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Effects of evolutionary thermal environment on temperature-preference relationships in fishes

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Synopsis

Fishes exhibit a perplexing variety of temperature-preference relationships, ranging from positive to negative functions of acclimation temperature. However, these relationships tend to be consistent within species even across broad geographic ranges. We developed and tested an hypothesis that temperature-preference relationships are related to the amplitude of the annual thermal-cycle experienced by species during their recent evolutionary histories. Species experiencing annual cycles of relatively high amplitude (temperate species) were predicted to exhibit temperature-preference relationships that are positive functions of acclimation temperature. Those with low thermal amplitudes, such as cold stenotherms, or relatively high short-term amplitudes, such as tropical mesotherms, were predicted to exhibit relationships that are either independent or negative functions of acclimation temperature. This hypothesis was tested and strongly supported by a synthesis of studies from the literature. Of 42 species, for which data were available, 40 exhibited the class of temperature-preference relationships that we predicted on the basis of their thermal cycle. The concept of thermal guilds can be expanded by taking into consideration the capacity of fishes to adjust preferred temperatures through acclimation. This work shows the adaptive nature of temperature-preference behavior and may be useful for predicting general characteristics of temperature-preference relationships for the many species not yet examined in this regard.

Introduction

Water temperatures over the Earth vary so greatly in space and time that fishes only tolerate a subset of those temperatures and, therefore, are restricted in distribution to regions within their range of tolerance. Generally, fishes are well-adapted to environmental temperatures that they experience, leading to similarities in ecological responses to temperature. These similarities have led to the recognition of thermal response classifications (Magnuson et al. 1979) developed on the basis of the magnitude (e.g. polar, temperate, or tropical; and cold-, cool-,

or warm-water species) and range (e.g. eurythermal or stenothermal) of tolerated environmental temperatures. Within a range of tolerance, individuals select certain temperatures known as preferred temperatures when selected from a wide range of equally available temperatures (usually determined in the laboratory). Also, many species can survive a range of temperatures over the long term that would be lethal in the short term. This is accomplished through metabolic compensation during a gradual change to the new temperature (acclimation). Qualitative mechanisms of acclimation result in changes in temperature-preference and tol-

erance following exposure to different temperatures (Kelsch & Neill 1990). These temperature-preference relationships (as functions of acclimation temperature) have been characterized in the laboratory for a number of species.

There appears to be a genetic basis for temperature preference and ability to acclimate to temperature. For example, species with wide distributions, such as the bluegill, *Lepomis macrochirus*, exhibit relatively little geographic variation in temperature preference (Beitinger & Fitzpatrick 1979); however, small differences are expected among individuals and have been observed in some species (Hall et al. 1978, McCauley & Huggins 1979). Some evidence has suggested that preferred temperatures are optimal for performance (Kelsch & Neill 1990). Recently, a mechanism was developed that linked temperature-preference behavior to metabolic activity and ultimately natural selection (Kelsch 1996). Evidence showed that bluegills selected temperatures in proportion to the amount of metabolic power available to them for growth, activity, reproduction and other functions. Temperature selection by fishes appeared to be a process of selecting temperatures that maximize their available power (Kelsch 1996). Support for this idea comes from the work of Stauffer et al. (1980) who noted that optimal temperatures are related to optimal physiological performance and successful fish populations.

The problem

Fishes have evolved a perplexing variety of temperature-preference relationships. Essentially, the observed variety of relationships described by Zahn (1962) can be categorized into three classes on the basis of whether they are positive, independent, or negative functions of acclimation temperature. For example, species such as the bluegill tend to prefer warmer temperatures following exposure (acclimation) to warmer temperatures, giving them temperature-preference relationships that are positive functions of acclimation temperature (Figure 1). This seems to be an adaptive response to changing temperature. Other species such as the blue tilapia, *Oreochromis aureus*, prefer a narrow temperature

range regardless of acclimation temperature, resulting in temperature-preference relationships that are independent of acclimation temperature. This too seems adaptive because they select and occur only in environments with narrow temperature fluctuations. A few species, such as the guppy, *Poecilia reticulata*, exhibit the apparently mal-adaptive response of preferring cooler temperatures when acclimated to warmer ones, resulting in temperature-preference relationships that are negative functions of acclimation temperature. It is not clear how this latter response is adaptive.

This perplexing variety of temperature-preference relationships may be partially explained by the variety of types of metabolic compensation that have been observed during acclimation to temperature. Precht (1958) described three general types of metabolic compensation that have been observed in whole organisms. A model has been developed that describes how Precht's partial, no, and inverse compensation, would be expected to lead to temperature-preference relationships that are positive, independent, and negative functions of acclimation temperature (Kelsch & Neill 1990). However, justifying a seemingly mal-adaptive class of temperature-preference relationships (those with negative slopes) with a seemingly mal-adaptive type of metabolic compensation (inverse compensation) is not entirely satisfactory.

