

**CONTRIBUTIONS TO THE SCIENCE
OF ENVIRONMENTAL IMPACT
ASSESSMENT:**

**Three Papers on the Arctic Cisco
(*Coregonus autumnalis*)
of Northern Alaska**



BIOLOGICAL PAPERS OF THE UNIVERSITY OF ALASKA

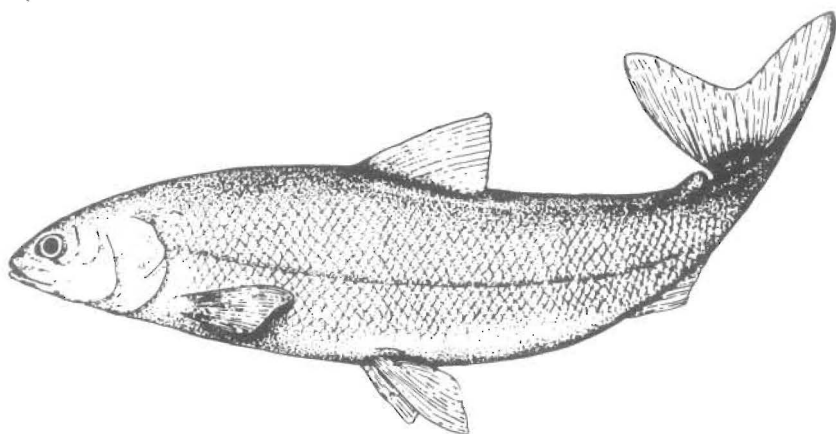
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Frontispiece

NASA image of western Prudhoe Bay taken in July 1982, showing the 3.9-km artificial causeway in relation to the mainland shoreline and a natural barrier island (upper left corner). Image courtesy of the Geophysical Institute, University of Alaska.

EDITOR'S INTRODUCTION

Some readers might argue with the title of this issue of *Biological Papers of the University of Alaska*, by contending that a "science of environmental impact assessment" does not exist. Admittedly, much of the environmental assessment work stimulated in the U.S. by the National Environmental Policy Act of 1970, and elsewhere by other initiatives, has been lackluster—there has been science *in*, but not a science *of*, much of that work. Martin Holdgate succinctly criticized the vast exercises of environmental assessments in recent years:

... much effort has been devoted to the wrong kind of analysis and to collection of unnecessarily large quantities of data that have given rise to undue expectations and unsatisfactory predictions.¹

In applied ecological research, however, there is an ideal to which serious ecologists and environmental scientists aspire, often against formidable odds. That ideal is the capability to predict quantitatively and with increasing accuracy the results of environmental perturbations. Even as an aspiration this ideal deserves to be called the science of environmental assessment. It is especially satisfying to have the trio of cisco papers published together here, because they document progress toward the ideal more effectively as a suite of integrated studies than as publications scattered among several journals.

The history of the development of this Arctic cisco research is instructive because it has been extraordinary in several respects. In 1976, the Outer Continental Shelf Environmental Assessment Program (OCSEAP) undertook the ambitious task of studying the determinant processes in a representative barrier island-lagoon system of the Alaskan Beaufort Sea. Although OCSEAP's resources at the time were considerable, they were finite, so that a careful screening method was needed to select only the major processes and system components for continued field investigation each season. LGL² ecologists assumed the team leadership role in the multidisciplinary and multi-institution effort in Simpson Lagoon, and applied the techniques of Adaptive Environmental Assessment¹ to this annual screening exercise. Arctic cisco met three essential criteria to qualify as subjects for research: they were important components of the system, they were harvested for human consumption, and they were likely to be affected by coastal development associated with petroleum activities.

¹Holling, C. S. [Ed.] 1978. Adaptive Environmental Assessment and Management. Wiley and Sons, New York xix + 377 pp.

²LGL is a private company specializing in ecological research, with offices in Canada and the U.S. The name of the firm is derived from the initials of its three co-founders.

The first extraordinary aspect of the cisco research is that it continued for 5 years (1977-81) under OCSEAP, a program which elsewhere in Alaska rarely provided more than one or two seasons' survey and inventory effort for biological characterizations. Had the cisco research been suspended after two seasons, no coherent story could be told here. The coherence of the story presented in the first paper is enhanced by a second extraordinary circumstance: it was an unexpected bonus to discover continuous, reliable, and long-term catch records from the Colville River fishery.

