TEMPERATURE PREFERENCE OF JUVENILE ARCTIC CISCO

(COREGONUS AUTUMNALIS) FROM THE ALASKAN BEAUFORT SEA,

IN RELATION TO SALINITY AND TEMPERATURE ACCLIMATION

by

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ABSTRACT

Horizontal-thermal-gradient apparatus of previously undescribed design was used to determine the temperature preference of juvenile arctic cisco, Coregonus autumnalis, as a function of acclimation temperature and acclimation-test salinity. Mean preferred temperature ranged from 11.5 C for fish acclimated to 5 C/5 ppt to 15.4 C for the 15 C/15 ppt acclimation group. Estimated final temperature preferenda were 13.5 C at 30 ppt and 15.6 C at 15 ppt. Preferred temperatures at 5 and 30 ppt were lower (P<0.05) than that at 15 ppt. Qualitative observations of fish in the acclimation tanks suggested that physiologically optimal temperatures of juvenile arctic cisco also exceed 10 C over the salinity range of 5-30 ppt.

These results are consistent with the summer distribution of arctic cisco in the Alaskan Beaufort Sea: fish concentrate near shore in a narrow band of relatively warm water of moderate salinity.

INTRODUCTION

The arctic cisco, Coregonus autumnalis, is one of the most abundant anadromous fishes in Alaskan arctic waters. From spawning areas in the Mackenzie River system (Hatfield et al. 1972; O'Neill et al. 1981) and possibly other major river systems of the North Slope region, juveniles migrate into the nearshore waters of the Beaufort Sea where they live during the ice-free period from mid-June to early September (Craig and Haldorson 1980). Freshwater runoff along with intense solar heating make these shallow coastal habitats relatively warmer and less saline than deeper offshore waters (Truett 1980). Nearshore areas also serve as primary summer feeding grounds for arctic cisco due to shoreward and longshore transport of invertebrate-rich ocean waters (Griffiths and Dillinger 1980).

The abundance of arctic cisco and other anadromous species in the warm-water areas during summer has prompted speculation as to the effects of temperature on the migration and distribution of these fishes. In response, we conducted a laboratory study of the temperature preference of juvenile arctic cisco as a function of both acclimation temperature and acclimation-test salinity. Although a multitude of temperature-preference data has been published (Coutant 1977), none is available for this species nor any other high-arctic coregonine. Temperature preferences were measures in a horizontal-thermal-gradient apparatus of previously undescribed design.

MATERIALS AND METHODS

Arctic cisco (83-136 mm) were taken by fyke net from the Beaufort
Sea near Prudhoe Bay, Alaska, during July and August 1981. The fish
were flown the day of their capture to a laboratory in Fairbanks. Water
temperature and salinity during transport and during an initial 48-hour
holding period at the laboratory were maintained at levels similar to
those recorded in the field at time and place of capture (i.e., 5-8 C
and 10-25 ppt).

Groups of 20-25 fish were held in 450-liter filtered aquaria under
constant light. (At the latitude -- approximately 70° N -- and season
of fish collection, day length was 24 hours.) Dechlorinated tap water
supplemented with Instant Ocean^R salts was used in all phases of the
experiment. Conditions of acclimation were organized in a 3x3 design
-- salinities of 5, 15 and 30 ppt (+ 2 ppt) versus temperatures of 5,
10 and 15 C (+ 0.5 C); however, owing to numerous logistical problems
the 5 ppt/15 C acclimation group was never tested. Groups were brought
to their specific acclimation conditions by incrementally adjusting
temperature and salinity at the rates of 2 C/day and 5 ppt/day, respectively.
Fish were maintained at their final acclimation levels for a minimum
of ten days prior to testing. During the acclimation period they were
fed to satiation 2-3 times daily on a mixture of commercial freeze-dried
euphausids and brine shrimp. Once testing of a particular group began,
fish were fed to satiation 20-30 minutes before the beginning of each
temperature-preference trial.

Test Apparatus

Horizontal thermal gradients were formed in an elongate chamber made from a 5-m length of transparent polyvinyl chloride (PVC) Excelon[R] pipe with an internal diameter of 102 mm. Lying within this primary structure, and extending its entire length along the bottom, were three smaller tubes -- a 12.7-mm-diamter PVC pipe flanked by two 15.9-mm-diameter titanium pipes (Fig. 1). A 50-mm-wide slit in the top of the primary tube permitted the investigator free access to any portion of the chamber.

