agency,
National Health and Environmental Effects Research Laboratory,
Mid-Continent Ecology Division, 6201 Congdon Boulevard, Duluth, Minnesota 55804, USA*

GARY W. OEHLERT

*Department of Applied Statistics, University of Minnesota,
1994 Buford Ave., St. Paul, Minnesota 55108, USA*

Abstract.—Multisource fish-sampling data and U.S. Geological Survey temperature data from streams throughout the United States were used to investigate the influence of derived thermal regime variables on the presence or absence of 15 common warmwater fish species. The 3-year average annual thermal regime was calculated for streams where presence or absence was known for these 15 species. Six variables estimated to be of biological importance to the winter and summer survival and recruitment of a species, including measures of feeding and nonfeeding periods, were calculated from these thermal regimes. Stepwise discriminant analysis and multiple regression were used to select optimal variables for creating multivariate models. Parametric and nonparametric multivariate discriminant analyses were then performed to test our ability to correctly classify presence or absence using the thermal variables. These statistical empirical models were able to correctly predict presence or absence with greater than 90% accuracy for 13 of 15 species. Nonparametric (*K*th nearest neighbor) analyses had marginally more accurate predictions than parametric (linear) analyses. This technique may allow for an improved estimation of potential changes in distribution under various global warming scenarios.

A recent United Nations Intergovernmental Panel on Climate Change report (IPCC 1995) has provided new information substantiating the likelihood of global climate change. The effect of climate change on freshwater ecosystems, including effects on freshwater fish, will be profound (Magnuson et al. 1997). Temperature will be a primary factor in determining which freshwater fish species will be most affected. One potential effect of climate change is modification of the geographic distribution of fish species. To predict this modification, it is necessary to estimate temperature tolerances of fishes and then relate these tolerances to the changing environment.

Previous investigations have used field data to estimate maximum temperature tolerances of fishes (Eaton et al. 1995), which in turn were used to

project the effects of global warming on fishes in lakes (Stefan et al. 1994, 1995) and streams (Eaton and Scheller 1996). In general, the prevalence of warmwater fish was predicted to increase in the United States and that of coldwater fish to decrease under conditions of increased maximum temperatures. It is likely that some warmwater fishes would benefit as a result of the moderating effect that global warming would have on stressful low temperature conditions prevalent during the winter at the boundaries of their current range. However, relatively little research has been done on the low temperature tolerances of most freshwater fish species.

There is evidence that warmwater fish do not feed or feed only sporadically and eat very little at temperatures below 6–10°C (e.g. Johnson and Charlton 1960; Keast 1968; McComish 1971; Shuter et al. 1980, 1989). For example, Keast (1968) lists the temperatures at which black bullhead *Ameiurus melas*, black crappie *Pomoxis nigromaculatus*, pumpkinseed *Lepomis gibbosus*, rock bass *Ambloplites rupestris*, and largemouth bass *Micropterus*

* Corresponding author: rmscheller@students.wisc.edu

¹ Present address: Department of Forest Ecology and Management, University of Wisconsin–Madison, Madison, Wisconsin 53706, USA.

cropterus salmoides start feeding as about 6.5, 6.5, 8, 8.5, and 8.5°C, respectively. Death at low temperatures has been observed to be a function of the duration of winter nonfeeding temperatures, which results in depletion of energy stores (Johnson and Charlton 1960; Shuter et al. 1989; Johnson and Evans 1991) or osmoregulatory dysfunction (Johnson and Evans 1996), or both. In addition to longer-term effects resulting from energy depletion, there is evidence that mortality among some species from acute physiological stress occurs at temperatures between 0°C and 4°C. Sheehan et al. (1990) found that young-of-the-year green sunfish *Lepomis cyanellus*, bluegill *L. macrochirus*, and largemouth bass were relatively intolerant to low temperature. All green sunfish died as temperature was reduced from 5°C to 4°C, bluegills suffered mortalities of 32%, 8%, and 4% at 0, 2, and 4°C, respectively, and largemouth bass experienced 4%, 0%, and 12% mortality at 0, 2, and 4°C. In 30-d laboratory exposures. Johnson and Evans (1996) observed mortality among white perch *Morone americana* to increase from 11% at 4°C to 71% at 2.5°C during 150 d of exposure to low temperatures. A number of studies have documented or demonstrated that smaller fish or young of the year are more vulnerable than larger fish to overwinter mortality (Toneys and Coble 1979; Post and Evans 1989; Shuter et al. 1989), and that good growth conditions in the preceding summer reduce this vulnerability.