The third extraordinary development in the course of the cisco research grew out of the investigators' frustrations in searching the Colville River system for spawning Arctic cisco. The search was made because the petroleum industry's eventual needs for millions of cubic meters of gravel were expected to be met by mining the material from the lower reaches of larger rivers on the North Slope. The consequences of such gravel mining for populations of fish (such as Arctic cisco) that might be obligate spawners in restricted locations there were not known, but thought to be potentially severe. The alternative to continuing the expensive search for cisco in the Colville system was the stock assessment study, combining catch data, mark-recapture studies, and application of a population model in the first of the papers.

Laboratory experiments on temperature preference, reported in the second of these papers, grew out of debate among the investigators over the reasons behind the observed concentrations of Arctic cisco and other anadromous species in the narrow band of shallow water immediately adjacent to shorelines. One theory, the eventual null hypothesis, was that this clustering was strictly an edge effect, not causally related to the presence of warmer, less saline water in this coastal band. The alternative explanation was that the coastal edge effect was incidental, and that the fish were selecting preferred temperature and salinity conditions. The difference between these explanations was more than academic at the time of the debate (1980) because existing and planned gravel causeways projecting out from the Beaufort Sea coast (Frontispiece, p. iv) were then regarded as potentially interdicting or delaying fish migrations parallel to the shoreline. Discrimination between the two hypotheses would provide some basis for predicting the responses of fish to artificial spits and coastal configurations. If the edge effect prevailed, the route taken by an imaginary migrating fish would be lengthened by an increment equivalent to twice the combined lengths of all causeways between starting point and destination. The magnitude of the effect of one or more structures on fish could be estimated and, if the swimming speed were known, total delay could be calculated. If, on the other hand, fish respond primarily to physical characteristics of water masses, the interplay between causeways and fish migration would be mediated by more subtle and complex processes and events associated with coastal winds and currents impinging on natural and artificial

shorelines. The experimental phase of the research and its results encouraged the investigators to continue their research into a post-OCSEAP phase.

In 1981, as the OCSEAP funding was exhausted, the investigators obtained support from another government agency and from industry to investigate fish behavior in relation to the extended gravel causeway of the Prudhoe Bay Waterflood Project then under construction, as reported in the third paper. From a scientific perspective, this was an unusual opportunity. The same ecologists who had made predictions about the effects of causeway-induced changes in water mass characteristics on migrating fish in their OCSEAP reports could now develop real experience to verify, reject, or refine those earlier predictions.

The causeway problem was particularly attractive for tying together previously independent lines of inquiry devoted to the Arctic cisco. The problem was challenging logistically, with its requirements for simultaneous physical oceanographic measurements and fish sampling. Conceptually, it posed a question of degree of effect in a way not offered by certain sweepstakes aspects of environmental perturbations—estimating direct loss by burial of so many hectares of benthic invertebrate habitat by gravel fill causeways is a trivial example. By the same token, the causeway did not seem to threaten the resource seriously, and therefore its investigation did not appear likely to threaten the industry's freedom of action in building a number of these structures. Evidence of industry's willingness to try engineering solutions ("mitigative measures") is the breach designed into the Prudhoe Bay causeway, discussed briefly in the third paper here.

In the context of the improbable background and train of events since 1976, applied ecological studies on Arctic cisco developed to the level of understanding presented here. This level of understanding may be challenged as it stands, or be superseded rapidly. In any event, these three studies are a noteworthy synthesis of field and laboratory investigations, supported by iterative refinements of mathematical modeling, and post-development continuity of research.

The current pace of petroleum industry development in arctic Alaska and Canada should be creating many analogous opportunities for the continuity of pre- and post-development studies that would lead to refining the predictive skills of applied ecology. Regrettably, most of these opportunities appear to be passed over, perhaps deliberately, and perhaps owing to apprehensions about how the results would reflect on the industry. The results of the cisco research illustrate that such apprehensions are sometimes unwarranted.