Fig. 1

Gradients were established by pumping coolant (ethylene glycol) through one titanium pipe while simultaneously pumping hot water through the other in the opposite direction (Fig. 1). This countercurrent arrangment for heat exchange was augumented by heterogeneous insulation of the titanium pipes: the upstream third of each was bare; the second third was spirally wrapped with 6.4-mm-thick clear vinyl so that the proportion of bare conductive surface progressively decreased; and the downstream third was completely insulated with vinyl wrap. This system produced linear to slightly sigmoidal gradients as great as 18 C (Fig. 2), with specific gradients obtainable through adjustments in the temperature and flow rate of the liquid within each heat exchanger. Compressed air, bubbled from the central PVC line via 0.5-mm holes at 20-cm intervals, prevented cross-sectional thermal variation in addition to providing aeration. A screen of plastic mesh prevented fish from contacting the heat exchangers and aeration pipe.

Fig. 2

Each of four such gradient tanks (mounted one above another) was marked off at intervals of 50 cm, to give 10 stations. A copper-constantan thermocouple submerged at each station was interfaced with a Baily Instruments Inc. digital thermometer (Model BAT-12; display accuracy =

0.1 C) to provide data on water temperature. Florescent light reflected off a white backround provided low-level, uniform illumination from the side of the tank opposite the observer.

Experimental Procedure

A single fish was netted at random from the desired acclimation group and placed in a pre-formed gradient at the temperature corresponding with that of acclimation. The salinity in the gradient was homogeneous and equal to the acclimation salinity ($\pm$ 1 ppt). In order to accomodate initial disorientation that might have led to the fish rushing headlong into areas of stressful temperature, small blocking nets were placed in the gradient at points equivelent to the acclimation temperature $\pm$ 3.0 C. The blocking nets were removed after 30 minutes and the fish was given an additional 90 minutes to habituate to the test apparatus. The fish's position in the gradient tank was then recorded in tenths of a division between each marked station (e.g., 1.6, 3.7, etc.) every 2 minutes for 60 consecutive minutes. Gradient temperatures were recorded at the beginning of each trial and after the 10th, 20th and 30th observations. Temperature between adjacent thermocouples and between observations taken at a single thermocouple was assumed to vary linearly. Temperatures observed or calculated (if between thermocouples) for each positional observation were tabulated and the median taken as the preferred temperature for that particular trial. Frequency distributions based on temperature (1 C increments) and position (50-cm increments) were also calculated. Fish from a particular acclimation group were tested in a minimum of two different gradient tanks which were oriented in opposite directions, and gradients within specific tanks were varied among trials in order to detect any bias, other than temperature, that may have affected spatial

distribution. Analysis of variance, Student's t test and Duncan's multiple-range test (Ostle and Mensing 1975) were used to evaluate differences amoung acclimation groups.

RESULTS

Temperature Preference Trials

Individual cisco tended to generate monomodal frequency distributions with respect to temperature. Strongly platykurtic distributions (i.e., those with a moment coefficient of kurtosis greater than 1.0 and position-ally covering more than 80% of the gradient) were removed from the data base because the median temperature in such cases more likely reflected the distribution of gradient temperatures than the fish's temperature preference. Most of the seven (of 110) trials that were rejected on this basis involved fish that appeared highly stressed and unable to adapt to the test apparatus. The results of three other fish were also discarded because their distributions were sharply truncated at either end of the gradient.

Plots of sample variance against standard fish length indicated that size had a negligible effect on temperature-frequency distribution. The possibility of temperature re-acclimation during the course of any experimental trial was discounted because examination of consecutive observations provided no indication of consistent drift in the temperature at which fish were observed. Variation in preferred temperature among gradients and test tanks proved to be non-significant (P>0.10); therefore, data within acclimation groups were pooled for furthur analysis.