Our objectives were to: (1) present a conceptual model that explains the perplexing variety of tem-

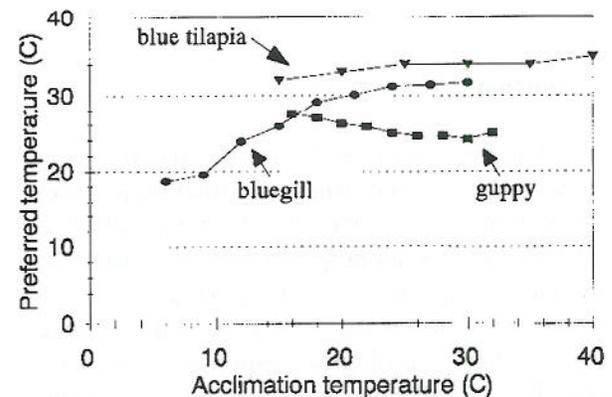


Figure 1. Examples showing the diversity of temperature-preference relationships in fishes [data sources: bluegill and blue tilapia, Kelsch & Neill (1996); guppy, Zahn (1962)].

perature-preference relationships in fishes on the basis of thermal regimes in which they evolved and live, and (2) to present a test of this model by comparing classes of temperature-preference relationships, predicted on the basis of the thermal regime experienced by species, with observed relationships using data from the literature.

The model

We have developed an hypothesis that predicts classes of temperature-preference relationships on the basis of environmental temperature variation experienced by a species through its recent evolutionary history (Figure 2). We predicted that species experiencing thermal cycles of relatively high amplitude and duration (long-cycle) would have temperature-preference relationships that are positive functions of acclimation temperature. Species that experience low annual thermal-amplitude but may be exposed to temperature fluctuations on a daily or sub-seasonal basis (short-cycle), and species that normally experience minimal temperature fluctuations (no cycle) were predicted to have temperature-preference relationships that are independent or negative functions of acclimation tem-

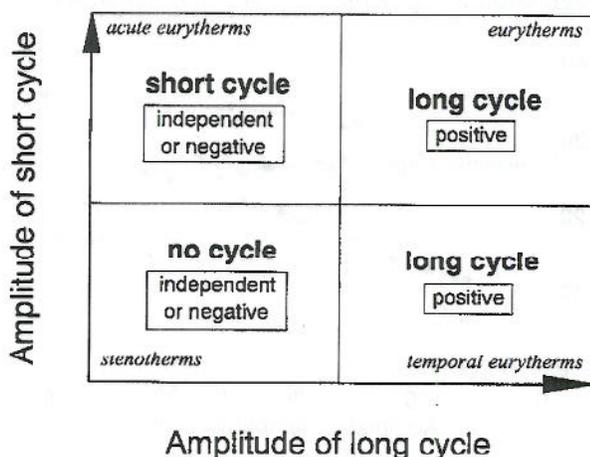


Figure 2. Model hypothesizing the relationship between temperature-preference and the duration and amplitude of thermal cycles experienced by fishes. Bold indicates our categorization of fishes on the basis of environmental and recent temperatures and boxes indicate our prediction of the slope of the relationship between preferred and acclimation temperatures

perature. According to this model, some eurytherms may have broad temperature tolerance only if given time for acclimation (temporal eurytherms), some may have a broad temperature tolerance without an ability to acclimate (acute eurytherms), and some may share both characteristics (eurytherms).

The rationale for these predictions is that because time is required for acclimation to occur, only species that evolved experiencing gradual long-term temperature changes (e.g. temperate species) would have the time necessary to make metabolic changes that would result in substantial shifts in preferred temperatures or ranges of tolerance. Species that experience their greatest thermal extremes over the short term (e.g. some tropical species) must have a broad range of tolerance to survive relatively rapid temperature changes without time for acclimation to adjust thermal preferences or tolerances, and species that live in relatively constant temperatures or select constant temperatures would not require, nor be expected to evolve, broad tolerances or the ability to shift tolerances through acclimation, and may be stenothermal.

Methods

To test the hypothesis that temperature-preference relationships are related to the thermal regimes of recent evolutionary history, we first conducted a literature review to identify the approximate duration and amplitude of thermal cycles experienced by selected species. From this information, we predicted whether species would be expected to exhibit positive temperature-preference relationships or not. We then did an independent literature review to determine the observed classes of temperature-preference relationships for these species, if such information was available, and tested the hypothesis by comparing predicted versus observed classes. A high degree of agreement between predicted and observed classes of temperature-preference relationships would provide support for our hypothesis.

Prediction of temperature-preference relationships

We initially restricted our search for information on magnitude and duration of thermal cycles to 110 fishes listed in a compilation of temperature preference data by Coutant (1977), because we anticipated that temperature-preference relationships may have been determined for many of these species. Coutant's paper included sources and useful information on final preferred temperatures, and upper and lower avoided temperatures but gave no hint as to what temperature-preference class species might belong, thus minimizing the likelihood of bias in evaluating thermal regimes experienced by fishes. An effort was made to ensure that judgments regarding thermal regime were blind; having been made solely by an author (JAJ) with no previous experience in thermal ecophysiology of fishes, nor any preconceived perceptions as to what class of temperature-preference relationship species might exhibit. While the literature review for temperature-preference relationships was being conducted, such relationships and corresponding information regarding thermal regimes were discovered for nine additional species. These species were included in the test of the model in the same manner as described in this section.

We categorized species experiencing thermal cycles of relatively high amplitude and living in regions or habitats estimated to have an annual temperature fluctuation of greater than 5 °C as long-cycle species, and predicted that they would have temperature-preference relationships that are positive functions of acclimation temperature. Species that experience less than an estimated 5 °C change in annual thermal amplitude but are exposed to short-term temperature fluctuations on a daily or sub-seasonal basis (short-cycle), and species that normally experience less than 5 °C change in either annual or short-term temperature fluctuations (no-cycle) were predicted to have temperature-preference relationships that were independent or negative functions of acclimation temperature.