D. W. Norton, July, 1983

AN ASSESSMENT OF THE COLVILLE RIVER DELTA STOCK OF ARCTIC CISCO—MIGRANTS FROM CANADA?

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ABSTRACT

To help interpret observed population changes of Arctic cisco in the Colville River Delta of Alaska, the Deriso model was applied to 15 years of catch and fishing effort records from the local commercial fishery. The model can provide a predicted sequence of catch values that closely mimics the historical record. Although survival and lag time parameters giving the best fit predictions appear reasonable, the high value giving best fit for the recruitment parameter would indicate a strongly density-dependent stock-recruitment relationship, and is suspect. Similar analyses of fishery data collected in future years may help determine whether the observed population fluctuations are attributable to normal population cycles or to environmental variables. The construction of a 3.9-km long causeway in the vicinity, and the operation of the local fisheries are both tentatively discounted as environmental causes for the observed fluctuations, but extreme sea ice conditions in certain years are implicated.

A theory that Arctic cisco in Alaska are representatives of a Canadian stock from the Mackenzie River is proposed, and the evidence is reviewed.

KEY WORDS: Arctic cisco, *Coregonus autumnalis*, life cycle, Beaufort Sea, stock assessment, commercial and subsistence fisheries.

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INTRODUCTION

The Arctic cisco, *Coregonus autumnalis*, is both one of the most abundant and valued of the anadromous fishes occurring along the North Slope of Alaska. As a subsistence fish, it is considered to be "much fatter, larger, and more tasty" than other common whitefish (Flossie Hopson, Conservation and Environmental Protection Office, North Slope Borough, pers. comm., 1980). In Alaska, Arctic cisco are presently a mainstay of seasonal subsistence fisheries at the village of Nuiqsut in the Colville River Delta and in the vicinity of Barter Island, Alaska. The former is a fall-winter fishery, whereas the Barter Island fishery operates during summer (Griffiths et al. 1977). Helmericks' commercial fishery (permitted to take a maximum of 50,000 Arctic cisco annually) has operated continuously since 1967 in the Colville Delta in fall and early winter and provided the largest body of data for this study. In the Mackenzie River valley of Canada the Arctic cisco also represents an important component of the domestic fishery (Hatfield et al. 1972).

The Arctic cisco ranges from northern Europe and Siberia to western arctic North America. In the latter region, it is distributed along the arctic coast from about Point Barrow, Alaska to Bathurst Inlet, Northwest Territories, Canada (Fig. 1). The distribution is apparently centered in brackish waters around the Mackenzie (Canada) and Colville (Alaska) River Deltas, habitats which are used for overwintering following summer feeding dispersals into the nearshore Beaufort Sea. In the Mackenzie River system, Arctic cisco range as much as 1,600 km upstream of the delta (Liard River) during late summer-fall spawning runs (O'Neil et al. 1981). This run is similar to those reported for Arctic cisco in Siberia, where the fish migrate over 1,500 km from the sea to spawning areas in the upper parts of the Yenisei River (Nikolsky and Reshetnikov 1970). Following spawning, adult Arctic cisco in Siberia, and probably in the Mackenzie River, undertake post-spawning migrations to delta regions where they overwinter (Wynne-Edwards 1952, Nikolsky and Reshetnikov 1970).

In conjunction with oil and gas development, numerous fish studies have been conducted in western arctic North America since the mid-1970's. Some of these studies have emphasized summer tagging programs (e.g. Bendock 1979, Doxey 1977, Craig and Haldorson 1981, Craig and Griffiths 1981a), with the recapture effort supplemented by fall-winter tag returns and catch data obtained from the Colville River commercial fishery. Craig and Haldorson (1981) used these data as the basis for population estimates which suggested that an 86 percent decline in the numbers of Arctic cisco overwintering in the Colville Delta occurred between 1976 and 1979. This observation was supported by the commercial catch data which, during 1979, dropped to 25 percent of its average during previous years. Again in 1980 the commercial catch and population estimates remained low similar to 1979 levels.

