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# Seasonal Temperature Preference of Adult Mountain Whitefish, Prosopium williamsoni

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SEASONAL TEMPERATURE PREFERENCE OF ADULT MOUNTAIN

WHITEFISH, PROSOPIUM WILLIAMSONI

by

Jean M. Ihnat

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

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Jean M. Ihnat

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by

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Utah State University, 1981

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Temperatures selected seasonally by adult mountain whitefish were measured in the laboratory in a horizontal gradient. Final preferendum estimates, based on acute (3-hour) preference tests conducted with fish acclimated to 5, 10, and 15 C each season, were 17.7 C (pre-spawning), 11.9 C (post-spawning), 9.9 C (winter), and 16.3 C (spring). Seasonal influence on temperature selection was evident on the basis of differences in final preferenda, covariance analysis of responses of laboratory-acclimated fish, and temperature selection by fish held at ambient river temperatures. Post-spawning and winter groups selected lower temperatures than did pre-spawning and spring groups. Pre-spawning fish selected temperatures unsuitable for embryo survival. Reproductive status as reflected by gonad size was evidently not a factor that influenced seasonal temperature selection of adult whitefish.

(42 pages)

# INTRODUCTION

Renewed interest in thermal requirements of fish has stemmed recently from more widespread and severe thermal changes in surface waters. Activities resulting in such changes include discharge into lakes and streams of heated water used in the cooling of power plants, release of water into streams from reservoirs, clearcutting on land adjacent to streams, and removal of water for irrigation and other purposes. Release of cold water from the hypolimnion of deep reservoirs reduces summer temperatures in the stream (Vanicek 1967). Clearcutting of forests along streams increases solar input with resulting increase in water temperature.

Survival and reproduction of fish species may be affected when water temperature is changed or unnaturally high temperatures are induced, as in a thermal plume from a power plant discharge. Knowledge of preferred temperatures and of upper and lower avoidance temperatures is useful in setting temperature standards and in predicting the behavior of fish in thermally altered areas (Coutant 1977). Laboratory determinations of preferred temperature are valuable because interactions of temperature selection with various factors such as season, social interactions, diel rhythms, photoperiod, feeding, chemicals, and infection can be examined under controlled conditions.

The preferred (or selected) temperature has been defined as the temperature most frequently occupied when a range of temperatures is available (Reynolds 1977). In short-term (acute) laboratory temperature preference tests the preferred temperature usually varies according to the recent thermal history (acclimation level) of the fish. In many species, selected temperatures increase with increasing acclimation temperature (Ferguson 1958; Cherry et al. 1975, 1977; Richards and Ibara 1978; Hall et al. 1979). Over time in a gradient, however, a fish eventually selects a temperature independent of prior acclimation level. This final temperature has been termed the final thermal preferendum (Fry 1947). The fish will remain at or near this temperature and become acclimated to it if given enough time. The final preferendum is often estimated in acute preference studies by graphically determining the point at which the acclimation and preferred temperatures are equal.

Short-term temperature preference studies have the disadvantage of testing fish while they are undoubtedly still under some metabolic stress resulting from their transfer to the gradient chamber. But if one desires to test the influence of acclimation temperature on preferred temperature, data must be collected as soon as possible after introducing the fish into the gradient. Within the first few hours of exposure to a thermal gradient the fish begins to gravitate towards its final preferendum and the influence of the original acclimation temperature is lost. The short duration of the tests also allows for testing of sufficient numbers of fish to provide reliable estimates of selected temperatures at various acclimation levels within a seasonal sampling period.

Several types of gradient chambers have been used in laboratory temperature preference studies. The two major categories are spatial and temporal gradients. Spatial temperature gradients are most commonly established either in long, shallow troughs (horizontal gradients) or in deep tanks (vertical gradients). Temporal gradients exist in electronic shuttleboxes, in which the fish controls the water temperature in the chamber by activating the flow of warm or cold water. In my study, a horizontal thermal gradient was used. Based on other studies, the horizontal gradient is satisfactory for determining temperature preference. McCauley (1977) and Huggins (1978) found that temperature preference data collected from horizontal gradients agreed well with that obtained from electronic shuttleboxes. Rainbow trout fry (Salmo gairdneri) selected the same final preferendum in vertical and horizontal gradients (McCauley and Pond 1971). Huggins (1978) found, however, that 12-month old rainbow trout selected significantly lower temperatures in a vertical gradient than they selected in either a horizontal gradient or shuttlebox. Temperature preference data acquired from various thermal gradient devices in the laboratory are valuable in predicting behavior of fish in their natural habitat. Neill and Magnuson (1974), Stauffer et al. (1975), and Magnuson et al. (1979) found that laboratory-determined preferred temperatures were in close agreement with temperatures occupied by fish in the field. Coutant (1975) reported that laboratory and field data agree fairly well when age of the fish is taken into account.

The mountain whitefish, Prosopium williamsoni, was selected for this study. This species is becoming increasingly popular as a sport fish, and the U. S. Environmental Protection Agency has recommended it as a key species on which studies should be conducted (Stalnaker and Gresswell 1974). The species is widely distributed in cool lakes and streams west of the Rocky Mountains in the United States and Canada (Jordan and Evermann 1902, Sigler and Miller 1963, McPhail and Lindsey 1970, Norden 1970, Moyle 1976).

Knowledge of thermal requirements of mountain whitefish is limited to reports of field observations on temperatures of waters inhabited by the species. Based on these observations, summer water temperatures where the species is found range from approximately 11 to 20 C (Rodeheffer 1935: Costley 1941; Sigler 1951; Gaufin et al. 1960; Posewitz 1960, 1962; Webb and Casey 1961; Bridges 1963; Sigler and Miller 1963; Hill 1965; Everhart and May 1973; Thompson 1974; Joseph et al. 1977). Juvenile whitefish have been collected in areas with temperatures of 12.2 to 20.6 C (Mullan 1976). Optimum temperatures for growth of whitefish fry range from 9 to 12 C (Stalnaker and Gresswell 1974; Rajagopal 1975, 1979). The upper optimum temperature for successful development of whitefish eggs is 6 C; embryo mortality is significant at 9 C and 100% at 12 C (Rajagopal 1975, 1979). Most reported spawning temperatures are below 5.6 C (Brown 1952, 1971, 1972; Breder and Rosen 1966; Thompson 1974; Thompson and Davies 1976).

Seasonal differences in temperatures selected by several fish species have largely been attributed to differing seasonal temperature acclimation levels (Sullivan and Fisher 1953, Barans and Tubb 1973, Otto et al. 1976), but some evidence of seasonal effects independent of thermal history has also been found. Sullivan and Fisher

(1953) and Otto et al. (1976) found that brook trout (*Salvelinus fontinalis*) and alewife (*Alosa pseudoharengus*) selected temperatures rose in the spring regardless of whether acclimation temperatures increased, decreased, or remained constant. Selection of higher temperatures in the spring could be due to anticipation of greater food intake associated with warming spring temperatures after a long period of reduced feeding. Changing photoperiods might contribute to seasonal differences in temperature selection (Richards et al. 1977, McCauley and Huggins 1979). The influence of photoperiod and temperature on gonadal maturation is well known (Hoar 1969), and these factors are frequently manipulated to stimulate the fish to spawn outside the normal spawning season. In turn, temperature selection during the spawning season may be influenced by hormones involved in gonadal maturation (Hesthagen 1979). Spawning adults might subordinate their own preference to the needs of embryos.

The objectives of my study were to determine if mountain whitefish respond similarly to other species in laboratory temperature preference experiments. Effects of acclimation temperature and season on acute temperature selection of adult mountain whitefish were examined.

The following hypotheses were tested:

1. Preferred temperatures of whitefish will increase with increasing acclimation temperatures.

2. Seasonal differences, independent of differences attributable to acclimation level, exist in temperatures selected.

a. Fish select higher temperatures in the spring than during fall and winter.

b. Fish in early fall (pre-spawning) select temperatures approximately the same or lower than those selected by fish in late fall (post-spawning).

c. Fish select lower temperatures in winter than during the other seasons.

3. Changes in gonosomatic index (GSI) correlate with seasonal changes in preferred temperatures.

In a symposium on the history and methodologies of temperature preference studies, Richards et al. (1977) made several recommendations in an attempt to standardize techniques and facilitate comparisons among studies. These recommendations were followed in my study where relevant.

# METHODS

## Fish Collection and Laboratory Holding Facilities

Electrofishing equipment was used to collect adult mountain whitefish from the Blacksmith Fork River, Utah, in October and December, 1980, and in February and April, 1981. Each season captured fish were divided into four groups of approximately 15 to 20 fish each. Body total length ranged from 275 to 442 mm. One group was held in Logan River water at ambient photoperiod and water temperature. The rest of the fish were divided equally in numbers and placed in three separate fiberglass holding tanks. Water temperatures in the holding tanks were regulated to maintain acclimation temperatures each season of 5, 10, and 15 C. Temperatures were initially set at ambient field temperature at the time of collection. The desired thermal acclimation levels were attained by changing the holding water temperature 1 C per day.