Characterization of temperature-preference relationships

Published temperature-preference relationships were then examined and classified to test our predictions. Temperature-preference data were taken from tables or estimated from temperature preference curves drawn by authors. Preferred temperatures were determined or estimated from published data at acclimation intervals ranging from 3 to 6 °C over the range of the experiment. Any experiment with a range of acclimation less than 6 °C was not included due to the questionable nature of assessing slopes on such a narrow range of data. For those species studied more than once, the analysis was done separately and results compared.

Prior to the literature review, we developed objective criteria for classifying temperature-preference relationships on the basis of slopes calculated from published data (Figure 3). To establish whether observed temperature-preference relationships were positive functions of acclimation temperature or not, we calculated the slopes of each published relationship for comparison with the slope of a second curve established to delimit positive relationships from independent and negative relationships. We calculated slopes for each species by performing a regression analysis on \ln by \ln transformed data

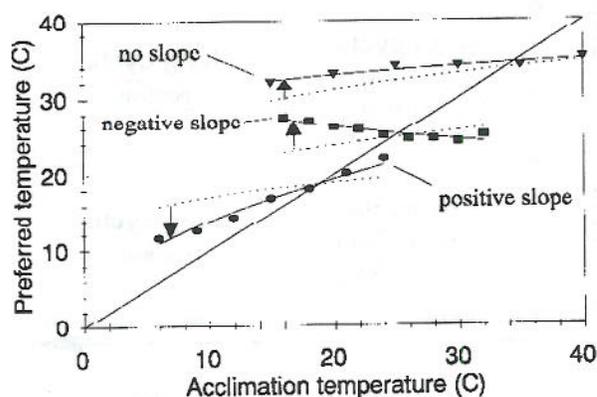


Figure 3. Examples showing criteria and methods used to objectively determine whether slopes of temperature-preference relationships were positive or not. Symbols show data for three representative species, solid curves show the functions fit to the data to determine slopes of temperature-preference relationships, and dashed lines delimit the boundaries between positive and non-positive slopes.

from published studies. The data were ln transformed to improve the fit of this linear analysis on relationships that are typically curved. We selected this method of characterizing temperature-preference relationships rather than other published and perhaps better methods (Cincotta & Stauffer 1984) because it gave us a single meaningful parameter (slope) with which to compare relationships. As a measure of the relative amount of variation explained by this method, R^2 values were calculated.

Separate curves for each species were calculated and used to delimit positive from negative and independent temperature-preference relationships. We selected this method of delimiting positive and non-positive slopes, rather than defining significant relationships as positive, because raw data from the literature were often unavailable, making the latter method unsatisfactory. Such curves and their slopes were calculated by performing a regression analysis on ln by ln transformed values taken from a line with a slope of 0.2 drawn through points calculated for each acclimation temperature and the final preferred temperature for the species. (We selected the modest positive value of 0.2 to delimit positive from independent relationships because it was unlikely that any species would have a slope of exactly 0.0.) A temperature-preference relationship was defined as positive if it was significant and its ln-transformed slope was greater than the ln-transformed slope of the delimiting relationship for the species (Figure 3). All data transformations, statistical analyses, and graphs were done using Quattro Pro (Borland International¹) and Statmost (Datamost Corporation²) for Windows.

Results

Usable information for both habitat and temperature-preference relationship was collected for forty-two species distributed among 11 families (Table

1). The data were not representative of the diversity of temperature-preference relationships in fishes because most studies have been done in North America and the majority of species studied were temperate species experiencing long thermal cycles.

Results strongly supported our hypothesis. Observed slopes agreed with predicted slopes for 40 of the 42 species tested. Thirty-two species were predicted to be long-cycle, four no-cycle, and six short-cycle (Figure 4). The Mozambique tilapia was one species for which our prediction was incorrect. Our assessment was that it experienced a relatively low annual-temperature-cycle causing us to predict that its temperature-preference relationship would not have a positive slope. The observed relationship, although not significant, was positive with a slope of 0.210 (Table 1). Also, the goldfish, *Carassius auratus*, was predicted to have a relationship with a positive slope on the basis of its thermal regime; however, its observed relationship had a slope of 0.136, just under our predicted limit of 0.137. The rainbow trout had mixed results with three of four studies supporting our hypothesis. Although we found data for relatively few species and four families were represented by only one species, members of only one of the 11 families exhibited different classes of

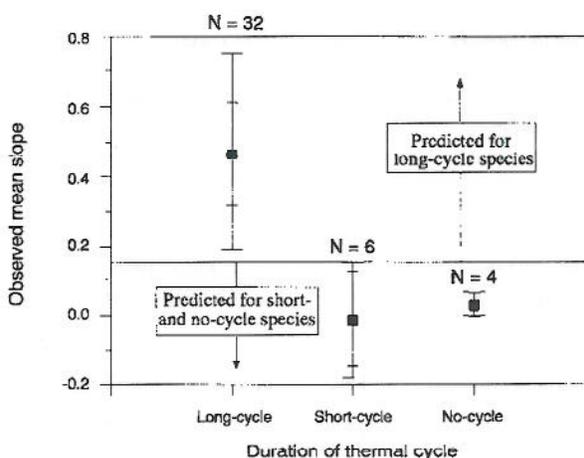


Figure 4. Observed means (symbols), standard deviations (short bars), and ranges (long bars) of slopes of temperature-preference relationships for species experiencing long-, short-, or no-cycle thermal regimes. The horizontal line represents the mean slope of curves delimiting positive from non-positive relationships.

¹ Borland International, Inc. 1992. Quattro pro for windows: users guide. Borland International, Inc., Scotts Valley. 455 pp.