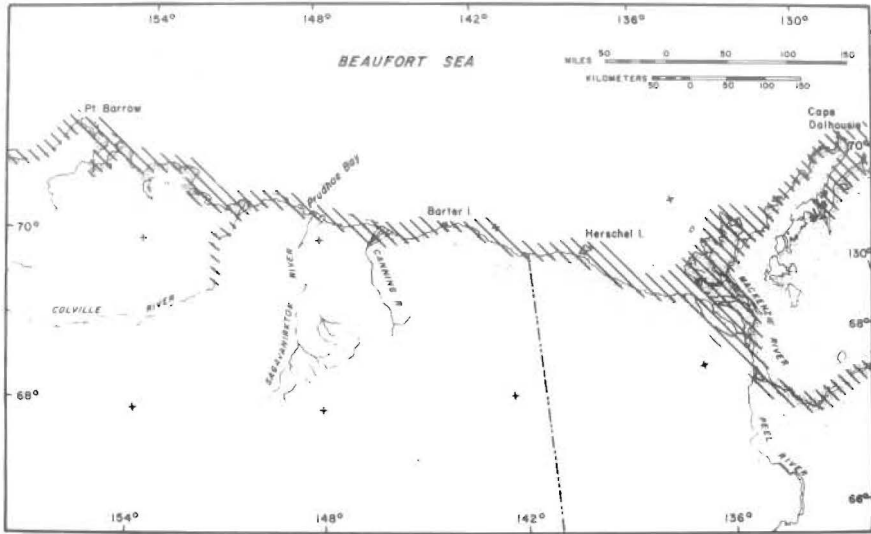


Fig. 1. The distribution (hatched area) of the Arctic cisco (*Coregonus autumnalis*) in Alaska and Canada (after Morrow 1980).

The apparent Arctic cisco decline coincided with both the first consequential offshore oil and gas development, and with the resettlement of the village site of Nuiqsut at the head of the Colville Delta (Fig. 2) beginning in 1973. The offshore petroleum development included the construction in 1975 of the solid-fill causeway just west of Prudhoe Bay. Originally 1.3-km long, it was extended offshore by an additional 1.5 km in 1976, and further extended by 1.1 km in 1981 (see Frontispiece). Given that causeways might directly impede fish migrations parallel to the shore, or indirectly affect anadromous fish by altering longshore currents and local temperature and salinity regimes, there was some belief expressed that the decline in abundance of Arctic cisco might in some way have been related to this structure.

The resettlement of Nuiqsut undoubtedly increased the local take of fish, including Arctic cisco. Craig and Haldorson (1981) estimated that the Nuiqsut harvest was of similar magnitude to that occurring in Helmericks' commercial fishery in the Colville Delta. The increase in the take of fish from the Colville Delta raised the question of overfishing as a major factor contributing to the observed decline. Reliable information about the population dynamics and biology of the Alaskan stock of Arctic cisco was needed before any causality could be ascribed to the apparent decline.