The area around the holding tanks was enclosed by a wooden framework covered with black plastic. Low intensity lighting was provided by three evenly-spaced 15-watt incandescent lamps suspended from the ceiling of the enclosure. Lights were turned on one-half hour before sunrise and off one-half hour after sunset. Photoperiod was adjusted several times during the acclimation period to coincide with the ambient photoperiod. The photoperiod was kept constant after testing began.

Richards et al. (1977) recommended that in testing for seasonal effects, fish should either be tested immediately after collection or held at ambient photoperiod and river temperature before testing. Whitefish tested at ambient river temperatures were held for two days before testing. Testing was completed within ten days of collection. Fish acclimated to temperatures higher than ambient field temperature were held for at least seven days at the desired acclimation level before testing was begun. Fish acclimated to temperatures lower than ambient field temperature were held at least one month at the desired acclimation temperature before testing was begun.

Fish were fed 3-mm Silver Cup dry trout chow ($\geq$ 38% protein) once each day in early to late afternoon or evening. Fish were not fed on the day of testing. Juvenile whitefish that had learned to eat the artificial food were placed in each tank of newly captured fish to help train them to feed. Examination of fish after testing revealed that none had completely empty intestines and indicated that some feeding was occurring.

## Experimental Apparatus and Methods of Testing

The testing apparatus consisted of a stainless steel trough, 4.5 m long, 27 cm wide, and 10 cm deep (Figure 1). Water depth was maintained at 9 cm. The trough area was enclosed by black plastic to eliminate extraneous lighting and human disturbance. Fish were observed through a small aperture in the plastic curtain. Lighting was provided by six evenly-spaced 15-watt incandescent lamps. Light intensity was set at a level just high enough (less than 1 lux) to permit observation of the fish.

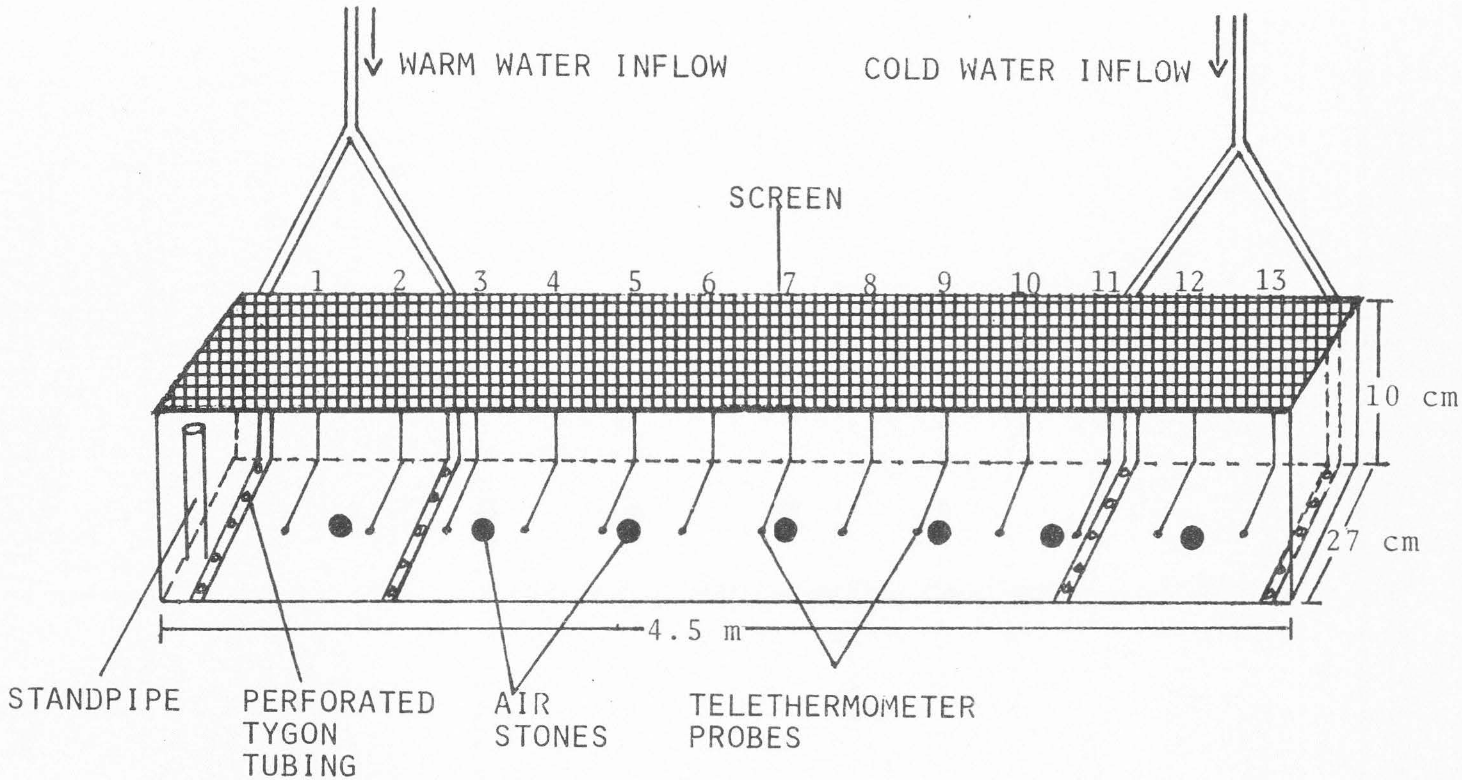


Figure 1. Horizontal gradient apparatus.

Heated water (50 C) was introduced at a rate of approximately 600 ml/min at one end of the trough through perforated Tygon tubing anchored in the bottom of the trough. Chilled water (4-5 C) entered at a rate of approximately 800 ml/min at the opposite end of the trough.

Water flowed out of the trough through a standpipe at the warm end of the gradient. The trough was covered with 25-mm mesh hardware cloth to prevent escape of the fish during the habituation period.

Air stones placed at 60-cm intervals along the bottom of the trough helped maintain dissolved oxygen levels at saturation, assured vertical mixing, and provided a linear temperature gradient. Temperature in the 9-cm water column varied less than 1 C. A temperature range of approximately 15 C existed in the gradient for all fish tested. The range was set so that the temperature to which each fish had been acclimated was located near the center of the gradient when possible. Temperatures occupied by the fish were measured to the nearest 0.1 C with telethermometer probes anchored in the bottom of the trough at 35-cm intervals.

The following test procedure was used: A fish was placed in the gradient at a point corresponding to the acclimation temperature of that fish. The fish was then left undisturbed for 1.5 hr. This time period was chosen after preliminary testing indicated that upon introduction fish either attempted to escape, swam excitedly, or remained motionless. An hour or more after introduction into the chamber, most fish became calm and began exploring the gradient without attempting to escape. For the next hour, fish position and water temperature at that position were recorded at one-minute intervals. For each fish tested, temperature readings were then grouped into one-degree (Centigrade) intervals. The interval containing the most observations was identified as the mode. The mean of all readings in the one-degree modal interval was taken as the selected temperature for that fish.

At the end of the test period, the gradient was altered by changing the flow rate of the warm or cold water or both. For fish in the warm end of the gradient, warm water flow was increased. For those in the cold end, cold water flow was increased. Positions and temperatures occupied during this 30-min control period were recorded to determine whether the fish was responding to temperature, or selecting a position in the trough for some other reason. Positions and temperatures occupied during the control period were plotted against time and compared with those occupied during the test period to judge the responsiveness of an individual fish.

Criteria used for discarding data for a particular fish were as follows:

1. Evidence of disease, injury, or abnormal swimming.

2. Failure of a fish to change positions in the trough within 30 min of the beginning of the test period.

3. More or less equal time spent in all available temperatures.

4. Rapid swimming back and forth in the trough and attempting to escape for the first 30 min of the test period.

5. Failure of a fish to respond to the changing temperature

during the control period.

After testing was completed each fish was killed and then weighed on a triple-beam balance. Gonads were then removed and weighed to compute the gonosomatic index (GSI) for each fish. GSI values were computed as follows:

GSI = (gonad weight/total body weight) x 100

Total length (mm) and sex were also recorded.

## Statistical Analyses

The computer program, Minitab (Ryan et al. 1980), was used to calculate means modes, and standard deviations of occupied temperatures. The Statistical Program Package (STATPAC) compiled at Utah State University by Rex L. Hurst (unpublished) was used for all other statistical analyses. Ambient seasonal temperature-preference data were analyzed in a completely-randomized-design analysis of variance (STATPAC/BASIC). The effects of acclimation temperature and season were analyzed in a 3 x 4 factorial analysis of variance (STATPAC/LIBRARYA). The program used standard multiple regression methodology (Draper and Smith 1966). Regression and covariance analyses were performed using STATPAC/BASIC.