Mean temperature preferendum ranged from a high of 15.4 C for fish acclimated to 15 C/15 ppt to a low of 11.5 C for the 5 C/5 ppt acclimation group (Table 1, Fig. 3). Arctic cisco acclimated to 15 C preferred temperatures that were higher (P<0.05) than those preferred by either the 5 C or 10 C acclimation groups; however, there was no significant

Fig. 3
Table 1

(P>0.05) difference in thermal preference between fish acclimated to 5 and 10 C. The mean temperature preferendum was significantly (P<0.05) higher than the temperature of acclimation in all groups with the exception of those acclimated to 15 C. The final temperature preferendum, defined as the point at which the temperature-preference trendline intersects the 45° diagonal (Fry 1947), was graphically estimated to be 15.6 C at 15 ppt and 13.5 C at 30 ppt (Fig. 3).

Preferred temperatures at salinity extremes of 5 and 30 ppt were lower (P<0.05) than that at 15 ppt (Fig. 4).

Behavioral Observations

Behavior of the fish in the acclimation tanks suggested that physiologically optimal temperatures exceed 10 C. Fish acclimated to 15 C appeared alert, perceptive and proved to be extremely elusive during capture attempts. When slowly pursued about the holding tank the majority of individuals tended to form cohesive, well-organized schools. Such characteristics suggest a rather sophisticated degree of both muscular and neurological capability consistant with a poikilotherm operating under optimal thermal conditions. Frenzied feeding activity and a comparatively high rate of food consumption (fish fed to apparent satiation actively accepted food within two hours were undoubtedly linked to elevated metabolic rates induced by the high temperature. Of approximately 45 fish acclimated to 15 C for a period of 10-20 days, the only fatalities involved individuals that jumped out of the holding tanks.

Conversely, arctic cisco acclimated to 5 C appeared lethargic and lacked the locomotory agility noted in their 15 C counterparts. Tenuous schools, consisting of loose aggregates of 6-8 individuals, persisted no longer than several seconds. Feeding behavior was casual, and these fish,

once satiated, refused food for at least the next 6-8 hours. A mortality rate of approximately 0.5 fish/day was noted in all of the 5 C acclimation groups.

These qualitative differences were very apparent when comparisons were made between the 5 and 15 C and between the 5 and 10 C acclimation groups. Differences between the 10 and 15 C groups were subtle except with regard to schooling behavior, which was substantially more conspicuous in the 15 C groups. There were no mortalities in the 10 C acclimation groups.

Within temperature-acclimation groups, differences in performance among salinity groups were not detected.

DISCUSSION

Thermal preferenda of arctic cisco varied between 11.5 and 15.4
C, depending on the temperature of acclimation and the salinity at which
the fish were acclimated and tested. Given that preferred temperatures
are typically highest for juveniles of a species (Coutant 1977) and under
conditions that simulate summer photoperiod/seasonality (Sullivan and
Fisher 1953; Zahn 1963), our results may represent maximum values of
temperature preference for arctic cisco.

Current literature suggests, for fish in general, a strong correl-
ation between preferred temperature and the optimum for physiological
performance (Brett 1971) in such terms as maximum potential for growth
(Jobling 1981), maximum sustainable swimming speed (Fry and Hart 1949;
Brett 1967), maximum distance moved as a result of electrical stimulation
(Fisher and Elson 1950), and , most importantly, maximum scope for
activity (Brett 1964; Beamish 1970a). Thermal optima reflect the com-
bination of an underlying positive effect of temperature on biochemical
reaction rates and inherent physiological limitations (e.g., increasing
net cost of oxygen delivery) which come into play as temperature approaches
the upper lethal limits of the organism. From this perspective the
enhanced survival, schooling, feeding and locomotory performance noted
in arctic cisco acclimated to 10 and 15 C qualitatively corroborate the
thermal preferenda (11.5-15.4 C) determined from the gradient experiments.

The tendency for arctic cisco to select highest temperatures at
intermediate salinities is similar to that reported for the threespine
stickleback, Gasterosteus aculeatus (Garside et al. 1977). In the latter
case, intermediate salinities were those isosmotic for the species,
suggesting that thermoregulatory behavior may compensate for osmotic

stress. The potential severity of such stress is indicated by the obser-

vations of Rao (1968): in terms of oxygen consumption, the cost of osmo-

regulation for rainbow trout (Salmo gairdneri) reached 20-27% of total

metabolic demand as environmental salinity diverged from isosmocity.