The present study describes a multivariate statistical procedure for selecting variables and predicting the presence or absence of 15 fish species using thermal regime criteria developed from fish collection records and U.S. Geological Survey (USGS) stream monitoring station temperature files.

Methods

Data sources.—Our analysis is based on two data sources: (1) weekly average stream temperatures, which are drawn from the USGS National Water Data Storage and Retrieval (WATSTORE; Showen 1980) files of stream monitoring stations, and (2) multisource fish-sampling events in close proximity to USGS monitoring sites. These fish data are obtained from a variety of sources (i.e., state fisheries or natural resource agencies, universities) from throughout the contiguous United States. The unique fish collection and water temperature regime combinations for each species are derived from the Fish and Temperature Database Matching System (FTDMS) database (Eaton et al.

1995). Criteria for spatially matching stream monitoring sites and fish collection records are given in that report.

Thermal regime derivation.—Fish-sampling records for each species were matched with weekly USGS stream temperature data for the entire sampling year in which fish were collected, starting with week of the year 38 (in late September), plus, when available, the two previous sampling years of USGS stream data. A 3-year mean was thought to better represent the thermal experience of the fish species collected because we assumed that these species were resident at that site. Additionally, a 3-year average would mitigate anomalies that might occur within a single year.

Weekly temperatures of corresponding weeks of the three years were averaged to create an annual thermal regime consisting of 52 average weekly stream temperatures. In cases when USGS temperature data were not available for the full three years, only two complete years (25% of all regimes) or one year (7% of all regimes) of data were considered acceptable. If one or two consecutive weeks of data within a year were missing (a common occurrence in USGS datasets), an average of the previous and next weeks' average temperature was used for the missing weeks. These three year averages, which are associated with one or more sampling events, are referred to as 'annual thermal regimes' in this study.

Fish presence or absence.—If a given species was captured at any time during an annual thermal regime, the species was considered to be present during all of that annual thermal regime. If not, the annual thermal regime was assigned an absence value for that species. It is recognized that false absences may occur due to inadequate or insufficient sampling. However, only streams that were adequately sampled by professional fisheries or natural resource biologists for the 15 species chosen were used as the basis for this study. Because our fish data are derived from external sources, we are dependent on their evaluation of their sampling methods as thorough and complete for all species analyzed.

The data analyzed for each species was limited to annual thermal regimes within those watersheds in which that species was known to occur (Boschung et al. 1983). The subregion watershed classification system developed by Maxwell et al. (1995) provided the watershed boundaries used for determining whether to include or exclude "absence" thermal regime values for each species. Subregion watersheds were considered the poten-

tial (i.e., unimpeded or feasible access) geographic range of each species, and thermal regimes found outside of this range were not included in the final analysis. As a consequence, the total number of sites available to each species is unique. This seemed the best way to allow for inclusion of sites which are absences due to thermal conditions and to provide for expansion of a species' range under climate change conditions. Nevertheless, some of our absence values may result from factors unrelated to temperature (e.g., river size, flow, competition, habitat, etc.).

Thermal regime variables.—From each annual thermal regime classified as to presence or absence for each of the 15 species, we derived six variables which were considered potentially important components or attributes of warmwater fishes' thermal experience. These six variables, designated TOTAL, >8C, ≤8C, FACTOR, WEEK8C, and WEEK2C, are defined below and were largely based on the limited low temperature effects information described previously.