² Datamost Corporation. 1995. Statmost statistical analysis and graphics: users guide. Datamost Corporation, Salt Lake City. 852 pp.

Table 1. Species analyzed to test our model for which both data regarding thermal regimes (thermal habitat source) and temperature-preference relationships (preferred temperature source) were available from the literature. Included are observed cycle of thermal regime experienced by the species (observed cycle), final preference, predicted and observed slopes of temperature preference relationships, and statistics related to the fit of our ln by ln transformed regression analysis of observed temperature-preference data. Multiple rows are given for species studied more than once.

	observed cycle	thermal habitat source	final prefer.	predicted slope	observed slope	R ²	p	preferred temperature source	
Cyprinidae									
1	long	Hubbs & Lagler (1958)	29.0	> 0.106	0.482	0.96	< 0.0001	Cherry et. al. (1975)	
		central stoneroller	Burr (1980)	26.6	> 0.154	0.643	0.95	0.0001	Cherry et. al. (1977)
2	long	Hubbs & Lagler (1958)	28.1	> 0.137	0.136	0.84	0.0293	Fry (1947)	
		goldfish	Scott & Crossman (1979)						
3	long	Gilbert & Burgess (1980a)	27.2	> 0.120	0.411	0.99	< 0.0001	Cincotta & Stauffer (1984)	
		satinfin shiner							
4	long	Hubbs & Lagler (1958)	29.4	> 0.111	0.402	0.95	< 0.0001	Cherry et. al. (1975)	
		spotfin shiner	31.0	> 0.149	0.402	0.88	< 0.0001	Cherry et. al. (1977)	
5	long	Hubbs & Lagler (1958)	32.6	> 0.130	0.488	0.95	0.0011	Pitt et al. (1956)	
		common carp	Scott & Crossman (1979)						
6	long	Jenkins & Lachner (1980)	15.3	> 0.218	0.673	0.99	0.0007	Cherry et. al. (1975)	
		bluehead chub							
7	long	Scott & Crossman (1979)	23.8	> 0.133	0.340	0.95	0.0002	Cincotta & Stauffer (1984)	
		golden shiner							
8	long	Scott & Crossman (1979)	27.6	> 0.110	0.395	0.90	0.0003	Cherry et. al. (1975)	
		rosyface shiner	Gilbert & Burgess (1980b)	26.1	> 0.164	0.340	0.88	0.0005	Cherry et. al. (1977)
9	long	Gilbert (1980a)	21.0	> 0.179	0.743	0.95	0.001	Cherry et. al. (1977)	
		telescope shiner							
10	long	Stauffer et. al. (1980)	25.3	> 0.136	0.408	0.98	0.0002	Stauffer et. al. (1980)	
		northern redbelly dace							
11	long	Scott & Crossman (1979)	28.4	> 0.108	0.370	0.93	0.0001	Cherry et. al. (1975)	
		bluntnose minnow	Lee & Shute (1980a)	28.4	> 0.146	0.463	0.96	< 0.0001	Cherry et. al. (1977)
12	long	Scott & Crossman (1979)	29.0	> 0.136	0.455	0.94	0.0014	Cherry et. al. (1975)	
		fathead minnow	Lee & Shute (1980b)	26.2	> 0.156	0.431	0.88	0.0016	Cherry et. al. (1977)
13	long	Zahn (1962)	26.2	> 0.189	0.244	0.69	0.0103	Zahn (1962)	
		rosy barb							
14	long	Cincotta & Stauffer (1984)	24.6	> 0.130	0.343	0.99	< 0.0001	Cincotta & Stauffer (1984)	
		blacknose dace							
15	long	Hensley & Courtenav (1980a)	20.2	> 0.199	0.493	0.74	0.0063	Zahn (1962)	
		bitterling							
Catostomidae									
16	long	Scott & Crossman (1979)	27.1	> 0.120	0.687	0.92	0.0002	Cincotta & Stauffer (1984)	
		white sucker	Lee & Kucas (1980)						
17	long	Buth & Murphy (1980)	28.6	> 0.152	0.681	0.86	0.0009	Cherry et. al. (1977)	
		northern hog sucker							
Ictaluridae									
18	long	Scott & Crossman (1979)	27.3	> 0.111	0.404	0.98	< 0.0001	Richards & Ibara (1978)	
		brown bullhead	Glodek (1980a)						
19	long	Scott & Crossman (1979)	30.5	> 0.107	0.324	0.87	0.0003	Cherry et. al. (1975)	
		channel catfish	Glodek (1980b)						
Salmonidae									
20	no	Fechhelm et. al. (1983)	13.7	< 0.125	0.025	0.08	0.582	Fechhelm et. al. (1983)	
		Arctic cisco							
21	no	Scott & Crossman (1979)	14	< 0.203	0	1	< 0.0001	Brett (1952)	
		chum salmon							

Table 1. Continued.