We attempted to describe the apparent population dynamics of the Arctic

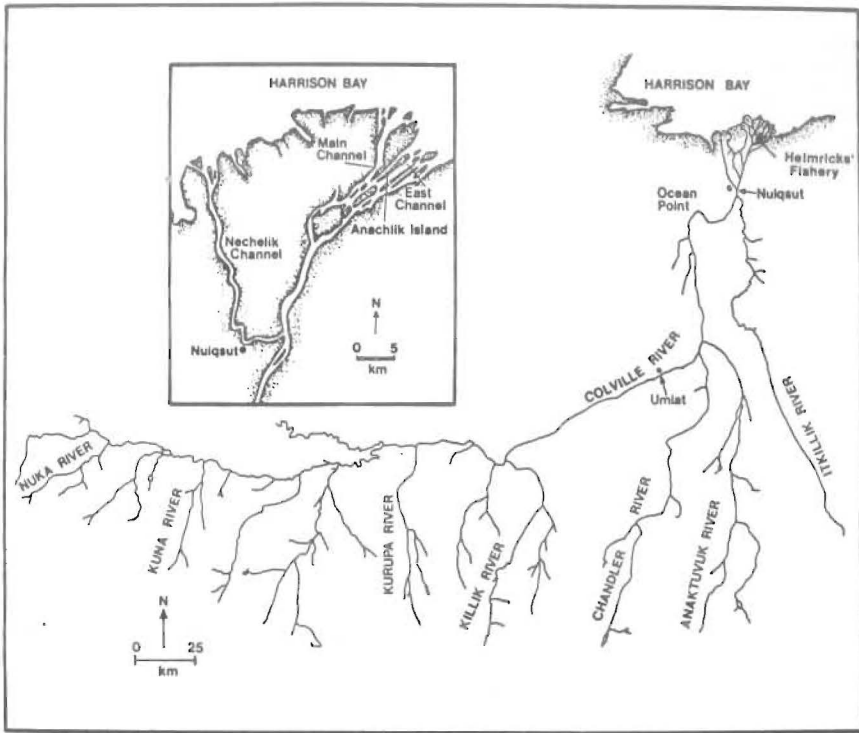


Fig. 2. The Colville River of Alaska with detail of the delta region (inset) showing major fishing sites.

cisco. Although our main purpose was to contribute to the understanding of the biology of this species, another goal was to evaluate whether the observed decline could best be explained by population attributes, overfishing, or impacts resulting from environmental conditions.

MATERIALS AND METHODS

The Deriso Model

Deriso (1980) provided a major breakthrough in the methodology of assessing population dynamics. His contribution was the derivation of a model incorporating features such as time lags, growth, mortality and recruitment (all of which can be related to biological processes) whose parameters could be estimated from a time series of catch per unit effort (CPUE) data. Prior to Deriso's work, such dynamic pool models could be constructed, but required a

time series of accurate age composition data (seldom available) as opposed to simple CPUE data.

The Deriso model, simply stated, says that a given year's biomass will be the survivors of the previous year's stock, corrected for weight growth, plus new recruits. When numbers are modeled instead of biomass, the Deriso model can be simplified to:

$$C_{t+1} = l(1 - qE_t + m)C_t - l^2m(1 - qE_{t-1})C_{t-1} \\ + q(1 - m)R[(1 - qE_{t-1} - k)C_{t+1} - k/q]$$

where the variables are:

$$C_t = \text{CPUE during year } t \\ E_t = \text{effort during year } t \\ R(.) = \text{recruitment function with } R(s) = \\ se^{a\beta s} \text{ (Ricker curve)}$$

and the parameters are:

$$l = \text{annual natural survival} \\ q = \text{catchability coefficient} \\ a, \beta = \text{Ricker recruitment parameters} \\ 1 - m = \text{fraction of spawners vulnerable to fishery} \\ \text{(allows for incomplete recruitment)} \\ k = \text{lag time between birth and recruitment} \\ (k + 1 = \text{age at recruitment})$$

We modeled numbers instead of biomass because number of fish caught (not biomass) was recorded by the fishery.

The Deriso model was applied to the time series of catch data from the Helmericks' commercial fishery dating from 1967. Parameters were estimated using Walters' (1981) Applesoft Basic computer program written for a 48K Apple II Plus® microcomputer with Disc-Operated System and a single disc drive. In this program, the approach is to use quasi-linearization and non-linear Newton's methods to estimate the set of survival and recruitment parameters that will make a predicted sequence of CPUE values agree best with the observed sequence (Deriso 1980, Walters 1981).

The Fishery

The Helmericks' commercial fishery in the Colville Delta has operated during fall and early winter in essentially the same fashion yearly since 1967. Fishing is conducted in the Main (Kupigruak) and East Channels of the river adjacent to Anachilik Island (Fig. 2) When the ice becomes thick enough to walk on, holes

are drilled and gill nets are set in a continuous series along the deep bottoms of the channels. The nets are typically 2 × 50 m, having either 7.6 cm (3 in) or 10.2 cm (4 in) stretched mesh. The smaller mesh is used in both channels, but the larger mesh is used exclusively in the Main Channel where broad and hump-back whitefish (*Coregonus nasus* and *C. pidschian*, species attaining larger size than the ciscoes) occur more commonly. Effort with the small mesh nets has comprised over 98 percent of the total soak time expended by the fishery over the 1967–81 period.

Fishing usually begins about the first of October and is terminated near the end of November. The nets are typically picked every day except Sunday. The catch is recorded by date and usually by location. Effort records are maintained by date and location. The nets are set and fished over the entire period, although they are occasionally moved. The nets are removed as the quota is approached or if the catches are considered too low to reward the fishing effort.