The TOTAL variable is defined as the cumulative temperature for all weeks within the annual thermal regime. We used the unit degree-weeks (DW), defined as the sum of the average weekly temperatures for the defined period, to quantify the cumulative temperature experienced during these thermal conditions. Degree-weeks integrates time and temperature over longer-term periods (months, seasons) within the annual thermal regime. The TOTAL variable quantifies the thermal regime over the entire annual cycle and was thought to take into consideration those physiological processes that occur gradually or serially over a long period of time (e.g., gonadal development and maturation) that result in important life cycle events such as reproduction. Although TOTAL is essentially equivalent to average temperature multiplied by the number of weeks in a year, the unit was retained to facilitate comparisons to the ≤8C and >8C variables.

Each annual thermal regime was subdivided based on whether the weekly average temperature is above 8°C (>8C variable) or equal to or below 8°C (≤8C variable). These variables are chosen to approximate the feeding and nonfeeding periods within the annual thermal regime. Although the temperature at which fish start feeding after overwintering has been reported to vary among species, variation in feeding activity with temperature also has been observed between different sizes of the same species (Keast 1968, 1977). At or below this temperature, warmwater fish are quiescent or

dormant and either don't grow or lose weight. Within a few degrees above this temperature, they become active and are capable of growth (Keast 1968). Thus the >8C variable quantifies the period of growth. The ≤8C variable quantifies the period within a year of zero or negative fish growth, analogous to the starvation period described by Shuter and Post (1990).

The FACTOR variable (dimensionless) is calculated by dividing the >8C variable into the ≤8C variable. Shuter and Post (1990) demonstrated that this proportion or coefficient may be critical in determining the northern limits of some warmwater fishes.

The WEEK8C variable is equal to the number of weeks at or below minimum critical feeding temperature (8°C). This is a measure of the time that fish experience zero growth or starvation. The rationale for this variable is that the duration of the nonfeeding period might be more important to survival than the actual temperature.

The WEEK2C variable, which is equal to the number of weeks at or below 2°C, was included to cover the possibility that very low temperature might cause mortality through osmoregulatory dysfunction (Johnson and Evans 1996) or other physiological mechanisms.

Statistical Analysis

Annual thermal regime data sets for each fish species were analyzed individually with multivariate statistical procedures using SAS statistical software (SAS Institute 1990). First, the annual thermal regime was rejected if all the weekly temperatures exceeded the minimum feeding temperature (no value for FACTOR; ≤8C and WEEK8C equal to zero). The relative influence of these omitted warm stream data sets was tested by assigning a value of one to the ≤8C variable and performing identical analyses. The addition of these annual thermal regimes, which constituted less than 7% of data for any species, did not substantially change the results. Specificity and sensitivity values calculated with both linear discriminant analysis (LDA) and nonparametric *K*th nearest neighbor (KNN) analysis were less than 2.4% different. Two variables were transformed to meet the assumptions of normality: the square root of FACTOR was substituted for FACTOR, and WEEK8C was substituted with the arcsine of the value of WEEK8C divided by the maximum value of WEEK8C (stratified by presence and absence). All variables were subsequently standardized (mean = 0, SD = 1). Next, several variable selection tech-

niques were used to identify which of the six thermal regime variables optimized the discriminant function analysis. The selection of optimal variables generally improves the performance of any subsequent discriminant function analyses. Stepwise discriminant analysis (forward selection, backward selection, and full stepwise) and a "best subsets" method (using Mallow's C_p and the relationship between regression and two-group linear discriminant analysis (see, for example, Kleinbaum et al. 1988) were used for variable selection. If multiple combinations of variables were chosen using these different methods, then each combination of variables, for each species, was saved for subsequent submission to our discriminant function analyses. These analyses allowed the selection of the optimal variables separately for each species and to reduce multicollinearity between variables.

Following the variable selection process, LDA and KNN analysis were performed on each of the unique combinations of variables to determine how successfully the derived thermal variables classified annual thermal regimes into presence or absence. Quadratic discriminant analysis and classification tree methods were also used for 7 of the 15 species, but these methods proved to be less accurate than LDA and KNN analysis. Prior probabilities were assumed to be equal in the analysis due to the uncertainty and difficulty of accurately estimating ecological priors (Williams 1983). A nearly unbiased classification was obtained using an n -fold (or leave-one-out) cross validation (Lachenbruch and Mickey 1968). In n -fold cross validation, n separate classification models are constructed, with n different data sets, with each data set having one observation from the full n -observation data set removed. For each of these n models, we classified the single data point that was not used in that model and found the error rate. Thus no data point was ever used to fit the model that was used to classify the data point.