The computer program Dataplot, written by Robert Bayn (unpublished) at Utah State University, was used for all graphs. The program drives a Calcomp 1051 plotter to produce graphs.

# RESULTS

During the observation period, fish demonstrated two general types of behavior. Some fish swam calmly back and forth in a small portion of the gradient and occasionally made an excursion to one of the extreme ends. Other fish remained almost stationary but at intervals of several minutes moved from one compartment to another, turning just often enough to remain in a particular portion of the gradient. Data for 19% of the total number of fish tested (210) were rejected on the basis of the criteria listed in the methods section. Ten fish were rejected when it was discovered during or after testing that they were injured or sick. Results for only four fish were rejected on the basis of their failure to follow the selected temperature down the chamber as the gradient changed during the control period. Most fish responded to the changing temperature and changed location in the chamber. Evidently water movement was not a factor in position selection by the fish because they oriented themselves at random in relation to the direction of water flow in the chamber.

Temperature selection data was first tested within each acclimation group for differences between the sexes. No statistically significant differences ($p \leq 0.05$) were detected, and data by sex were pooled for further analyses.

Richards et al. (1977) recommended that the entire frequency distributions of occupied temperatures be included in statistical reporting of results, especially where skewness is evident. In my study, pooled distributions of occupied temperatures were generally not normal (Figure 2). The histograms did, however, reflect differences in the ranges of temperatures selected by various groups of fish. Skewness coefficients for the pooled distributions ranged from -1.21 to +1.25 (Table 1), but no distinct pattern of skewness was evident. Examination of individual fish generally revealed greater precision in temperature selection than was indicated when all observations within a sample group were pooled (Figure 2, Table 1). Statistics for the pooled distributions (Table 1) are provided mainly to facilitate comparisons with other studies. Statistical comparisons in my study were based on modal preferred temperatures (Table 2, Appendix). The mode is assumed to describe the selected temperature since it is the temperature most frequently occupied when a range of temperatures is available (Richards et al. 1977). Selected temperatures (modes for individual fish) varied from 9.7 to 15.9 C for the pre-spawning fish acclimated to 10 C and from 5.0 to 18.9 C for the winter group acclimated to 5 C (Table 2, Appendix). The mean of pooled observations (Table 1) was generally very close ($\pm$ 0 to 1.6 C) to the mean of the modes (Table 2) for each group of fish. For example, the pooled mean for pre-spawning fish held at ambient temperatures was 12.5 C, and the mean of the modes was 12.8 C.

## Effect of Acclimation Temperature

Recent thermal history (acclimation level) usually influences the acute temperature preference of fishes. In my study the effect of acclimation temperature on preferred temperature was significant

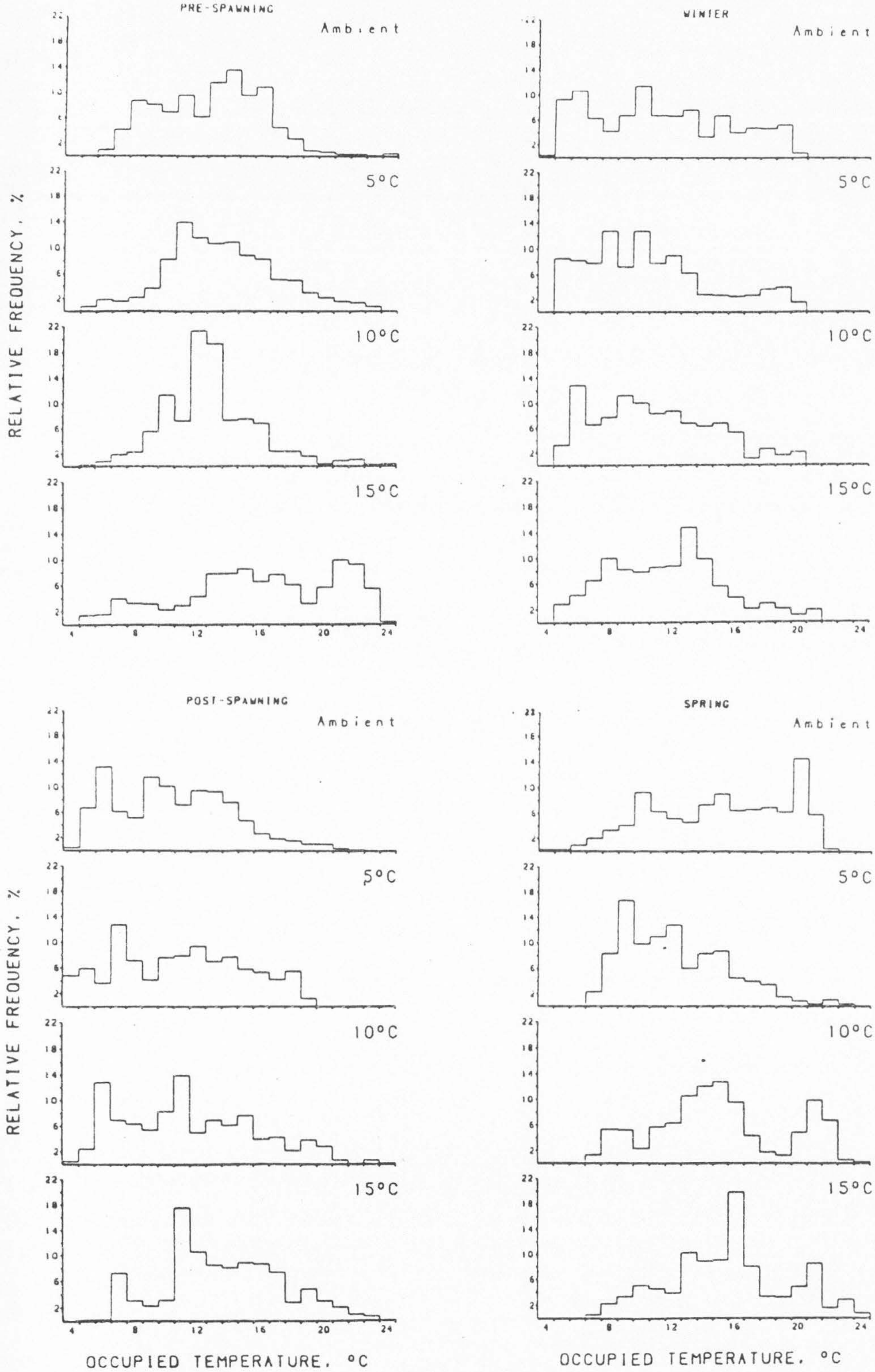


Figure 2. Histograms of temperatures occupied seasonally by adult mountain whitefish.

Table 1. Statistics for pooled observations of occupied temperature.

| Sample Group | Holding Temperature | Number of Observations[a] | Occupied Temperature, C Mean | Mode | Median | Standard Deviation | Skewness[b] |
|---|---|---|---|---|---|---|---|
| Pre-spawning (October) | ambient (9-11 C)[c] | 780 | 12.5 | 14 | 12.9 | 3.28 | -0.46 |
| | 5 C | 720 | 13.4 | 11 | 13.0 | 3.50 | +0.69 |
| | 10 C | 600 | 12.7 | 12 | 12.4 | 2.92 | +0.24 |
| | 15 C | 720 | 15.8 | 21 | 15.9 | 4.82 | -1.08 |
| | all acclimation levels | 2040 | 14.0 | 13 | 13.4 | 4.10 | +0.24 |
| Post-spawning (December) | ambient (4-8 C) | 720 | 10.4 | 6 | 10.1 | 3.62 | +1.22 |
| | 5 C | 660 | 10.9 | 7 | 11.0 | 4.08 | +0.96 |
| | 10 C | 720 | 11.4 | 11 | 11.0 | 4.19 | +0.10 |
| | 15 C | 540 | 13.4 | 11 | 13.1 | 3.69 | +0.65 |
| | all acclimation levels | 1920 | 11.8 | 11 | 11.5 | 4.15 | +0.19 |
| Winter (February) | ambient (4 C) | 600 | 11.1 | 10 | 10.6 | 4.33 | +0.25 |
| | 5 C | 600 | 10.5 | 9 | 9.9 | 3.98 | +0.38 |
| | 10 C | 600 | 10.7 | 6 | 10.3 | 3.75 | +1.25 |
| | 15 C | 600 | 11.6 | 13 | 11.6 | 3.67 | -0.38 |
| | all acclimation levels | 1800 | 10.9 | 10 | 10.5 | 3.83 | +0.23 |
| Spring (April) | ambient (7-10 C) | 540 | 14.9 | 20 | 15.1 | 4.23 | -1.21 |
| | 5 C | 600 | 12.1 | 9 | 11.6 | 3.29 | +0.94 |
| | 10 C | 600 | 14.9 | 15 | 14.6 | 4.13 | -0.02 |
| | 15 C | 600 | 15.4 | 16 | 15.5 | 3.69 | -0.16 |
| | all acclimation levels | 1800 | 14.2 | 16 | 14.0 | 4.00 | -0.45 |

[a] 60 observations were made for each fish

[b] Pearson's coefficient of skewness: (mean - mode)/ standard deviation

[c] Range of river water temperatures in the laboratory during the test period.