	observed cycle	thermal habitat source	final prefer.	predicted slope	observed slope	R ²	p	preferred temperature source
22 <i>Oncorhynchus mykiss</i> rainbow trout	long	Scott & Crossman (1979) Behnke (1980)	13.6	> 0.159 > 0.157	-0.018 0.562	0.97 0.90	0.0145 0.0138	Garside & Tait (1958) Javard & Anderson (1967)
			18.7	> 0.145	0.477	0.97	< 0.0001	Cherry et. al. (1975)
			19.7	> 0.179	0.628	0.99	0.0007	Cherry et. al. (1977)
23 <i>Oncorhynchus nerka</i> sockeye salmon	short	Scott & Crossman (1979)	14.4	< 0.198	0.024	0.00	0.872	Brett (1952)
24 <i>Oncorhynchus tshawytscha</i> chinook salmon	no	Scott & Crossman (1979)	12.3	< 0.247	0.030	0.05	0.628	Brett (1952)
25 <i>Salmo trutta</i> brown trout	long	Scott & Crossman (1979) Lee (1980a)	17.4	> 0.179	0.672	0.86	0.0235	Cherry et. al. (1977)
26 <i>Salvelinus fontinalis</i> brook charr	long	Scott & Crossman (1979) Hendricks (1980)	15.8	> 0.204	0.485	0.97	< 0.0001	Ferguson (1958)
			18.0	> 0.150	0.440	0.93	0.0004	Cherry et. al. (1975)
			16.0	> 0.211	0.492	0.98	0.0008	Cherry et. al. (1977)
27 <i>Salvelinus namaycush</i> lake charr	no	Goddard & Tait (1976)	11.7	< 0.167	0	1	< 0.0001	McCauley & Tait (1970)
Poeciliidae								
28 <i>Gambusia affinis</i> western mosquitofish	short	Lee & Burgess (1980)	33.7	< 0.153	-0.112	0.59	0.2101	Kelsch (unpublished)
29 <i>Poecilia reticulata</i> guppy	short	Coutant (1977)	24.6	< 0.189	-0.176	0.87	0.0002	Zahn (1962)
Gasterosteidae								
30 <i>Gasterosteus aculeatus</i> threespine stickleback	long	Burgess & Lee (1980)	16	> 0.155	0.222	0.95	0.0053	Garside et. al. (1977)
Centrarchidae								
31 <i>Ambloplites rupestris</i> rock bass	long	Scott & Crossman (1979) Cashner (1980)	30.6	> 0.174	0.439	0.88	0.0017	Cherry et. al. (1977)
32 <i>Lepomis cyanellus</i> green sunfish	long	Scott & Crossman (1979) Lee (1980b)	30.3	> 0.108	0.424	0.94	< 0.0001	Cherry et. al. (1975)
33 <i>Lepomis gibbosus</i> pumpkinseed	long	Scott & Crossman (1979) Lee (1980c)	31.1	> 0.107	0.399	0.99	< 0.0001	Cincotta & Stauffer (1984)
34 <i>Lepomis macrochirus</i> bluegill	long	Lee (1980d)	30.7	> 0.107	0.374	0.96	< 0.0001	Cherry et. al. (1975)
			31.4	> 0.147	0.211	0.97	< 0.0001	Cherry et. al. (1977)
			31	> 0.136	0.401	0.98	0.0001	Reynolds & Casterlin (1979)
35 <i>Micropterus dolomieu</i> smallmouth bass	long	Lee (1980e)	31.3	> 0.146	0.661	0.96	0.0007	Cherry et. al. (1975)
			30.3	> 0.157	0.472	0.85	0.0032	Cherry et. al. (1977)
36 <i>Micropterus punctulatus</i> spotted bass	long	Scott & Crossman (1979) Gilbert (1980b)	32.5	> 0.102	0.466	0.95	< 0.0001	Cherry et. al. (1975)
			31.2	> 0.160	0.268	0.91	0.0003	Cherry et. al. (1977)
37 <i>Micropterus salmoides</i> largemouth bass	long	Scott & Crossman (1979) Lee (1980f)	32.2	> 0.106	0.620	0.996	< 0.0001	Cincotta & Stauffer (1984)
Percidae								
38 <i>Perca flavescens</i> yellow perch	long	Scott & Crossman (1979) Lee (1980g)	24.2	> 0.155	0.311	0.99	0.0001	Ferguson (1958)
			21.4	> 0.182	0.316	0.995	0.0073	Cherry et. al. (1977)
Kyphosidae								
39 <i>Girella nigricans</i> opaleye	long	Ferguson (1958)	23.4	> 0.159	0.268	0.90	0.0053	Doudoroff (1938)
Cichlidae								
40 <i>Oreochromis aureus</i> blue tilapia	short	Hensley & Courtenay (1980b)	33.7	< 0.157	0.081	0.91	0.0031	Kelsch & Neill (1990)
41 <i>Oreochromis mossambicus</i> Mozambique tilapia	short	Hensley & Courtenay (1980c)	28.2	< 0.172	0.210	0.50	0.0754	Badenhuizen (1966)
Pleuronectidae								
42 <i>Pleuronectes platessa</i> plaice	long	Fry (1976)	16	> 0.136	0.150	0.996	< 0.0001	Fry (1976)

temperature-preference relationships. Salmonidae, with eight species, exhibited temperature-preference relationships in each of the three classes. This hints that the evolution of temperature-preference relationships may be relatively rapid.

Our method of establishing curves (as functions of a slope of 0.2) to delimit positive from non-positive slopes was supported by the results. All 48 relationships characterized as positive by this method had significant regressions (Table 1). By comparison, only four of nine relationships characterized as non-positive were significant. Two of these four slopes were 0.0 (artifacts of the way the data were reported in the literature) and one was negative leaving only 1 of 56 studies that had a significant regression that could possibly have been considered positive had we chosen some value smaller than 0.2.