Results

A summary of select univariate statistics for all variables is presented in Table 1. The model (or combinations of variables) that produced the highest specificity (ability of the model to accurately predict absence) and highest sensitivity (ability to accurately predict presence) for each species are highlighted in bold type. The TOTAL and >8C variables have presence values (means) greater than absence values for all 15 species. The TOTAL and >8C variables were selected as optimal model

variables for 8 and 6 species, respectively. The $\leq 8C$ variable has a presence value less than the absence value for 11 of 15 species (6 of 8 species when the variable was selected for the model). Brown bullhead, gizzard shad, rock bass and white crappie are the exceptions. The FACTOR variable (the ratio of no-growth to growth periods) has mean presence values lower than absence for 13 species (excepting brown bullhead and rock bass), reflecting longer relative growth periods for presence. The WEEK8C variable was universally chosen as an optimal model variable. The WEEK8C variable has mean presence values lower than absence values for all 15 species, and the range of presence values, notably the maximum, are reduced as compared with absence. The WEEK2C variable was selected as an optimal variable for 12 species. The mean presence values for WEEK2C are lower or equal to mean absence values for 9 of these 12 species, but the results for WEEK2C are difficult to interpret because they are highly skewed towards zero. There is considerable overlap in the ranges of values for presence and absence for all of our variables, although the range of absence values is generally greater than that of presence values. This may be an artifact of the larger sample sizes for absence. Normality was tested and confirmed for our variables, with the notable exceptions of the FACTOR and WEEK2C variables, which are positively skewed.

Multivariate analyses of the derived thermal variables were successful in classifying presence or absence. Table 2 presents the specificity and sensitivity of these two analyses for each species. Comparing the results from KNN analysis and LDA, we can see that KNN analysis tended to have greater specificity and sensitivity than the LDA. The KNN analysis accurately predicted both presence and absence with greater than 90% success for 12 of 15 species. Predictions by LDA were slightly lower: sensitivity was greater than 80% for 13 of 15 species, and specificity was greater than 80% for 14 of 15 species. A notable failure of both statistical procedures occurred in classifying presence or absence of rock bass. Specificity and sensitivity were 60% and 87% with KNN analysis and 71% and 65% with LDA.

Discussion

Thermal conditions occurring over a much longer period and influencing a wider range of physiological processes were considered in estimating low-temperature tolerances as compared with the high-temperature tolerances estimated previously

(Eaton et al. 1995). The results of this study support the hypothesis that low-temperature tolerances, in addition to the upper preferred temperature range, are important in determining the occurrence of warmwater species. The multivariate analysis technique used to obtain these results is unique in combining several thermal regime factors that have previously been shown only individually to influence the thermal tolerances, including overwinter survival, of warmwater fishes. Although the Fish Temperature Database Matching System was originally used to estimate species high-temperature tolerances, these data are also suitable for estimating cold thermal tolerances as used in the present analysis.

Clearly, we have not included all the other biological factors which may determine the ability of a population of a fish species to exist at a given location. However, the variables included in this study do successfully classify most presence or absences or, alternatively, are closely correlated with other factors that do discriminate between presence and absence. The addition of other environmental variables (e.g., stream flow, maximum tolerable temperature) could increase the sensitivity and specificity of this or similar analyses and may increase the ability to predict changes in distribution under altered conditions. No unusual aspects of the life history, biology, thermal responses, or habitat requirements or anomalies in the data set of rock bass (Scott and Crossman 1973) were found to explain the poor ability of the statistical methods to accurately classify presence or absence for this species.