RESULTS AND DISCUSSION

The Fishery

In 9 of the 15 years of record, the fishing effort followed a fairly regular pattern, with peak efforts ranging from 10 to 25 nets fished per day, and most effort being expended in October and November (Fig. 3). In three years (1968, 1971, 1976) maximum daily efforts were higher (31 to 41 nets fished per day) and in two of those years (1968, 1971) the peak daily efforts were sustained for longer than usual. The other three exceptional years (1978 to 1980) differed from all other years of record by the extension of fishing effort well into December (Fig. 3).

Although records of fishing effort distinguished between the two fishing sites, not all catch records for Arctic cisco indicated from which site they were taken. We therefore combined catch data from the Main Channel and East Channel for total annual harvest of the species (Fig. 4A). The resulting loss of resolution in these data is not significant. The levels of effort in the two channels covaried closely, with greater effort usually on the East Channel (Fig. 4B). Fishermen report that Arctic cisco use the shallower East Channel more heavily and that two species of whitefish and the least cisco (*Coregonus sardinella*) predominantly use the Main Channel.

The annual catch of Arctic cisco taken in the fishery (Fig. 4A) has ranged from a high of 71,575 in 1973 to a low of 9,268 in 1979. The catch levels over these years suggest a marked decline as described in the introductory section. During the same years, effort levels, although variable, have been roughly similar and thus do not account for the reduced fish catches (Fig. 4B)

Craig and Haldorson (1981) showed that the Arctic cisco taken in the commercial fisheries are moderately large (range in fork length: 240 to 380 mm) with

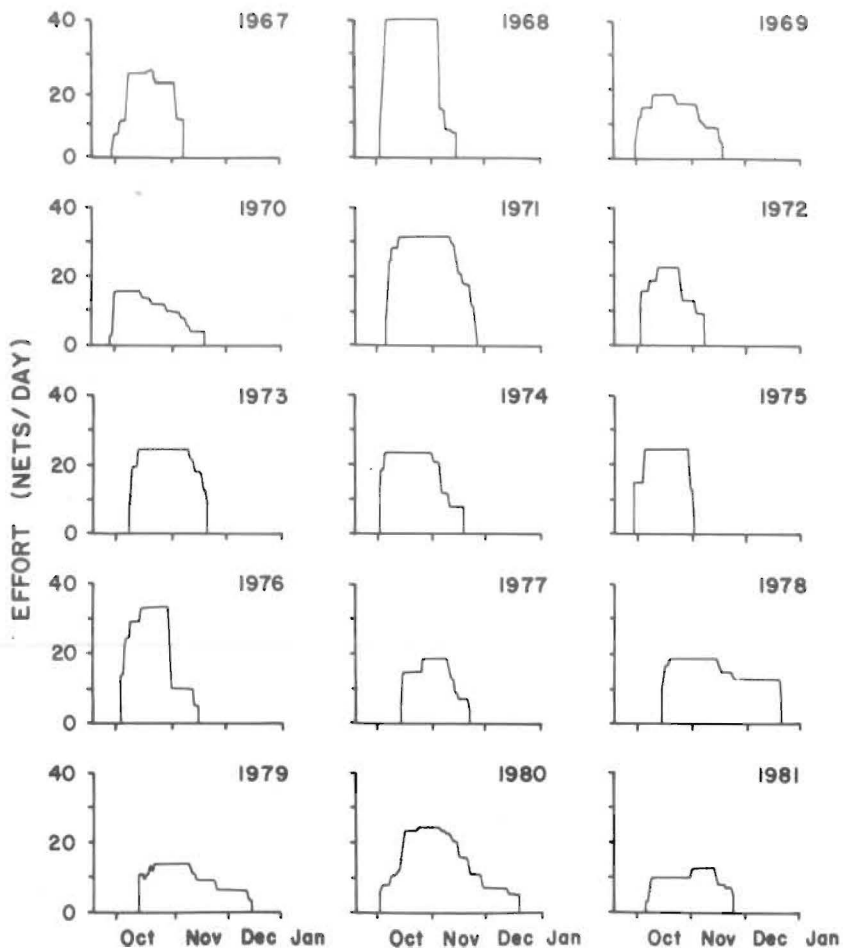


Fig. 3. Patterns of daily commercial fishing effort for the 15-year period of record for the Helmericks' commercial fishery.

most of the fish in the 280 to 340-mm range (Fig. 5). The ages of the catch range between three and ten years, but fish aged five to eight dominate the catch. Male and female Arctic cisco first attain sexual maturity at ages seven and eight, respectively (Craig and Haldorson 1981). Dominant age-size groups can be followed through the fishery in successive years (Fig. 5).