Discussion

Observed variation in temperature-preference relationships within species is not only due to real changes in preference with changing acclimation temperature but to variation among individuals and populations and to differences in methodology among the studies that we have reviewed. To reduce variation due to differences in methodology we have only included studies from the literature that are in some way comparable. However, such studies do vary in type of apparatus used in determining temperature preferences (vertical versus horizontal) and in source and age of experimental subjects (young vs. adult, hatchery vs. wild). We are not overly concerned about these differences because the relationship that we have hypothesized would only tend to be obscured rather than supported by such variation.

Thermal guilds

It has long been known that preferred temperatures are related to the magnitude of the thermal regime experienced by fishes. Consider, for example, that final thermal preferenda (Fry 1947, Reynolds & Casterlin 1979) are highly correlated with common-

ly available summertime temperatures. This is apparently the result of a combination of evolutionary adaptation to, and behavioral selection among, ambient temperatures. Behavioral selection among available temperatures is the short-term adaptive response exhibited by individuals, and evolutionary adaptation to temperature is the long-term response exhibited by populations. Accordingly, fishes have been categorized by magnitude of tolerated and preferred temperatures as cold, cool, or warm water species. It also is known that fishes vary in their tolerance to environmental temperature, ranging from broad tolerance (eurythermal) to narrow (stenothermal).

We have now shown that temperature-preference relationships appear to be related to the amplitude of thermal cycles to which species have recently been exposed. For a species to prefer or tolerate a wide range of temperatures it must have evolved mechanisms for maintaining homeostasis. These include mechanisms of tolerance that establish the breadth of tolerated temperatures at a given time and mechanisms of acclimation that over time may shift preferred and tolerated temperatures. Species that have evolved qualitative mechanisms of acclimation exhibit temperature-preference relationships that show a positively correlated change in preference with exposure to changing temperature.

Accordingly, thermal guilds of fishes can be considered on the basis of both amplitude and magnitude of their thermal cycles (Figure 5). We have selected final preferenda as a measure of the temperatures selected by species and as an index of the magnitude of temperatures to which species are adapted. In addition, we have selected slopes of temperature-preference relationships as an index of the amplitude of annual thermal cycles experienced by species.

This model adds another dimension for the separation of fishes into thermal guilds; one based on the ability of fishes to acclimate to temperature by shifting thermal preferenda. Most of the 42 species analyzed for this study fell into a group of warm eurytherms (Figure 5). Salmonids (20–27) formed an interesting cluster extending from cold stenotherms to cool eurytherms. Another notable group was the poeciliids (28–29) with negative slopes that would

be characterized as warm stenotherms according to this model.

Negative temperature-preference relationships

We still do not know why species such as the western mosquitofish, *Gambusia affinis*, and guppy have temperature-preference relationships with negative slopes. It is unlikely that mechanisms of acclimation evolved that shift preferences inversely with changing environmental temperature. However, it is possible that quantitative mechanisms of acclimation (those that do not directly result in changes in preference) result in temporary, inverse shifts in temperature preference. This may occur in species that have not evolved mechanisms of acclimation that result in shifts in thermal optima (and preference) and under circumstances where thermal optima for enzyme reaction rates vary about an integrated optimum (the final thermal preferendum). After exposure to cold temperatures, for example, an individual may benefit most by seeking a temperature close to optimum for the rate limiting reactions (higher than the final preferendum); at

least until those enzyme or substrate deficits were rectified. It is likely that reactions with thermal optima furthest from ambient temperatures (those inverse to the acclimation temperature) would be most limiting and that deficits would be most quickly rectified by temporarily seeking (preferring) temperatures inverse to acclimation temperatures.

Evolutionary basis for temperature selection

It appears that the evolutionary basis for temperature selection and tolerance in fishes is related to power available at various temperatures for functions such as reproduction, growth, activity, and survival. With the exception of brief forays, individuals are probably restricted in distribution to a range of temperatures where they have available power, i. e. where the cost of maintenance (standard metabolic rate) is less than the total amount of power that they can generate (active metabolic rate). Preferred temperatures of fishes are probably those that offer the greatest scope for activity (as developed by Fry 1947) and therefore, the greatest amount of available power (Kelsch 1996). Evolution should have favored individuals that were well adapted to available temperatures or selected those that offered the greatest available power because they would have surplus power that could be channeled into adaptive functions such as reproduction and survival (Ware 1982, Priede 1985).

With further study we suspect that the amplitude of the annual temperature cycle will be found to be positively correlated with the slope of the temperature-preference relationship, and that the amplitude of the short-term temperature cycle will be correlated with the range of thermal tolerance. Our rationale for these predictions is that species in thermal environments with low temperature variation would not gain any advantage by adjusting their metabolism or temperature preferences, where others should tend to evolve mechanisms that increase their metabolic efficiency following temperature change. For species that experience short-term temperature cycles, evolution should favor individuals with broad thermal tolerances that do not require time for acclimation. Species that ex-

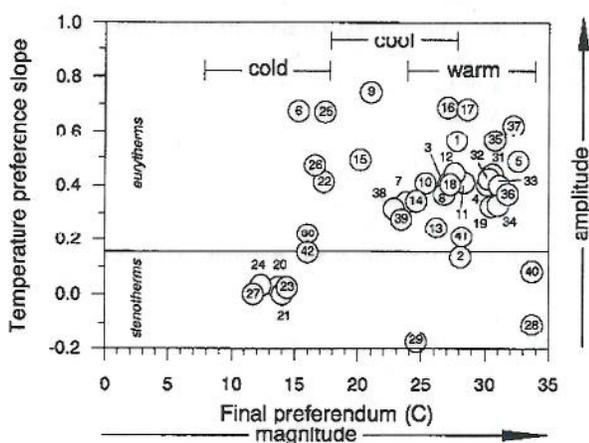


Figure 5. Model showing thermal guilds of fishes on the basis of magnitude (final preferendum) and amplitude (slopes of temperature-preference relationships) of thermal regimes experienced by fishes (mean slopes and final preferenda are plotted for species studied more than once). Bars indicate thermal niches for species typically designated as cold, cool, or warm temperate species (Manguson et al. 1979). The horizontal line is the mean slope of lines established for each species to delimit positive from non-positive slopes. Numbers refer to species in Table 1.