Table 2. Statistics for temperatures selected seasonally by fish held at ambient river temperatures and by fish acclimated in the laboratory to 5, 10, and 15 C. Temperatures selected by individual fish are listed in the appendix (Table 6).

| Sample Group | Holding Temperature | Number of Fish | Selected Temperature, C: Mean of Modes | Standard Deviation | Range of Modes |
|---|---|---|---|---|---|
| Pre-spawning (October) | ambient (9-11 C)[a] | 13 | 12.8 | 2.84 | 7.9 - 17.0 |
| | 5 C | 12 | 12.6 | 2.31 | 9.7 - 16.9 |
| | 10 C | 10 | 12.6 | 1.78 | 9.7 - 15.9 |
| | 15 C | 12 | 17.4 | 4.07 | 11.1 - 23.0 |
| | all acclimation levels | 34 | 14.3 | 3.68 | 9.7 - 23.0 |
| Post-spawning (December) | ambient (4-8 C) | 12 | 9.6 | 2.56 | 5.3 - 13.8 |
| | 5 C | 11 | 10.9 | 3.22 | 6.9 - 17.8 |
| | 10 C | 12 | 11.8 | 4.50 | 6.0 - 19.5 |
| | 15 C | 9 | 12.6 | 2.92 | 7.1 - 16.9 |
| | all acclimation levels | 32 | 11.7 | 3.64 | 6.0 - 19.5 |
| Winter (February) | ambient (4 C) | 10 | 10.8 | 3.62 | 4.8 - 16.5 |
| | 5 C | 10 | 10.0 | 3.95 | 5.0 - 18.9 |
| | 10 C | 10 | 9.9 | 3.24 | 5.8 - 15.0 |
| | 15 C | 10 | 11.4 | 2.60 | 7.6 - 15.0 |
| | all acclimation levels | 30 | 10.4 | 3.26 | 5.0 - 18.9 |
| Spring (April) | ambient (7-10 C) | 9 | 16.4 | 3.81 | 9.8 - 20.8 |
| | 5 C | 10 | 11.1 | 2.21 | 8.1 - 14.8 |
| | 10 C | 10 | 14.3 | 4.41 | 8.9 - 22.0 |
| | 15 C | 10 | 16.3 | 4.04 | 9.9 - 22.9 |
| | all acclimation levels | 30 | 13.9 | 4.19 | 8.1 - 22.9 |

[a] Range of river water temperatures in the laboratory during the test period.

at the 95% confidence level (Table 3). Fish acclimated to 5 C

Table 3. Factorial analysis of variance for effect of acclimation level and season on temperatures selected by fish acclimated in the laboratory to 5, 10, and 15 C.

| Source of Variation | Degrees of Freedom | Mean Square | F |
|---|---|---|---|
| Acclimation Temperature | 2 | 116.74 | 10.04 * |
| Season | 3 | 100.90 | 8.68 * |
| Acclimation Temperature x Season | 6 | 16.62 | 1.43 |
| Error | 114 | 11.63 | |
| Total | 125 | | |

* indicates significance at the 0.05 level of probability

selected temperatures several degrees higher than 5 C (Figure 3). The difference between selected and acclimation temperature generally decreased as acclimation temperature increased. Other researchers have made the same observation (Ferguson 1958, Cherry et al. 1975). Although fish acclimated to 15 C always selected mean temperatures higher than did fish acclimated to 5 C, the differences were statistically significant only during the pre-spawning and spring seasons. Fish acclimated to 5 C did not select significantly different temperatures than did fish acclimated to 10 C during any season. During the post-spawning and winter periods, selected temperatures did not increase with acclimation temperature ($p \leq 0.05$). Regression analysis substantiated the conclusion that the effect of acclimation temperature on selected temperature was significant only during pre-

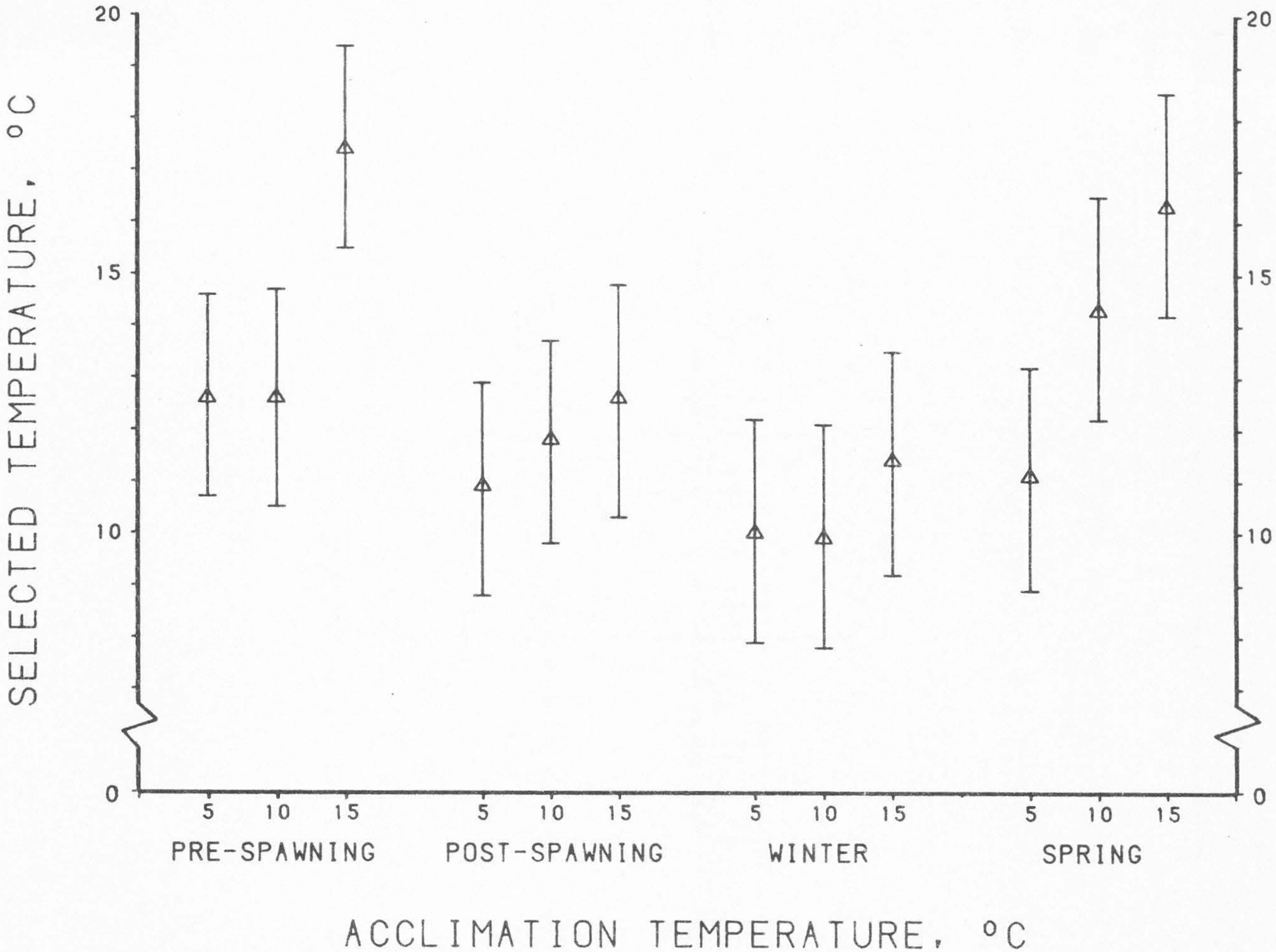


Figure 3. Temperatures selected seasonally at acclimation levels of 5, 10, and 15 C. Vertical lines represent 95% confidence intervals about the means (of modes for individual fish).

spawning and spring seasons, periods of falling or increasing temperature. The slope of the regression line describing the relation between selected and acclimation temperature was significantly different from zero only during the pre-spawning and spring seasons. Less than 30% of the variation in selected temperature could be explained by acclimation temperature in any season ($r^2$ = 0.30 in the pre-spawning group).

The data from the different lots of acclimated fish were used to estimate final preferenda. Final preferendum was estimated graphically for the pre-spawning and spring groups since acclimation level influenced temperature selection during those seasons. Geometric means of modal selected temperatures were plotted against acclimation temperature for pre-spawning and spring groups (Figure 4).