Based upon Craig and Haldorson's (1981) examination of about 200 specimens taken each year from the commercial catch during 1977-79, sexually mature fish comprised an estimated 49 to 57 percent of the catch. In 1976, only

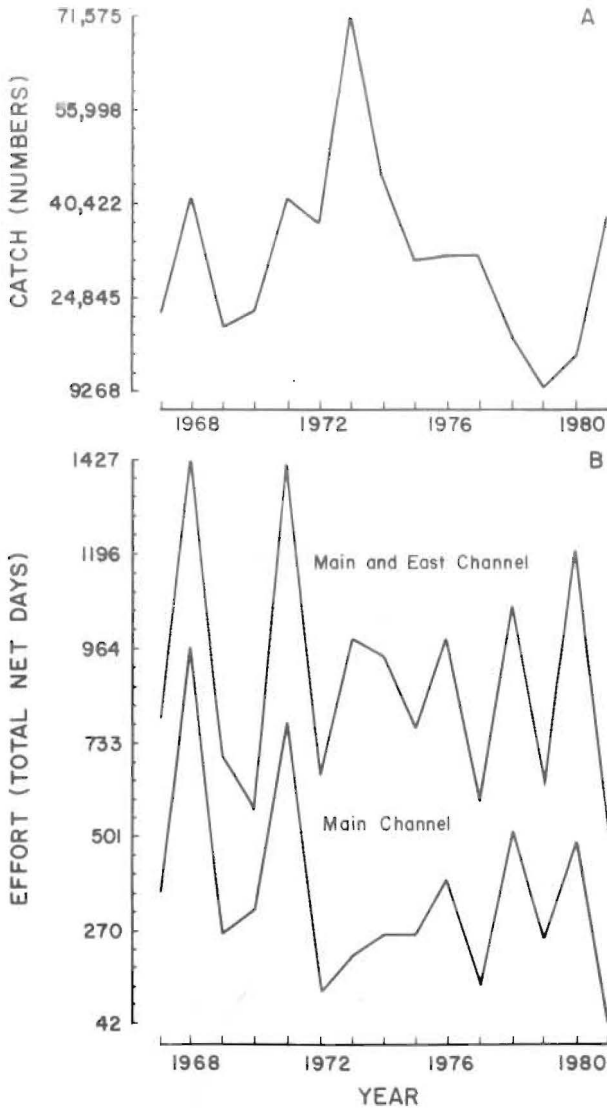


Fig. 4. Patterns of annual catch (A) and fishing effort (B) for the Helmericks' commercial fishery, 1967-1981.