perience substantial thermal amplitudes with the time for major adjustments should have been favored if they had evolved mechanisms capable of adjusting their thermal optima and temperature preferences over time, resulting in slopes that are proportional to the amplitude of annual temperature cycle.

We did not test these predictions due to the difficulty of quantifying the amplitude of thermal cycles experienced by fishes; however, with the exception of the telescope shiner, the seven species (6, 25, 9, 16, 17, 35, 37, see Figure 5) with the highest slopes all exhibited relatively wide latitudinal distributions, a factor consistent with our prediction.

This work demonstrates the adaptive nature of temperature-preference behavior and may be useful for predicting general characteristics of temperature-preference relationships for the majority of species not yet examined in this regard.

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References cited

- Badenhuizen, T.R. 1966. Temperatures selected by *Tilapia mossambica* (Peters) in a test tank with a horizontal temperature gradient. *Hydrobiol.* 30: 541-544.
- Behnke, R.J. 1980. *Salmo gairdneri* (Richardson), rainbow trout. p. 106. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Beitinger, T.L. & L.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature in fish. *Amer. Zool.* 19: 319-330.
- Brett, J.R. 1952. Temperature tolerance in young pacific salmon, genus *Oncorhynchus*. *J. Fish. Res. Board Can.* 9: 265-323.
- Burgess, G.H. & D.S. Lee. 1980. *Gasterosteus aculeatus* Linnaeus, threespine stickleback. p. 563. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Burr, B.M. 1980. *Campostoma anomalum* (Rafinesque), stone-roller. p. 143. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Buth, D.G. & R.W. Murphy. 1980. *Hypentelium nigricans* (Lesueur), northern hog sucker. p. 402. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Cashner, R.C. 1980. *Ambloplites rupestris* (Rafinesque), rock bass. p. 581. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Cherry, D.S., K.L. Dickson & J. Cairns, Jr. 1975. Temperatures selected and avoided by fish at various acclimation temperatures. *J. Fish. Res. Board Can.* 32: 485-491.
- Cherry, D.S., K.L. Dickson & J. Cairns, Jr. 1977. Preferred, avoided and lethal temperatures of fish during rising temperature conditions. *J. Fish. Res. Board Can.* 34: 239-246.
- Cincotta, D.A. & J.R. Stauffer, Jr. 1984. Temperature preference and avoidance studies of six North American freshwater fish species. *Hydrobiol.* 109: 173-177.
- Coutant, C.C. 1977. Compilation of temperature preference data. *J. Fish. Res. Board Can.* 34: 739-745.
- Doudoroff, P. 1938. Reactions of marine fishes to temperature gradients. *Biol. Bull.* 75: 494-509.
- Fechhelm, R.G., W.H. Neill & B.J. Gallaway. 1983. Temperature preference of juvenile Arctic cisco *Coregonus autumnalis* from the Alaskan Beaufort Sea. *Biol. Pap. Univ. Alaska* 21: 24-83.
- Ferguson, R.G. 1958. The preferred temperature of fish and their midsummer distribution in temperate lakes and streams. *J. Fish. Res. Board Can.* 15: 607-624.
- Fry, F.E.J. 1947. Effects of the environment on animal activity. *Publ. Ont. Fish. Res. Lab.* 68: 1-62.
- Fry, F.E.J. 1976. Thermal physiological effects in aquatic systems. pp. 101-117. *In: Electric Power Research Institute, Report of a Workshop on the Impact of Thermal Power Plant Cooling Systems on Aquatic Environments, volume 2, Technical and Topical Papers, Palo Alto.*
- Garside, E.T. & J.S. Tait. 1958. Preferred temperature of rainbow trout (*Salmo gairdneri* Richardson) and its unusual relationship to acclimation temperature. *Can. J. Zool.* 36: 563-567.
- Garside, E.T., D.G. Heinze & S.F. Barbour. 1977. Thermal preference in relation to salinity in the threespine stickleback, *Gasterosteus aculeatus* L., with an interpretation of its significance. *Can. J. Zool.* 55: 590-594.
- Gibson, M.B. 1954. Upper lethal temperature relations of the guppy, *Lebistes reticulatus*. *Can. J. Zool.* 32: 393-407.
- Gilbert, C.R. 1980a. *Notropis telescopus* (Cope), telescope shiner. p. 315. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Gilbert, C.R. 1980b. *Micropterus punctulatus* (Rafinesque), spotted bass. p. 607. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*
- Gilbert, C.R. & G.H. Burgess. 1980a. *Notropis analostanus* (Girard), satinfish shiner. p. 226. *In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.*