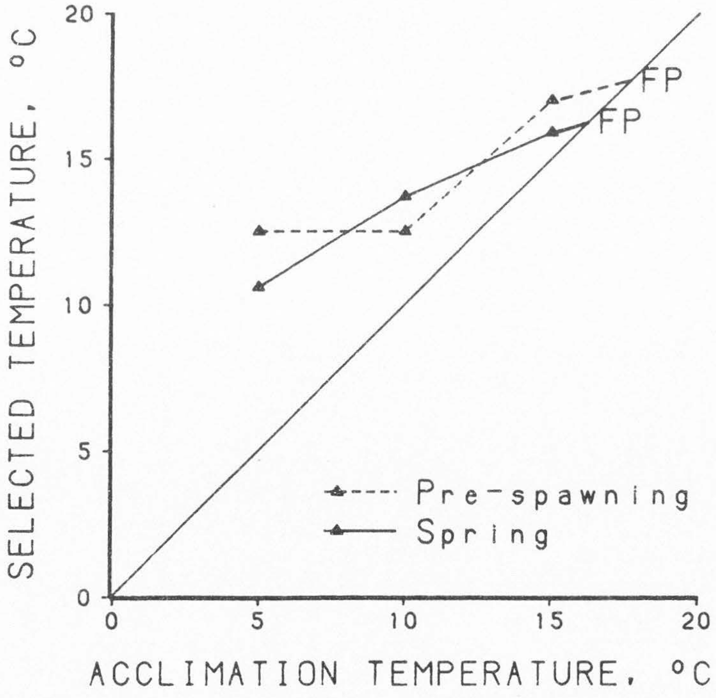


Figure 4. Geometric means (▲) of temperatures (modes) selected by pre-spawning and spring groups of fish acclimated to different temperatures, and final preferendum estimates (FP).

The points were connected and, by extrapolation, the final preferendum, i.e., the temperature at which acclimation temperature equals selected temperature, was estimated. Final preferendum was estimated as 17.7 C for the pre-spawning group and 16.3 C for the spring group. Since acclimation temperature did not influence temperature selection in the post-spawning and winter groups, the geometric mean of modal selected temperatures was considered the final preferendum. Final preferendum was 11.9 C for the post-spawning group and 9.9 C for the winter group. Final thermal preferendum, which by definition is independent of recent thermal history (Fry 1947), closely followed the seasonal trend of lowering ambient temperature from fall to winter and increasing from winter to spring (Figure 5).

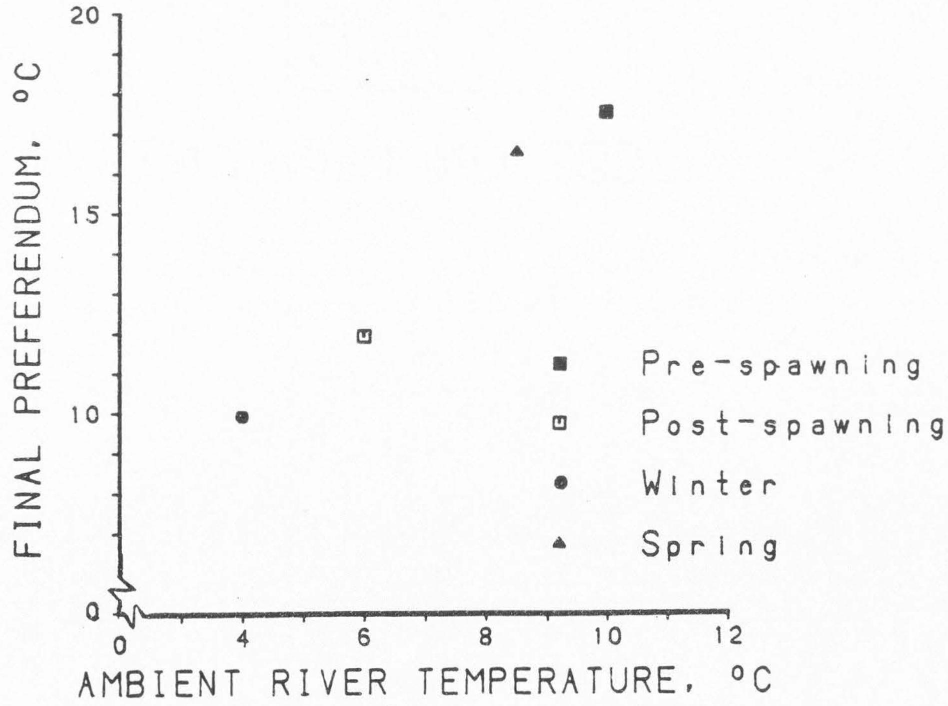


Figure 5. Comparison of seasonal final preferenda with seasonal changes in ambient river temperature.

Effect of Season

Factors that may influence seasonal temperature selection include ambient temperature and photoperiod, nutritional status, life stage, and reproductive status. Individual whitefish in my study occupied temperatures within ranges of approximately 5 C during the test period, regardless of acclimation level or season. When all temperatures selected each season by both ambient and acclimated fish were placed in 5-C temperature groups, seasonal differences were evident in selected temperatures (Figure 6). Percentages of post-

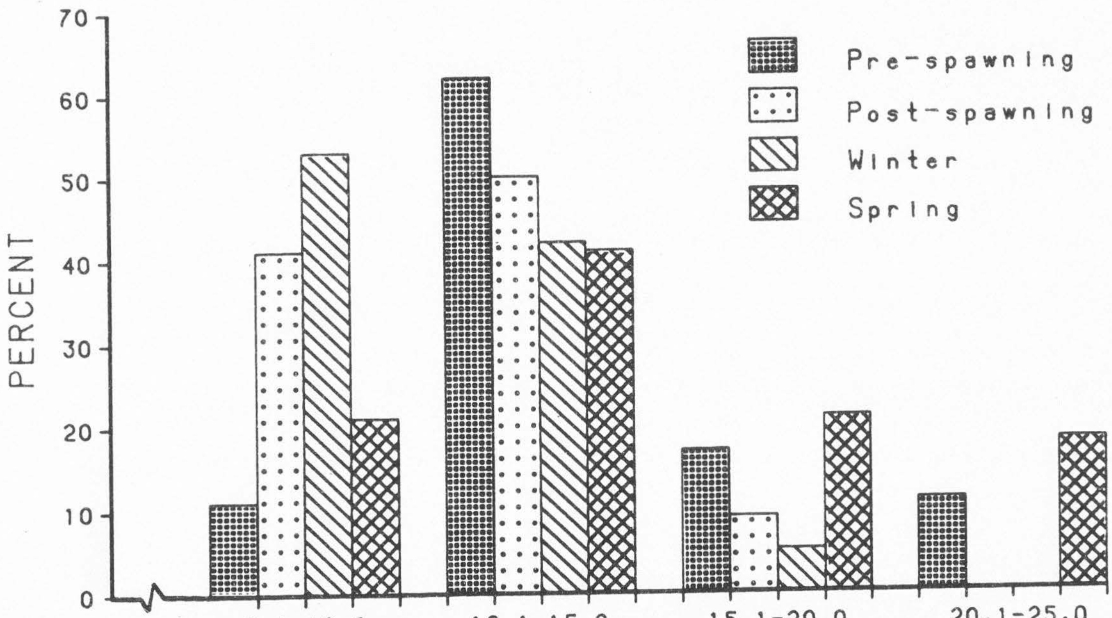


Figure 6. Percentages of seasonally selected temperatures (ambient and acclimated groups) within 5-C temperature categories.

spawning and winter selected temperatures in the 5.1 - 10.0 C category were much higher than the percentages of pre-spawning and spring temperatures in that category. None of the post-spawning and winter selected temperatures fell in the highest category (20.1 - 25.0 C). Largest proportions of selected temperatures for all but the winter seasonal group fell in the 10.1 - 15.0 C category.

Seasonal influence on temperature selection was also evaluated statistically with data on fish tested soon after collection (ambient groups). Differences among temperatures selected by these fish were significant at the 0.05 level of probability (Table 4 and Figure 7).

Table 4. Analysis of variance for effects of season on temperatures selected by fish held at ambient river temperatures.

| Source of Variation | Degrees of Freedom | Mean Square | F |
|---|---|---|---|
| Season | 3 | 87.35 | 8.66 * |
| Error | 40 | 10.08 | |
| Total | 43 | | |

* indicates significance at the 0.05 level of probability.

The mean temperature selected in the spring (16.4 C) was significantly higher than temperatures selected in the post-spawning (9.6 C) and winter (10.8 C) seasons but not significantly higher than that selected by the pre-spawning group (12.8 C). The difference between mean pre-spawning and post-spawning selected temperatures was not significant. In the winter, fish selected a mean temperature lower than that selected in the spring but not significantly different from temperatures selected during either of the other seasons (Figure 7).