Shuter and Post (1990) used bioenergetic models to demonstrate the importance of body size and duration of winter on the northern geographic limits for Eurasian perch, *Perca fluviatilis*, yellow perch, *Perca flavescens*, and smallmouth bass, *Micropterus dolomieu*. Near their geographic limits, overwinter survival was reduced by starvation of young of year because of restrictions imposed by shortened growing period and lengthened starvation period (see Lyons 1997 for a regional application of the model). Ten of the 15 species used in our study were determined by Shuter and Post (1990) as having a distribution potentially limited by overwinter starvation. Results of the statistical model in our study support the importance of relative growth conditions and shortened nonfeeding periods on distribution. Notably, the FACTOR variable, which is the ratio of nonfeeding to feeding potential, was chosen as an important variable for predicting the presence or absence of 12 spe-

cies. Presence values are lower than absence for 11 of the 12 selected species (rock bass is the exception) and 13 of the total 15 species, reflecting the importance of a relatively longer growing or feeding period or shortened nonfeeding period. The variable WEEK8C (nonfeeding or stressful cold temperatures) was chosen as an important predictive variable for all 15 species. All presence values were lower than absence values, which is consistent with our expectations that warmwater species would favor streams with shorter cold periods. Although the $>8^{\circ}\text{C}$ and $\leq 8^{\circ}\text{C}$ variables were chosen less often (eight and six species, respectively), the presence values for these variables show a pronounced tendency towards greater feeding periods and reduced nonfeeding periods for these warmwater species. The TOTAL variable, chosen for eight species, encompasses conditions experienced throughout the entire thermal regime. Presence values for TOTAL were consistently greater than absence values.

Other studies on the effects of low temperature on fishes have focused on resident lake populations. Consequently, 4°C has frequently been the minimum temperature available to investigators in these studies (e.g., Toney and Coble 1979; Post and Evans 1989). In our study, 39% of the streams available in our database sustain average temperatures of less than 4°C for at least 1 week. Our results highlight the important contribution that temperatures at or below 4°C can have on the presence or absence of warmwater fishes in streams. The WEEK2C variable, selected as a temperature previously shown to directly cause mortality, was selected as an important predictive variable for 12 species; 9 of these 12 species had presence values lower than absence values.

The analyses presented in this study describing the relationship between species presence or absence and thermal regime variables are empirical and correlative; therefore, deterministic interpretations are very difficult. Although we cannot infer causation or the relative importance of a variable as compared to the other variables, these results agree with known physiological or life history restrictions imposed by the affects of these different variables.

The somewhat greater success of the nonparametric KNN analysis is probably due to the non-normality of some of our variables. Unfortunately, the further application of the KNN method requires the use of the original data set used for calibration, whereas the formulae derived from LDA can be applied independently of the original data. Other

TABLE 1.—Descriptive statistics for the model variables selected for 15 warmwater fish species. Optimal model variables are in bold italic type face.

