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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Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 467

March 1982
ABSTRACT

Horizon tal-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 physiological" 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 in a near shore band of relatively warm water of moderate salinity.

Key Words: Temperature preference, arctic cisco, Beaufort Sea, salinity, summer distribution, behavior.
ACKNOWLEDGEMENTS

We wish to express our gratitude to Dave Norton of the Outer Continental Shelf Environmental Assessment Program's Arctic Projects Office (OCSEAP) for his support during all phases of the research. Thanks are also extended to the members of the Waterflood Monitoring Program survey team--Bill Griffiths, Dave Schmidt, Brad Adams, Terry Carpenter, Rob Dillinger and Dennis Hensel--who provided the fish for the experiment; to Scott Anderson for his statistical advice; to Amy Regis for her help in conducting the experiment; to Chuck Davis for his help in constructing the test apparatus; to Bonnie Bower for drafting the figures; and to the staffs of LGL Ecological Research Associates, Inc. (LGL) and LGL Alaska for their help and encouragement.

This study was funded partially by the Bureau of Land Management (BLM) through interagency agreement with the National Oceanic and Atmospheric Administration (NOAA), as part of the Outer Continental Shelf Environmental Assessment Program.
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 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). Despite a relatively homogeneous distribution of forage within the warm coastal regions of the Beaufort Sea, arctic cisco tend to concentrate in a narrow (20-50 m) corridor that lies adjacent to the shore, except in the vicinity of river deltas where the band can be from 1-4 km wide (Craig and Haldorson 1980). This corridor typically attains the highest temperatures locally available.

The abundance of arctic cisco and other anadromous species in 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 or any other high-arctic coregonine. Temperature preferences were measured 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-h
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 h.) Dechlorinated tap water supplemented with Instant Ocean® 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) Excelo® 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 diameter 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.

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 counter-current arrangement for heat exchange was augmented 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
Fig. 1. Schematic representation of one of the thermal gradient systems (above) and a cross-sectional view of a gradient tank (below).
produced *linear* to slightly *sigmoidal* gradients as great at 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.

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. Fluorescent light reflected off a white background 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 (± 1 ppt). In order to accommodate 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 equivalent to the acclimation temperature (± 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
Fig. 2. Water temperature versus location (at 50 cm intervals) for a typical horizontal thermal gradient.
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 Duncants multiple-range test (Ostle and Mensing 1975) were used to evaluate differences among 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 positionally 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 further 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
Table 1. Mean preferred temperature ± 1 standard error (sample size) for arctic cisco acclimated to various combinations of temperature and salinity.

<table>
<thead>
<tr>
<th>Acclimation Salinity (ppt)</th>
<th>Acclimation Temperature (°C)</th>
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<td>5</td>
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<td>5</td>
<td>11.5 ± 0.7 (12)</td>
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<td>10</td>
<td>13.7 ± 0.5 (10)</td>
<td>13.8 ± 0.4 (14)</td>
<td>15.4 ± 0.4 (16)</td>
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<td>30</td>
<td>12.8 ± 0.7 (11)</td>
<td>12.7 ± 0.6 (12)</td>
<td>14.1 ± 0.9 (10)</td>
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Fig. 3. Preferred temperature (+ 1 SE) versus acclimation temperature for acclimation-test salinities of 5 ppt (dotted line), 15 ppt (dashed line) and 30 ppt (solid line).
the 5 C or 10 C acclimation groups; however, there was no significant (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. 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 locomotor 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
Fig. 4. Preferred temperature (± 1 SE) versus acclimation-test salinity for acclimation; temperatures of 5°C (dashed line), 10°C (solid line) and 15°C (dotted line).
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 Optima

The major premise behind temperature preference studies is that fish, being mobile poikilotherms living in a heterothermal environment, will seek out temperatures that allow them to conduct their joint physiological and biochemical processes in the most optimal and efficient manner. Over the past several decades, a variety of studies concerned with the effects of temperature on the physiological mechanisms of fishes have tended to support this hypothesis. The classical bioenergetic experiments of Brett et al. (1969) demonstrated that growth, meal size and gross food conversion efficiency for sockeye salmon, *Onchorhynchus nerka*, were all maximized at the fish's preferred temperature of 15 C. Jobling (1981), using an accumulation of published data for 49 species of fish, concluded that there is good correlation between preferred temperature and the temperature that promotes maximal growth. Although such relationships between temperature and bioenergetics are dependent on other variables, the most obvious of which is food availability, they nonetheless represent an inherent physiological capability that could prove important in the trophic ecology of the species.