Seasonal effects were further examined by comparing results of ambient temperature fish with those of fish acclimated in the laboratory to different temperatures. Responses for fish acclimated to 5, 10, and 15 C were combined within each test period (Table 2 and Figure 8) to compare them with the ambient temperature groups. Seasonal differences among temperatures selected by the laboratory-acclimated fish were also significant at the 0.05 probability level (Table 3 and Figure 8). Seasonal trends similar to those noted in the ambient groups (Figure 7) were evident in the responses of laboratory-acclimated fish (Figure 8). Mean selected temperatures were higher in the pre-spawning and spring groups than in the post-spawning and winter groups. After adjusting for the effect of acclimation level, seasonal differences in selected temperatures were still significant for at least two seasons (Table 5). Hence, data on both acute temperature selection and final preferendum reflected a seasonal influence.

Table 5. Covariance analysis for effect of season on selected temperature.

| Source of Variation | Degrees of Freedom | Mean Square | F |
|---|---|---|---|
| Season | 3 | 103.73 | 8.74 * |
| Regression | 1 | 235.90 | 19.87 * |
| Error | 121 | 11.87 | |

* indicates significance at the 0.05 level of probability.

## Relation of Degree of Gonadal Development to Temperature Selection

Gonosomatic indexes were calculated to determine whether changes

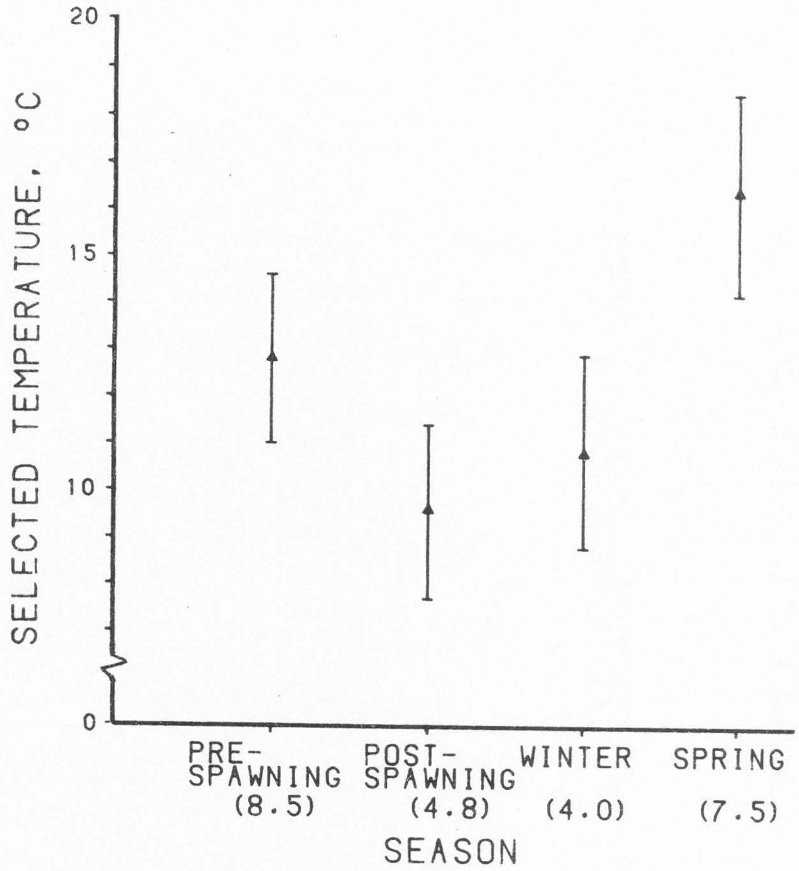


Figure 7. Mean temperatures selected seasonally by fish held at ambient river temperatures. Vertical lines indicate 95% confidence intervals. Ambient temperatures (C) at collection time are given in parentheses.

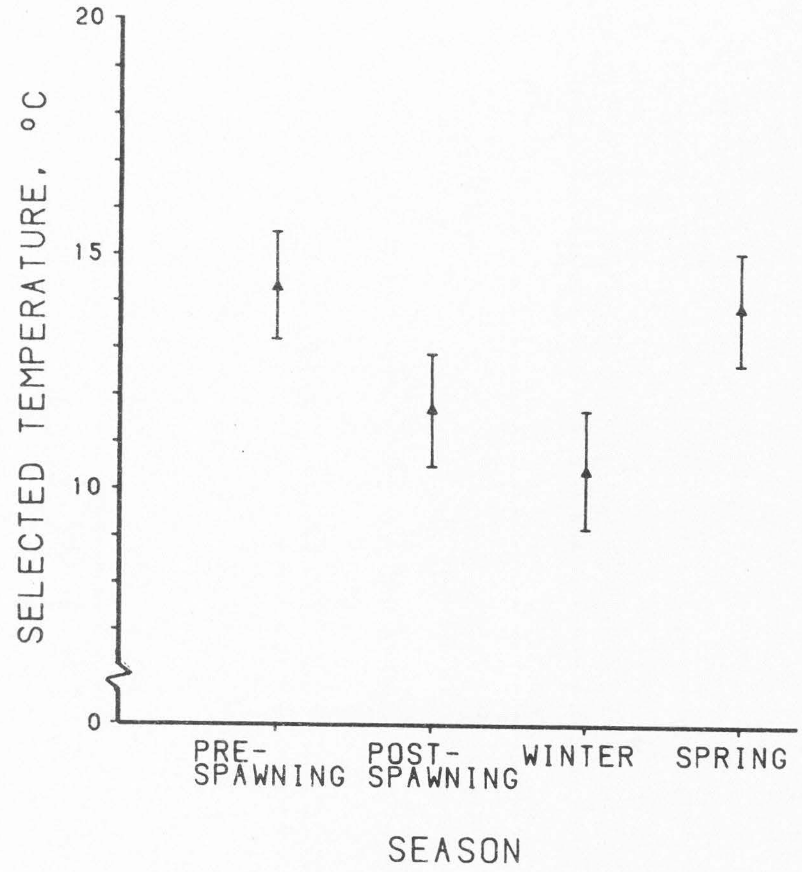


Figure 8. Mean temperatures selected seasonally by fish held at various acclimation temperatures, acclimation levels pooled within each test period. Vertical lines represent 95% confidence intervals.

in hormone level associated with gonadal development were related to temperatures selected seasonally. In populations of mountain whitefish in northern Utah, most spawning occurs in October and November. GSI values from the ambient test group of fish collected before spawning in October ranged from 16.3 to 22.6% for females and from 7.1 to 10.8% for males. Mean values were 19.2% (females) and 7.4% (males) (Figure 9). Lowest values were obtained in February (winter) and April (spring). Almost all fish had spawned by the time the December (post-spawning) collection was made. Only fish held at ambient temperature and photoperiod were used in the following comparisons of GSI with selected temperatures since GSI values changed in fish held in the laboratory under unnatural temperature regimes for longer periods of time. Males were excluded from the comparisons since there were only two males in the post-spawning (December) ambient temperature group. Although female GSI values were much lower in December (2.4%) than in October (19.2%), the mean selected temperatures for those two seasons did not differ significantly (Figure 9). Females tested in the spring (April) selected a higher mean temperature than did those tested in the winter (February), but GSI values were approximately equal during those two seasons.