Species		TOTAL (DW) ^c			>8C (DW) ^c			≤8C (DW) ^c		
Name ^a	Status (N) ^b	Mean	Range	Median	Mean	Range	Median	Mean	Range	Median
BLC	A (440)	655.0	159–1071	625	576.9	33–1063	547	78.1	6–200	74
	P (67)	741.0	569–1034	725	673.7	489–991	648	67.3	28–112	67
BLG	A (357)	622.6	159–1071	606	540.3	33–1063	526	82.3	6–200	78
	P (150)	770.6	358–1066	771	707.3	279–1059	703	63.4	7–117	64
BRB	A (230)	730.2	426–1071	731	669.1	369–1063	662	61.1	6–118	61
	P (40)	749.8	513–1034	719	681.8	463–991	641	68.1	37–112	70
CAP	A (308)	631.4	159–1063	606	547.6	33–1056	517	83.8	6–200	82
	P (199)	720.6	358–1071	727	655.0	279–1063	663	65.6	7–148	65
CCF	A (309)	630.9	159–1071	612	548.4	33–1063	529	82.5	6–200	79
	P (150)	753.6	431–1066	769	690.3	328–1059	704	63.3	7–148	63
FCF	A (204)	735.6	159–1071	757	672.9	33–1063	695	62.8	6–126	63
	P (48)	791.3	557–1066	792	730.7	500–1059	723	60.6	7–87	62
FWD	A (183)	694.0	159–1071	705	627.8	33–1063	633	66.3	7–126	67
	P (68)	746.5	515–1012	755	683.2	480–981	691	63.4	28–93	62
GIS	A (199)	714.0	159–1071	705	652.9	33–1063	631	61.1	7–126	59
	P (96)	779.4	590–1012	785	712.7	530–981	708	66.8	6–108	68
GOS	A (461)	659.2	159–1071	627	581.9	33–1063	549	77.4	6–200	73
	P (46)	738.2	426–896	731	668.4	393–836	657	69.8	33–112	70
GSF	A (361)	649.9	159–1071	620	570.0	33–1063	542	79.9	6–200	76
	P (104)	750.0	358–1066	761	685.6	279–1059	696	64.5	7–97	67
LMB	A (335)	607.0	159–1071	602	521.5	33–1063	520	85.5	7–200	81
	P (172)	782.1	358–1066	790	722.6	279–1059	726	59.6	6–148	60
RKB	A (141)	685.1	426–943	682	620.9	369–897	608	64.2	31–118	61
	P (68)	718.8	458–838	725	647.5	427–788	647	71.5	31–112	73
SAB	A (161)	706.4	159–1071	726	639.1	33–1063	650	67.4	7–126	69
	P (51)	772.0	513–1066	780	715.0	463–1059	717	57.0	7–86	58
WHB	A (153)	709.0	159–1071	723	642.3	33–1063	648	66.8	7–126	69
	P (75)	741.7	549–1012	755	678.3	500–981	692	63.5	28–95	62
WHC	A (231)	700.6	159–1071	694	637.0	33–1063	625	63.7	7–148	62
	P (94)	774.6	574–1063	782	709.7	522–1056	704	65.0	6–95	67

^a Species names: BLC = black crappie; BLG = bluegill; BRB = brown bullhead, *Ictalurus nebulosus*; CAP = common carp, *Cyprinus carpio*; CCF = channel catfish, *Ictalurus punctatus*; FCF = flathead catfish, *Pylodictis olivaris*; FWD = freshwater drum, *Aplodinotus grunniens*; GIS = gizzard shad, *Dorosoma cepedianum*; GOS = golden shiner, *Notemigonus crysoleucas*; GSF = green sunfish; LMB = largemouth bass; RKB = rock bass; SAB = smallmouth buffalo, *Ictiobus bubalus*; WHB = white bass, *Morone chrysops*; WHC = white crappie, *Pomoxis annularis*.

^b Species status: N = number of annual thermal regimes within a species geographic range in which a species was present (P) or absent (A).

^c DW = degree weeks, defined as the sum of the average weekly temperatures for the defined period.

multivariate statistical analysis methods were explored but found to be inadequate or unsuited to our data. Quadratic discriminant analysis was highly sensitive to normality and extrapolation. Classification regression trees did not provide adequate separation of presence or absence groups. Based on results presented in this paper, we conclude that KNN analysis or LDA could be applied to other species in the FTDS database with sufficient data to meet the criteria that minimum sample size exceed multivariate dimensionality by at least a factor of three (Williams and Titus 1988).

Summary

The results of this study present a statistical approach for predicting the presence and absence of 15 warmwater fish species based on various ther-

mal variables derived from annual thermal regimes. The ability of our statistical models to discriminate presence from absence strengthens our hypothesis that these potentially biologically significant thermal variables are important to a species' ability to populate a given location. This study used existing data to analyze the effects of derived temperature variables on species throughout their present thermal and geographic range in the United States. This method allows for assessment of thermal suitability (presence or absence) for a species based on measurements of year-round stream temperature or predicted annual thermal regimes. This methodology can be applied to predict changes in warmwater species population abundances or distributions due to climate change, such as the lake temperature models developed by Ste-

TABLE 1.—Extended.