Thermoregulatory behavior also exhibits a strong correlation with various aspects of activity. The maximum sustainable swimming speed of sockeye salmon (Brett 1967) and goldfish, *Carassius auratus* (Fry and Hart 1949); the maximum distance moved by Atlantic salmon, *Salmo salar*, and brook trout, *Salvelinus fontinalis*, as a result of electrical stimulation (Fisher and Elson 1950); and peaked levels of spontaneous activity for brook trout (Elson 1942), have all been reported to occur at respective preferred temperatures. One of the most ecologically important aspects of activity concerns its scope; i.e. that portion of available energy, exclusive of maintenance metabolism, which can be used for locomotion.
(attacking, escaping, migrating and all ancillary costs such as increased heart rate and breathing action). Measurements of oxygen consumption rates for sockeye salmon (Brett 1964) and *largemouth* bass, *Micropterus salmoides* (Beamish 1970a), again show a strong association between maximum scope for activity and preferred temperature.

These thermal optima reflect the combination 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 locomotor 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. Further experimentation, particularly in the areas of growth and scope for activity could ultimately confirm the existence of such thermal optima in arctic cisco.

Acclimation and Temperature Preference

In a constantly changing thermal environment the physiological character of fish undergoes continuous readjustment in an attempt to remain functionally cohesive with regard to temperature. These compensatory responses, which collectively represent the process of thermal acclimation, enable fish to perform more efficiently at new temperatures. Some adjustments such as changes in enzyme-substrate interaction and enzyme structure occur almost instantaneously (Hazel and Presser 1974). Other processes are slower, taking several hours to several weeks to complete their full transition; examples include biosynthesis of enzyme variants (Hochachka and Somero 1973), restructuring of cell membranes (Caldwell and Vernberg 1970) and shifts in blood chemistry (Houston and Dewilde 1968).

It is important to distinguish between the terms “most efficient” and “optimally efficient”. Fish which have been subjected to a particular temperature for several weeks will have most of their physiological processes shifted to operate best at that temperature; the fish are fully acclimated and are physiologically most efficient relative to that temperature. However, it’s optimum state, which represents some as yet
unexplained geneotypic characteristic of the species, may occur at a different temperature. The fish is thus faced with the choice of selecting from a thermal spectrum that is bounded by the temperature to which it is acclimated and the temperature to which it is genetically directed. The best response, given that all temperatures are available, would be to select a temperature close to its optimal-state yet near enough to the temperature of acclimation so as not to overstress the physiological process to which it is synchronized;

This acclimation-preferred-optimal temperature relationship can be viewed in terms of our trendline data for 15 ppt acclimated arctic cisco (Fig. 3). Fish acclimated to 10 C preferred a temperature of 13.8 C. However, physiological processes immediately begin reacclimating to this new temperature. Fish which subsequently become acclimated to 13.8 C will prefer a temperature of approximately 14.8 C (graphically estimated), again resulting in reacclimation—etc.

At some point the acclimation temperature equals the preferred temperature; this graphically corresponds to the point where the preferred temperature trendline intersects the 45° diagonal (Fig. 3). This final temperature preferendum (Tₚ) is indicative of the physiologically optimal temperature for the species. Beyond the Tᶠp selected temperatures will invariably be lower than the temperature of acclimation (Zahn 1967), albeit, our experiments did not cover a broad enough thermal regime to indicate such a trend. Preferred temperatures are thus higher than the temperature of acclimation below the Tᶠp and lower than the acclimation temperature above the Tₚ. Defined by Fry (1947) as "the temperature around which all individuals will ultimately congregate regardless of their thermal experience", Tᶠp "offers a convenient and meaningful index of the influence of temperature as a directive factor"; e.g. arctic cisco (at 15 ppt) acclimated to temperatures below 15.5 C will be biased toward warmer water while fish acclimated to temperatures above 15.5 C will be directed toward colder water.

The acclimation-preferred temperature relationship observed for arctic cisco is basically similar to that of other species (Zahn 1967). Likewise, the final temperature preferendum (13.5 and 15.5 C) are comparable to those for other juvenile salmonidiforms (Coutant 1977).
Photoperiod and Age

Arctic cisco were acclimated and tested under conditions of constant light which corresponded with the 24-day length indicative of the latitude (~70°N) and season of fish capture. 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 this species.

Feeding Regime

Food availability is another factor that can significantly affect thermoregulatory behavior in fish. The elevated metabolic rate that accompanies increased temperature is only sustainable given an adequate supply of energy. In cases where energy demand exceeds supply (i.e. low food availability and high metabolic rate), fish would be forced to either tap their body energy reserves or lower their metabolism by reducing ambient temperature. Since a net energy loss to the environment is biologically unfavorable, the latter response seems the most practical alternative. Food availability thus functions as a controlling and/or limiting factor in temperature selection. Javid and Andersen (1967) reported that brook trout, Salvelinus fontinalis and rainbow trout, Salmo gairdneri, significantly lowered their preferred temperatures within 24 hours after cessation of feeding and subsequently returned to pre-starvation levels within 24 hours after the resumption of feeding. They also noted an increase in the temperatures preferred by starved Atlantic salmon, Salmo salar, but attributed this behavior to a positive phototaxic response to stress.