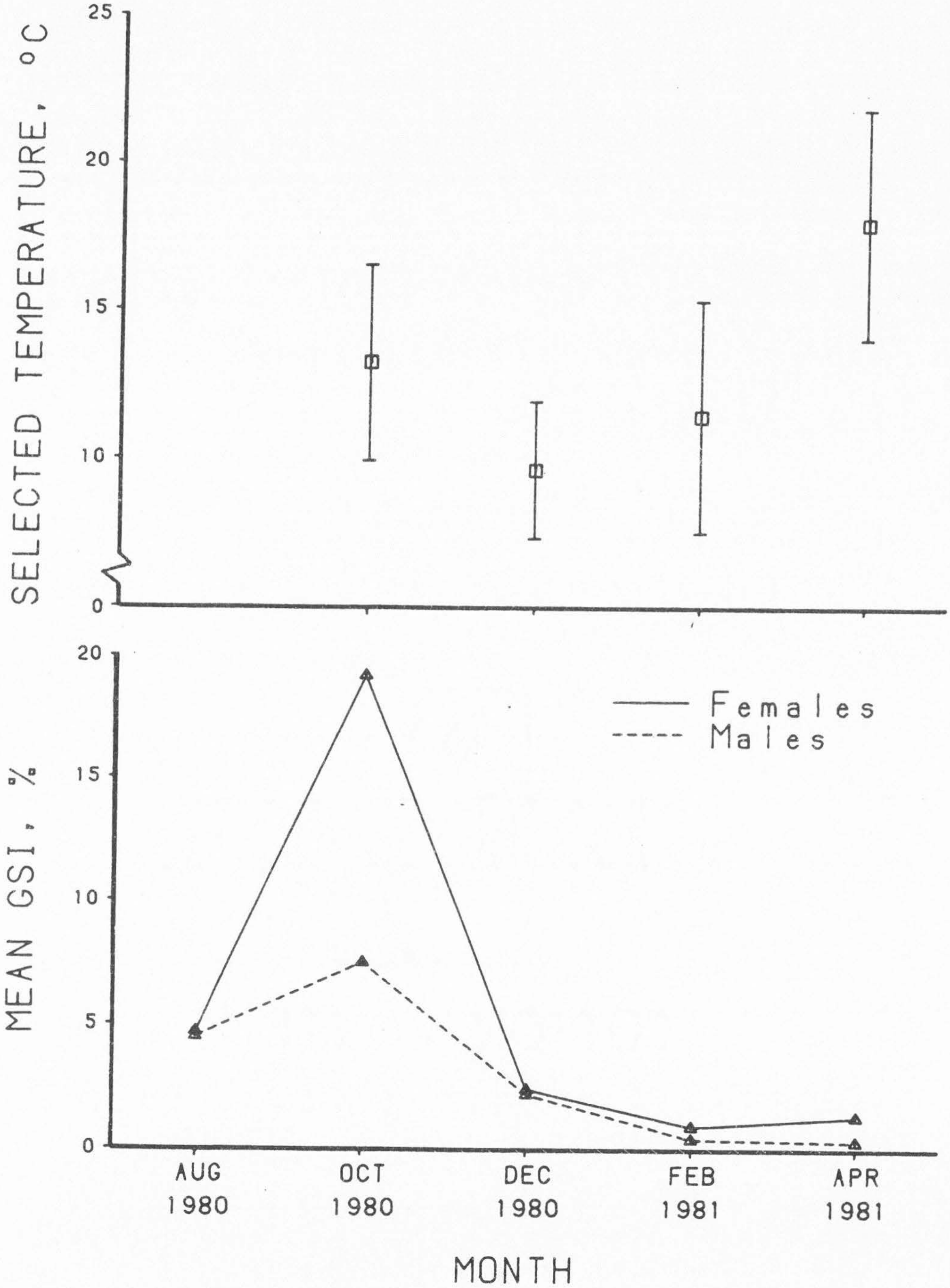


Figure 9. Mean temperatures (□) selected by females and mean GSI values (▲) for males and females. Vertical lines represent 95% confidence intervals. All fish included in this figure were collected at different seasons of the year and held at ambient river temperatures until they were tested.

# DISCUSSION

Precision in acute temperature selection by individual mountain whitefish in my study was generally fairly low (Appendix). Lack of greater precision is perhaps due to the thermally unstratified environment of the Blacksmith Fork River, a typical mountain stream ideal for stenothermic coldwater species. The population is not normally exposed to thermal gradients of any magnitude as are many warmwater species. However, another coldwater species, rainbow trout (Salmo gairdneri) also tested in a horizontal gradient chamber (Huggins 1978) exhibited less variability in acute temperature selection than did the whitefish in my study. Other species have shown variation similar in magnitude to the whitefish in acute temperature selection (Richards and Ibara 1978, Ehrlich et al. 1979). Even fish that normally utilize thermal cues in daily movements or spawning migrations sometimes demonstrate rather imprecise responses to thermal gradients in the laboratory (Brett 1952). Brett (1956) postulated that such fish might be capable of perceiving slight differences in temperatures but only do so under certain stressful conditions such as during migrations or when subjected to high environmental temperatures. The amount of variation in temperature selection is generally reduced over time as the individual begins to disregard acclimation temperature and select its final preferendum.

Another possible reason for the wide variation in temperature selection noted in whitefish as well as other species is the apparatus used to determine preference. A species may be rather precise in its temperature selection but conditions in the horizontal gradient may be so foreign to the individual fish that preferred temperature is very low in its hierarchy of needs. Perhaps it is under excessive stress from the shallow water depth or limited space within the chamber. Hence, better methods and apparatus are needed to define preferred temperature and reduce the variability found in this and many other studies.

Although considerable variation was evident in whitefish acute temperature selection, data were adequate for examining the influence of acclimation temperature on selected temperature. Fish that have been temperature acclimated will generally initially select temperatures near the acclimation temperature when placed in a thermal gradient. If the acclimation temperature is lower than the final preferendum for the species, the fish will fairly rapidly move into warmer portions of the gradient (Coutant 1975). In my study, most whitefish acclimated to 5 C selected temperatures several degrees higher than 5 C regardless of season. As acclimation temperature increased above 5 C, only pre-spawning and spring groups consistently selected temperatures higher than acclimation. In contrast, post-spawning and winter groups acclimated to 15 C selected temperatures lower than 15 C (Figure 3). The reasons for these differing responses are not known, but field temperatures were fairly constant in December and February (the post-spawning and winter groups), whereas temperatures were decreasing in October (pre-spawning) and increasing in April (spring). Perhaps the stress or stimulus of changing field temperatures in October and April created the greater sensitivity to acclimation temperatures exhibited by whitefish during those seasons.

The seasonal differences in selected temperatures noted in the laboratory may have been related to the nutritional status of the fish. The post-spawning and winter groups selected lower temperatures than did the pre-spawning and spring groups. Some feeding occurred in the laboratory during all seasonal test periods, but based on observed body condition, energy reserves were low in whitefish following spawning and during the winter months. Also, examination of stomach and intestine contents of a sample of fish from each collection period indicated that feeding in the field was heavier in pre-spawning and spring than during the post-spawning and winter periods. When food is withheld from fish in the laboratory some species select lower temperatures than they would otherwise select (Dyzan 1959, Javaid and Anderson 1967, Ehrlich et al. 1979). Selection of lower temperatures when food intake is restricted is a means of balancing energy intake with energy loss.

Exact thermal requirements for gonadal development of mountain whitefish are not known, but exposure to unnaturally high temperatures for an extended period of time during the fall could be detrimental to normal maturation or development of whitefish gametes. In walleye, Stizostedion vitreum, gamete viability was affected by acclimation temperature of the adult fish (Hokanson 1977). Viability of walleye gametes was highest in the range of temperatures at which spawning most frequently occurred. In my study, gamete viability in the sex organs was not monitored, but it was hypothesized that mountain whitefish would select temperatures favorable to embryo survival during the spawning season and that gonadal hormone levels might be instrumental in directing the fish into those favorable temperatures. Degree of gonadal maturity has been used by other researchers as an index of gonadal hormone levels. Baggerman (1959) correlated gonadal maturation with salinity preference of sticklebacks (*Gasterosteus aculeatus*). No correlation between GSI and seasonally selected temperatures was evident for mountain whitefish (Figure 9).

Spawning of mountain whitefish normally occurs in the fall when water temperature has decreased to approximately 6 C (Brown 1952, 1971, 1972; Breder and Rosen 1966; Thompson 1974; Thompson and Davies 1976). Mountain whitefish in Phelps Lake, Wyoming, began spawning when the lake temperature was approximately 11 C. A second spawning pulse was observed when the lake temperature had fallen to 6.9 C (Hagen 1970). In my study, mean temperatures (acute preferendum) of 12.8 C (ambient group) and 14.3 C (pooled acclimation levels) were selected by adults in the pre-spawning season (Figures 7 and 8, Table 2). Only one fish of 47 tested in the pre-spawning group selected a temperature lower than 9 C. The estimated final preferendum for pre-spawners was 17.7 C (Figure 4). Final preferendum for the post-spawning group was 11.9 C. In contrast, the reported upper optimum temperature for normal development of whitefish eggs is 6 C (Rajagopal 1975, 1979). Rajagopal (1975) observed 8.7% mortality at 6 C, 34.4% mortality at 9 C, and 85.1% mortality at 10 C of whitefish eggs after 36 days of incubation in the laboratory. Mortality was 100% by day 14 for eggs held at 12 C. Chances for normal development of whitefish embryos would be very poor, therefore, if mature adults selected the temperatures they seemed to prefer in the laboratory tests. Some species of fish tend to congregate in the warm waters of thermal effluents as ambient temperature decreases (Coutant 1975, Hokanson 1977). Results of my study suggest that adult mountain whitefish could also be attracted to thermal discharge areas during the spawning period and thus either block the spawning act itself or hinder embryo survival. The close agreement between selected temperatures in laboratory and field studies lends credence to this concern. Hence, caution should be used in discharging warm water into mountain whitefish habitat during the fall spawning period.

# CONCLUSIONS

1. The mountain whitefish selected temperatures in the laboratory with moderate precision in comparison with studies on other species, but much variability was evident.

2. The effect of acclimation temperature on selected temperature varied seasonally.

3. Seasonal differences in temperature selection were evident.

4. Adults during the pre-spawning period in October and in the December post-spawning period preferred temperatures that would be lethal to most whitefish embryos.