Species		FACTOR			WEEK8C (weeks)			WEEK2C (weeks)		
Name ^a	Status (N) ^b	Mean	Range	Median	Mean	Range	Median	Mean	Range	Median
BLC	A (440)	0.193	0.006–3.818	0.122	17.1	1–48	18	3.1	0–26	0
	P (67)	0.104	0.029–0.208	0.100	16.1	5–25	17	2.9	0–14	1
BLG	A (357)	0.217	0.006–3.818	0.141	18.1	1–48	19	3.3	0–26	0
	P (150)	0.098	0.006–0.288	0.092	14.2	1–30	15	2.3	0–16	0
BRB	A (230)	0.100	0.006–0.319	0.096	15.8	1–28	17	4.4	0–22	1
	P (40)	0.104	0.041–0.208	0.107	15.6	5–24	17	2.8	0–15	0
CAP	A (308)	0.228	0.006–3.818	0.155	17.3	1–48	18	2.3	0–26	0
	P (199)	0.109	0.007–0.426	0.099	16.4	1–30	17	4.1	0–20	1
CCF	A (309)	0.223	0.006–3.818	0.140	17.5	1–48	18	2.9	0–26	0
	P (150)	0.102	0.006–0.426	0.095	15.1	1–27	16	3.3	0–20	1
FCF	A (204)	0.128	0.006–3.818	0.096	15.8	1–48	16	4.2	0–26	1
	P (48)	0.087	0.007–0.136	0.093	13.6	1–25	14	2.5	0–17	0
FWD	A (183)	0.142	0.006–3.818	0.105	17.5	1–48	18	5.0	0–26	1
	P (68)	0.095	0.029–0.148	0.095	16.3	5–26	16	4.1	0–20	2
GIS	A (199)	0.130	0.006–3.818	0.097	16.3	1–48	18	5.2	0–26	1
	P (96)	0.097	0.006–0.205	0.095	14.4	1–21	15	1.6	0–13	1
GOS	A (461)	0.189	0.006–3.818	0.120	17.0	1–48	18	3.1	0–26	0
	P (46)	0.106	0.059–0.208	0.103	16.6	7–28	16	2.7	0–22	1
GSF	A (361)	0.206	0.006–3.818	0.128	17.0	1–48	18	2.9	0–26	0
	P (104)	0.101	0.006–0.285	0.096	15.4	1–30	16	2.9	0–16	1
LMB	A (335)	0.228	0.007–3.818	0.151	18.9	1–48	19	3.5	0–26	0
	P (172)	0.091	0.006–0.426	0.086	13.1	1–30	14	2.1	0–21	0
RKB	A (141)	0.110	0.040–0.319	0.099	17.8	6–28	19	5.8	0–22	2
SAB	P (68)	0.112	0.047–0.208	0.109	16.5	7–26	17	2.7	0–21	1
	A (161)	0.145	0.006–3.818	0.106	17.1	1–48	17	4.6	0–26	1
WHB	P (51)	0.083	0.007–0.134	0.088	15.2	1–24	15	4.1	0–17	2
	A (153)	0.146	0.006–3.818	0.105	17.0	1–48	17	4.4	0–26	1
WHC	P (75)	0.096	0.029–0.148	0.096	16.5	5–25	16	4.6	0–17	2
	A (231)	0.137	0.006–3.818	0.100	16.7	1–48	18	4.9	0–26	1
	P (94)	0.094	0.006–0.148	0.096	15.0	1–22	16	2.5	0–14	1

TABLE 2.—Specificity (percent absence correctly predicted as absence) and sensitivity (percent presence correctly predicted as presence) of *K*-nearest neighbor (KNN; priors = 0.5; *K* = 15) and linear discriminant analysis (LDA; priors = 0.5).

Species	KNN		LDA	
	Specificity	Sensitivity	Specificity	Sensitivity
Black crappie	100	100	99	90
Blue gill	97	99	98	99
Brown bullhead	83	90	86	78
Common carp	96	97	100	93
Channel catfish	98	99	99	97
Flathead catfish	96	100	100	90
Freshwater drum	100	90	98	87
Gizzard shad	100	98	100	91
Golden shiner	100	98	100	96
Green sunfish	100	100	100	91
Largemouth bass	97	99	93	95
Rock bass	60	87	71	65
Smallmouth buffalo	99	96	100	88
White bass	99	93	100	81
White crappie	100	96	100	93

fan et al. (1995). Modeling techniques are currently being developed for predicting the effects of climate change on stream thermal regimes that will, in turn, provide the basis for estimating impacts on fisheries resources.