- Gilbert, C.R. & G.H. Burgess. 1980b. *Notropis rubellus* (Agassiz), rosyface shiner. p. 302. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Glodek, G.S. 1980a. *Ictalurus nebulosus* (Lesueur), brown bullhead. p. 443. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Glodek, G.S. 1980b. *Ictalurus punctatus* (Rafinesque), channel catfish. p. 446. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Goddard, C.I. & J.S. Tait. 1976. Preferred temperatures of F_3 to F_5 hybrids of *Salvelinus fontinalis* + *S. namaycush*. J. Fish. Res. Board Can. 33: 197-202.
- Hall, L.W. Jr., C.H. Hocutt & J.R. Stauffer, Jr. 1978. Implication of geographic location on temperature preference of white perch, *Morone americana*. J. Fish. Res. Board Can. 35: 1464-1468.
- Hendricks, M.L. 1980. *Salvelinus fontinalis* (Mitchill), brook trout. p. 114. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Hensley, D.A. & W.R. Courtenay, Jr. 1980a. *Rhodeus sericeus* (Pallas), bitterling. p. 357. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Hensley, D.A. & W.R. Courtenay, Jr. 1980b. *Tilapia aurea* (Steindachner), blue tilapia. p. 771. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Hensley, D.A. & W.R. Courtenay, Jr. 1980c. *Tilapia mossambica* (Peters), Mozambique tilapia. p. 774. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Hubbs, C.L. & K.F. Lagler. 1958. Fishes of the Great Lakes region. Univ. Mich. Press, Ann Arbor. 213 pp.
- Javald, M.Y. & J.M. Anderson. 1967. Thermal acclimation and temperature selection in Atlantic salmon, *Salmo salar* and rainbow trout, *S. gairdneri*. J. Fish. Res. Board Can. 24: 1507-1513.
- Jenkins, R.E. & E.A. Lachner. 1980. *Nocomis leptoccephalus* (Girard), bluehead chub. p. 213. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Kelsch, S.W. 1996. Temperature selection and performance by bluegills: evidence for selection in response to available power. Trans. Amer. Fish. Soc. 125: 948-955.
- Kelsch, S.W. & W.H. Neill. 1990. Temperature preference versus acclimation in fishes: selection for changing metabolic optima. Trans. Amer. Fish. Soc. 119: 601-610.
- Lee, D.S. 1980a. *Salmo trutta* Linnaeus, brown trout. p. 109. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980b. *Lepomis cyanellus* Rafinesque, green sunfish. p. 591. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980c. *Lepomis gibbosus* (Linnaeus), pumpkinsced. p. 593. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980d. *Lepomis macrochirus* Rafinesque, bluegill. p. 597. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980e. *Micropterus dolomieu* Lacépède, smallmouth bass. p. 605. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980f. *Micropterus salmoides* (Lacépède), largemouth bass. p. 608. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. 1980g. *Perca flavescens* (Mitchill), yellow perch. p. 713. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. & G.H. Burgess. 1980. *Gambusia affinis* (Baird & Girard), mosquitofish. p. 538. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. & J.R. Shute. 1980a. *Pimephales notatus* (Rafinesque), bluntnose minnow. p. 340. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. & J.R. Shute. 1980b. *Pimephales promelas* Rafinesque, fathead minnow. p. 341. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Lee, D.S. & S.T. Kucas. 1980. *Catostomus commersoni* (Lacépède), white sucker. p. 375. In: D.S. Lee et al. (ed.) Atlas of North American Freshwater Fishes, N. C. State Mus. Nat. Hist., Raleigh.
- Magnuson, J.J., L.B. Crowder & P.A. Medvick. 1979. Temperature as an ecological resource. Amer. Zool. 19: 331-343.
- McCaulley, R.W. & J.S. Tait. 1970. Preferred temperature of yearling lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 27: 1729-1733.
- McCaulley, R.W. & N.W. Huggins. 1979. Ontogenetic and non-thermal seasonal effects on thermal preference of fish. Amer. Zool. 19: 267-272.
- Pitt, T.K., E.T. Garside & R.L. Hepburn. 1956. Temperature selection of the carp (*Cyprinus carpio* Linn.). Can. J. Zool. 34: 555-557.
- Procht, H. 1958. Concepts of the temperature adaptation of unchanging reaction systems of cold-blooded animals. pp. 50-78. In: C.L. Prosser (ed.) Physiological Adaptation, Amer. Physiol. Soc., Washington, D.C.
- Priede, I.G. 1985. Metabolic scope in fishes. pp. 33-64. In: P. Tyler & P. Calow (ed.) Fish Energetics: New Perspectives, Johns Hopkins Univ. Press, Baltimore.
- Reynolds, W.W. & M.E. Castorlin. 1979. Behavioral thermoregulation and the 'final preferendum' paradigm. Amer. Zool. 19: 211-224.
- Richards, F.P. & R.M. Ibara. 1978. The preferred temperatures of the brown bullhead *Ictalurus nebulosus* with reference to its orientation to the discharge canal of a nuclear power plant. Trans. Amer. Fish. Soc. 107: 288-294.

- Scott, W.B. & E.J. Crossman. 1979. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184, Ottawa. 966 pp.
- Stauffer, J.R. Jr., E.L. Melisky & C.H. Hocutt. 1980. Temperature preference of the northern redbelly dace *Phoxinus eos*. Arch. Hydrobiol. 90: 121-126.
- Ware, D.M. 1982. Power and evolutionary fitness of teleosts. Can. J. Fish. Aquat. Sci. 39: 3-13.
- Zahn, M. 1962. Die Vorzugstemperaturen zweier Cypriniden und eines Cyprinodonten und die Adaptationstypen der Vorzugstemperatur bei Fischen. Zool. Beitr. 7. 15-25.