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# APPENDIX

Table 6. Modal and mean temperatures selected over 60-min test period by individual adult mountain whitefish.

| Season | Selected Temperature (C) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acclimation Level | | | | | | | | | | | |
| | Ambient River Temperature | | | 5 C | | | 10 C | | | 15 C | | |
| | Mode | Mean | SD[a/] | Mode | Mean | SD | Mode | Mean | SD | Mode | Mean | SD |
| Pre-spawning | 7.9 | 8.2 | 0.60 | 11.1 | 12.7 | 3.34 | 12.7 | 11.8 | 1.62 | 16.9 | 15.3 | 3.15 |
| | 13.7 | 11.9 | 3.30 | 13.9 | 13.5 | 2.90 | 9.7 | 10.4 | 1.32 | 20.9 | 20.0 | 3.28 |
| | 12.9 | 14.2 | 2.20 | 14.6 | 13.8 | 3.80 | 12.9 | 13.5 | 2.43 | 21.5 | 14.3 | 5.66 |
| | 12.1 | 12.2 | 2.93 | 11.9 | 13.5 | 1.98 | 12.8 | 13.6 | 3.49 | 11.1 | 12.9 | 4.83 |
| | 9.8 | 11.4 | 2.58 | 10.8 | 10.9 | 1.12 | 12.1 | 12.5 | 0.71 | 22.0 | 17.2 | 6.11 |
| | 11.1 | 11.2 | 1.90 | 11.0 | 13.4 | 2.45 | 11.1 | 10.9 | 3.00 | 16.0 | 15.5 | 3.64 |
| | 13.9 | 14.1 | 2.52 | 10.2 | 13.0 | 4.25 | 15.0 | 14.2 | 4.37 | 23.0 | 16.6 | 6.48 |
| | 9.3 | 11.2 | 2.34 | 16.9 | 16.6 | 2.98 | 15.9 | 14.6 | 2.24 | 12.8 | 13.4 | 3.84 |
| | 15.9 | 13.7 | 2.93 | 12.9 | 13.7 | 3.13 | 11.9 | 11.6 | 1.95 | 20.9 | 20.6 | 1.48 |
| | 17.0 | 14.1 | 3.86 | 16.0 | 16.2 | 3.54 | 12.0 | 13.6 | 2.77 | 13.8 | 14.1 | 2.67 |
| | 16.9 | 15.6 | 3.32 | 12.7 | 13.3 | 3.01 | | | | 14.9 | 14.1 | 3.65 |
| | 14.0 | 14.7 | 1.06 | 9.7 | 9.6 | 2.05 | | | | 15.0 | 16.0 | 3.00 |
| | 12.1 | 10.5 | 2.59 | | | | | | | | | |
| Post-spawning | 13.0 | 12.6 | 1.69 | 10.0 | 10.1 | 4.15 | 12.9 | 11.7 | 1.84 | 13.9 | 14.0 | 3.29 |
| | 5.3 | 8.8 | 5.11 | 17.8 | 12.8 | 5.37 | 19.0 | 14.4 | 4.78 | 10.8 | 11.2 | 1.37 |
| | 9.2 | 11.1 | 2.97 | 11.9 | 11.8 | 3.14 | 7.1 | 7.7 | 2.28 | 14.9 | 16.7 | 3.09 |
| | 6.1 | 6.3 | 0.29 | 7.8 | 10.6 | 4.51 | 13.8 | 13.6 | 1.94 | 11.9 | 14.2 | 3.55 |
| | 10.0 | 9.6 | 2.85 | 9.8 | 10.8 | 2.64 | 9.8 | 10.3 | 2.02 | 10.9 | 12.8 | 2.87 |
| | 10.1 | 11.8 | 3.63 | 7.1 | 7.2 | 0.31 | 15.0 | 14.8 | 2.47 | 16.9 | 17.4 | 1.07 |
| | 8.0 | 10.5 | 3.91 | 13.9 | 13.1 | 1.92 | 10.1 | 11.9 | 3.72 | 7.1 | 7.6 | 0.66 |
| | 9.1 | 9.8 | 2.44 | 9.9 | 8.1 | 3.14 | 19.5 | 16.0 | 3.86 | 11.9 | 12.6 | 2.43 |
| | 7.9 | 10.6 | 3.99 | 6.9 | 10.8 | 4.87 | 10.9 | 9.7 | 2.20 | 14.9 | 14.2 | 2.08 |
| | 13.8 | 11.3 | 3.61 | 12.0 | 11.5 | 3.96 | 11.0 | 12.8 | 3.89 | | | |
| | 10.4 | 10.1 | 2.49 | 12.3 | 13.0 | 3.57 | 6.1 | 5.9 | 0.41 | | | |
| | 11.9 | 12.6 | 3.13 | | | | 6.0 | 8.3 | 3.49 | | | |
| Winter | 8.9 | 11.3 | 3.70 | 9.8 | 10.3 | 3.12 | 11.9 | 13.1 | 2.40 | 8.0 | 9.7 | 2.01 |
| | 11.8 | 13.0 | 4.06 | 12.8 | 11.6 | 4.37 | 7.9 | 9.3 | 2.54 | 13.0 | 14.4 | 3.78 |
| | 12.9 | 12.2 | 4.45 | 10.0 | 9.6 | 3.51 | 10.0 | 9.3 | 1.49 | 12.9 | 13.0 | 4.14 |

Table 6. Continued.

| Season | Selected Temperature (C) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Acclimation Level | | | | | | | | | | | |
| | Ambient River Temperature | | | 5 C | | | 10 C | | | 15 C | | |
| | Mode | Mean | SD | Mode | Mean | SD | Mode | Mean | SD | Mode | Mean | SD |
| | 10.9 | 10.0 | 3.45 | 5.0 | 6.8 | 2.28 | 5.8 | 9.9 | 4.17 | 13.0 | 11.6 | 3.20 |
| | 10.1 | 9.9 | 0.65 | 11.9 | 11.9 | 1.24 | 15.0 | 11.6 | 4.24 | 15.0 | 14.0 | 4.41 |
| | 5.7 | 8.8 | 3.93 | 10.0 | 9.1 | 2.56 | 9.9 | 10.6 | 2.92 | 7.6 | 7.0 | 1.32 |
| | 4.8 | 5.3 | 0.75 | 6.0 | 7.9 | 2.08 | 14.9 | 16.2 | 1.99 | 14.1 | 13.2 | 2.58 |
| | 12.8 | 10.4 | 2.95 | 8.0 | 8.3 | 1.61 | 5.8 | 6.5 | 1.32 | 10.0 | 11.2 | 3.02 |
| | 14.0 | 14.7 | 3.08 | 7.9 | 12.5 | 4.02 | 9.0 | 10.7 | 3.80 | 9.1 | 9.7 | 2.13 |
| | 16.5 | 15.1 | 4.15 | 18.9 | 16.8 | 2.66 | 9.0 | 10.2 | 1.96 | 11.1 | 11.9 | 1.20 |
| Spring | 19.7 | 18.3 | 1.75 | 12.0 | 11.9 | 1.22 | 14.9 | 14.3 | 2.26 | 22.9 | 16.5 | 5.19 |
| | 17.9 | 15.9 | 2.92 | 13.9 | 13.5 | 1.77 | 13.0 | 10.1 | 2.64 | 16.1 | 14.2 | 3.48 |
| | 14.0 | 12.6 | 3.33 | 8.9 | 12.3 | 4.11 | 22.0 | 18.4 | 3.03 | 13.9 | 14.0 | 2.61 |
| | 20.1 | 19.3 | 2.32 | 14.8 | 11.8 | 1.57 | 12.8 | 14.5 | 2.16 | 16.0 | 15.4 | 2.40 |
| | 9.8 | 10.5 | 1.02 | 11.0 | 14.3 | 4.07 | 14.1 | 12.7 | 4.63 | 14.0 | 14.6 | 1.82 |
| | 16.0 | 14.0 | 3.50 | 9.8 | 11.9 | 3.88 | 11.8 | 14.4 | 3.24 | 9.9 | 12.8 | 3.98 |
| | 11.9 | 11.8 | 2.84 | 12.0 | 12.2 | 2.42 | 20.9 | 20.2 | 2.19 | 15.7 | 15.7 | 0.23 |
| | 17.0 | 13.6 | 4.22 | 8.1 | 12.3 | 4.11 | 16.0 | 15.0 | 0.86 | 20.8 | 18.9 | 1.89 |
| | 20.8 | 18.4 | 2.69 | 8.8 | 9.8 | 2.93 | 8.9 | 9.7 | 2.38 | 20.9 | 15.6 | 5.38 |
| | | | - | 11.2 | 11.1 | 3.31 | 8.9 | 12.7 | 4.50 | 13.2 | 16.5 | 2.96 |

a/ SD represents standard deviation about the mean.