At salinity extremes, the selection of a lower temperature would reduce

standard metabolism and partially offset the elevated oxygen demand created

by osmotic loading. Higher oxygen concentrations at lower temperatures

might also prove beneficial in supporting increased metabolism. Our

experimental temperature gradients were accompanied by relatively linear

dissolved oxygen gradients ranging from approximately 9 mgO_2/liter at

20 C to 15 mgO_2/liter at 5 C. Farmer and Beamish (1969) likewise found

that oxygen consumption rates for Tilapia nilotica were lowest under

isosmotic conditions. Yet, this species, when acclimated from 15 to

30 C, showed a preferred-temperature trend essentially opposite that

of arctic cisco and threespine stickleback: selected temperatures were

lowest at intermediate salinities (Beamish 1970b). Such contrasting

results lead one to consider the importance of habitat and niche diversity

when assessing the species-specific effects of temperature and salinity

interactions.

Regardless of the variation induced by salinity and acclimation

temperature, the selected temperatures of juvenile arctic cisco either

approach or exceed the upper limits of the thermal spectrum typically

available to them during the summer season. Moderately saline (18-25

ppt), nearshore waters of the Alaskan Beaufort Sea reach an annual maximum

temperature of 10-12 C during the month of August (Craig and Haldorson

1980), although temperatures as high as 15 C have been reported (D. Schmidt,

pers. comm.). Given these environmental conditions and the results of

our gradient experiments, temperature would seem to play a role in the summer distribution of this species. Valtonen (1970) presumed a similar role of thermal preference in the tendency of juvenile Coregonus nasus to occupy warm nearshore waters along the coast of the Bay of Bothea, Finland.

During the summer, arctic coastal waters not only provide the highest temperatures locally available, but also generate intense trophic support for the fish species that occupy them. This simultaneous occurence of elevated temperature and abundant forage no doubt confers an ecological advantage in terms of growth potential. Jobling (1981), using an accumulation of published data for 49 species of fish, concluded that there is good correlation between preferred temperature and the temper-ature that promotes maximum growth. Assuming this relationship holds for arctic cisco, juveniles are ecologically and physiologically positioned to make optimal use of their limited feeding season.

Although our experiments implicate temperature as an environmental determinant in the summer distribution of arctic cisco, it is only one of many factors that can affect population movement. Variables such as abundance of forage, shallowness of nearshore waters, substrate composition or the dynamics of coastal currents may compete directly with temperature in determining specific patterns of dispersion and migration. Laboratory studies have demonstrated that behavioral thermo-regulation in fishes can be modified by a variety of biotic and abiotic factors (Reynolds and Casterlin 1979). Yet, while the exact ecological role of temperature will depend upon temporal and spatial integration of both species and environmental characteristics, the strong thermal dependency of physiological mechanisms in fishes demands its serious

consideration. In the case of arctic cisco, preference for warm waters along the Beaufort Sea coast would appear to be a sensible adaptive strategy in that it would enable them to realize their physiological potential and thereby maximize the probability of successfully coping with a rigorous environment.

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Table 1. Mean preferred temperature ± 1 standard error (sample size) for arctic cisco acclimated to various combinations of temperature and salinity.

ACCLIMATION SALINITY (ppt)	ACCLIMATION TEMPERATURE (°C)		
	5	10	15
5	11.5 ± 0.7 (12)	12.8 ± 0.6 (15)	–
10	13.7 ± 0.5 (10)	13.8 ± 0.4 (14)	15.4 ± 0.4 (16)
30	12.8 ± 0.7 (11)	12.7 ± 0.6 (12)	14.1 ± 0.9 (10)

FIGURES

Figure 1. Schematic representation of one of the thermal gradient systems (above) and a cross-sectional view of a gradient tank (below).

Figure 2. Water temperature versus location (at 50 cm intervals) for a typical horizontal thermal gradient.

Figure 3. Preferred temperature ($\pm$ 1 SE) versus acclimation temperature for acclimation-test salinities of 5 ppt (dotted line), 15 ppt (dashed line) and 30 ppt (solid line).

Figure 4. Preferred temperature ($\pm$ 1 SE) versus acclimation-test salinity for acclimation temperatures of 5 C (dashed line), 10 C (solid line) and 15 C (dotted line).

Hot Reservoir

Cold Reservoir

Air

Air

Plastic Mesh

PVC Air Line

Titanium Heat Exchangers

Preferred Temperature - °C

Acclimation-Test Salinity - ppt