Acknowledgments

Naomi Detenbeck and J. Howard McCormick provided help with preliminary data analysis and important advice on fish biology.

References

- Boschung, H. T., J. D. Williams, D. W. Gotshall, D. K. Caldwell, and M. C. Caldwell. 1983. The Audubon Society field guide to North American fishes, whales, and dolphins. Knopf, New York.
- Eaton, J. G., and six coauthors. 1995. A field information-based system for estimating fish temperature tolerances. *Fisheries* 20(4):10–18.
- Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41: 1109–1115.
- IPCC (Intergovernmental Panel on Climate Change). 1995. Climate change 1995: the science of climate

- change. Cambridge University Press, Cambridge, UK.
- Johnson, M. G., and W. H. Charlton. 1960. Some effects of temperature on the metabolism and activity of the largemouth bass, *Micropterus salmoides* Lacépède. *Progressive Fish-Culturist* 22:155–163.
- Johnson, T. B., and D. O. Evans. 1991. Behavior, energetics, and associated mortality of young-of-the-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. *Canadian Journal of Fisheries and Aquatic Sciences* 48:672–680.
- Johnson, T. B., and D. O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. *Transactions of the American Fisheries Society* 125:466–471.
- Keast, A. 1968. Feeding of some Great Lakes fishes at low temperatures. *Journal of the Fisheries Research Board of Canada* 25:1199–1218.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition between two centrarchid fishes. *Evolutionary Biology* 10:333–395.
- Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analysis and other multivariable methods. PWS-Kent, Boston.
- Lachenbruch, P. A., and M. A. Mickey. 1968. Estimation of error rates in discriminant analysis. *Technometrics* 10:1–10.
- Lyons, J. 1997. Influence of winter starvation on the distribution of smallmouth bass among Wisconsin streams: a bioenergetics modeling assessment. *Transactions of the American Fisheries Society* 126:157–162.
- Magnuson, J. J., and eleven coauthors. 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield region. *Hydrological Processes* 11:825–871.
- Maxwell, J. R., and five coauthors. 1995. A hierarchical framework of aquatic ecological units in North America (Nearctic Zone). U.S. Forest Service General Technical Report NC-176.
- McComish, T. S. 1971. Laboratory experiments on growth and food conversion of the bluegill. Doctoral dissertation. University of Missouri, Columbia.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1958–1968.
- SAS Institute. 1990. SAS/STAT user's guide: DISCRIM and UNIVARIATE procedures, release 6.10. SAS Institute, Cary, North Carolina.
- Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa.
- Sheehan, R. J., W. M. Lewis, and L. R. Bodensteiner. 1990. Winter habitat requirements and overwintering of riverine fishes. Illinois Department of Conservation, Federal Aid in Sport Fish Restoration, Project F-79-R, Final Report, Springfield.
- 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).
- 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 dolomieu* Lacépède. *Journal of Fish Biology* 35:765–780.
- Shuter, B. J., J. A. MacLean, F. E. J. Fry, and H. A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. *Transactions of the American Fisheries Society* 109:1–34.
- Shuter, B. J., and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* 119:314–336.
- Stefan, H. G., M. Hondzo, J. G. Eaton, and J. H. McCormick. 1994. Predicted effects of climate change on fishes in Minnesota lakes. *Canadian Special Publication of Fisheries and Aquatic Sciences* 121.
- Stefan, H. G., M. Hondzo, J. G. Eaton, and J. H. McCormick. 1995. Validation of fish habitat model for lakes. *Ecological Modelling* 82:211–224.
- Toneys, M. L., and D. W. Coble. 1979. Size-related, first winter mortality of freshwater fishes. *Transactions of the American Fisheries Society* 108:415–419.
- Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. *Ecology* 64:1283–1291.
- Williams, B. K., and K. Titus. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. *Ecology* 69:1275–1285.