We believe that the feeding regime employed during these experiments essentially negated the controlling and/or limiting effects of food availability; arctic cisco were fed to satiation 2-3 times daily during acclimation periods and 20-30 minutes prior to each temperature preference trial. If one further assumes that a reduction in thermal preferenda is the typical response to lowered feeding rates, then the temperatures
selected by our well-fed arctic *cisco* may, as was the case with photoperiod and age, represent maximum values for the species.

**Salinity Effects**

The tendency for arctic *cisco* to select highest temperatures at intermediate salinities is similar to that reported for the threespine sticklebacks, *C. aculeatus* (Garside et al. 1977). In the latter case, intermediate salinities were those *isomotic* for the species, suggesting that *thermoregulatory* behavior may compensate for osmotic stress. The potential severity of such stress is indicated by the observations of Rao (1968): in terms of oxygen consumption, the cost of *osmoregulation* for rainbow trout (*Salmo gairdneri*) reached 20-27% of total metabolic demand as environmental salinity diverged from *isomoticity*. 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 mgO₂/liter at 20 C to 14 mgO₂/liter at 5 C.

Farmer and Beamish (1969) likewise found that oxygen consumption rates for *Tilapia nilotica* were lowest under *isomotic* conditions. Yet, this species, when acclimated from 15 to 30 C, showed a preferred temperature trend essentially opposite that of arctic *cisco* and threespine sticklebacks: 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.

This preferred temperature-salinity relationship has an ecological compliment. Throughout the summer arctic *cisco* occupy the warm, brackish water corridor along the coastline. At intermittent intervals wind-driven incursions of arctic ocean water cause a rapid decrease in temperature while simultaneously increasing salinity (Craig and Baldorson 1980). Conditions are thus ‘either warm and brackish (higher preferenda at intermediate salinities) or cold and saline (lower preferenda at high
salinities). This occurrence further confounds the role of salinity in altering thermal preferences. Salinity may act as an osmotic stress which must be compensated for through changes in ambient temperature (referenda), or it may act as a signaling stimulus; forewarning the fish of an ensuing change in temperature and thus acting as a thermal acclimation catalyst.

Ecological Implications

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 annual maximum temperatures 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 experiments it seems reasonable to assume that temperature plays a role in the distribution of this species. The thermal structure of the coastal environment would consistently result in an orientation bias in favor of a shoreward movement. Valtonen (1970) presumed a similar role of thermal preference in the tendency of juvenile Coregonus nasus to occupy the warm nearshore waters along the coast of the Bay of Bothia, Finland.

During 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 occurrence of elevated temperature and abundant forage no doubt confers an ecological advantage in terms of growth potential. Assuming that the previously noted correlation between preferred temperature and the temperature for maximum growth (Jobling 1981) holds for arctic cisco, juveniles are ecologically and physiologically positioned to make optimal use of their limited feeding season.

Several studies have inferred that thermal preferenda may be reflective of spawning optima (Banner and Hyatt 1975, Smith 1975). This is an interesting correlation in light of the migratory patterns of adult
**cisco.** Mature fish undergo extensive upstream spawning runs in the Mackenzie River during July and August, reaching areas as far as 725km up-river (Stein et al. 1973, Griffiths et al. 1975). Suspension of feeding during the migration lasts until spawning is completed (Hatfield et al. 1972). Runs are finished by the middle of October, with spent fish subsequently moving back downstream to overwinter in the vicinity of the estuary delta (O'Neil et al. 1981).

Measurements taken around the Mackenzie River delta show July-August temperatures ranging from 11-18 C, decreasing to 7-9 C by the end of September (P. Craig, pers. comm.). It is likely that such temperatures occur in the more southerly reaches of the river system. Assuming a slight lag in seasonal temperature decay as one moves upstream, arctic cisco might well encounter their warmest waters during this critical spawning period.

Lack of larval arctic cisco in up-river areas during the spring breakup suggests that fry are transported downstream during the spring flood and rear in the lower reaches of the Mackenzie (O'Neil et al. 1981). Stein et al. (1973) located nursery grounds at the head of the Mackenzie River delta. Nursery utilization, another critical period in a fishes life cycle, could again correspond with seasonally high temperatures of around 15 C.

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 thermoregulation in fishes can be modified by territoriality (Beitinger and Magnuson 1975), bacterial infection (Reynolds et al. 1976), photoperiod (Sullivan and Fisher 1954), competition and niche availability (Fleming and Laverster 1956), food availability (Javid and Anderson 1977), age (Coutant 1977) and salinity (Beamish 1970b). Yet despite such complex interactions field studies have demonstrated temperature to be an important factor in controlling environmental distributions (Fry 1937, Dendy 1948, Hancock 1949).

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 demand its serious consideration. In the case of juvenile 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 vigorous environment.