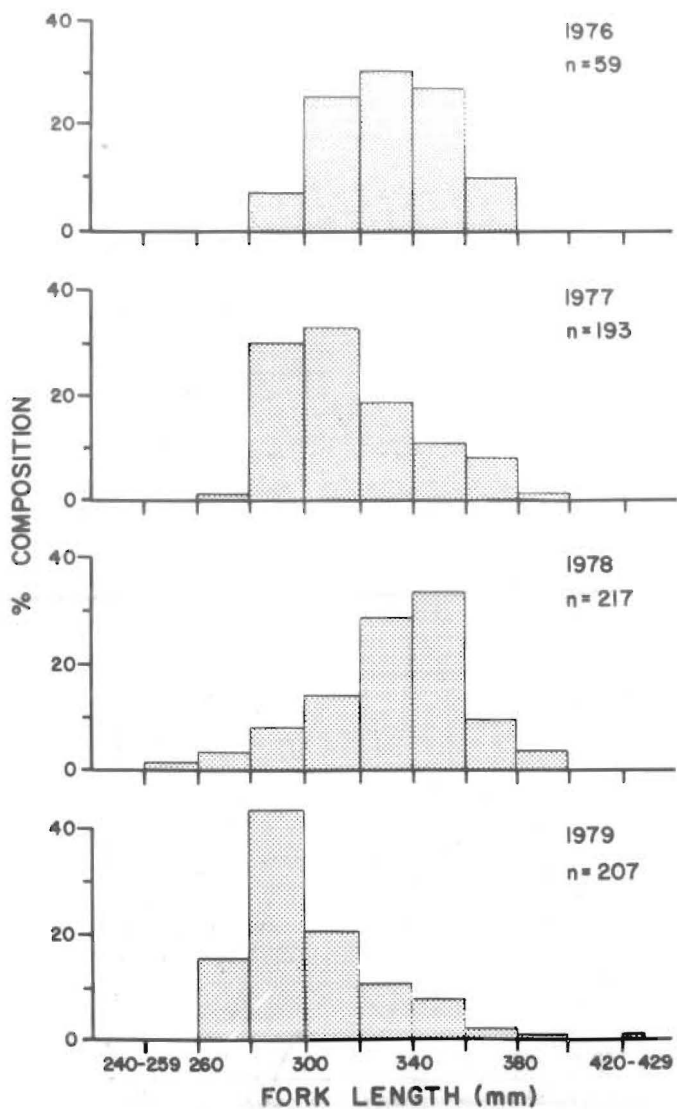


Fig. 5. Size distribution of Arctic cisco taken in the Helmericks' commercial fishery, 1976-1979 (after Craig and Haldorson 1981).

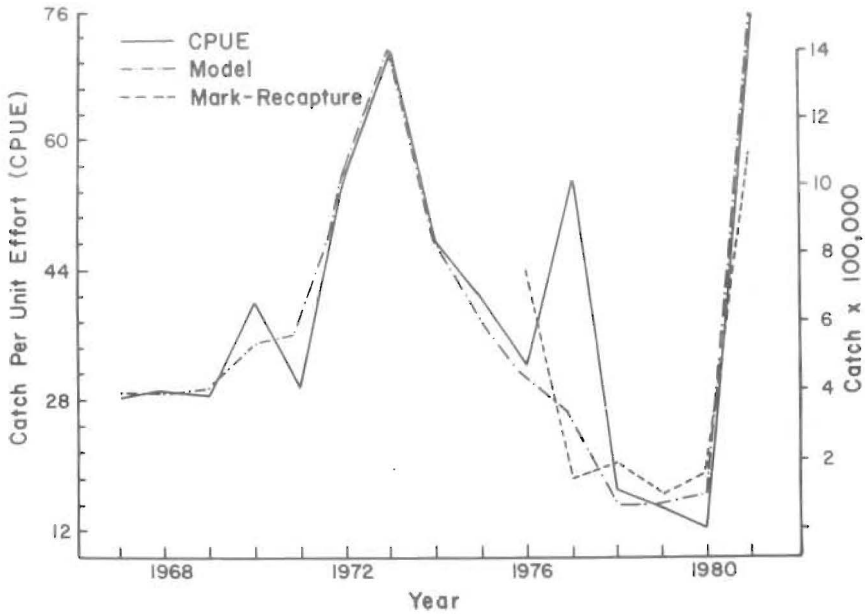


Fig. 6. Population trends of Arctic cisco (*Coregonus autumnalis*) based upon CPUE, Model, and Mark-recapture data from the Helmericks' commercial fishery, 1967-1981.

12 percent of the catch was estimated to have been sexually mature, but the sample consisted of only 59 fish. More significantly, no fish in spawning condition and no spawned-out fish were found in any of the samples examined by Craig and Haldorson (1981), despite the probability that this species' spawning period immediately precedes and may extend into the fishing season. When requested in 1979 to supply any spawned-out fish, the fishermen provided only nine fish out of the entire catch, of which only one spawned-out male and two "possibly" spawned-out females were confirmed by Craig and Haldorson (1981). The autumn commercial fishery in the Colville Delta therefore harvests essentially a non-spawning segment of the Arctic cisco population.

The Model

Peak population levels of catchable Arctic cisco according to CPUE data occurred in 1973 and 1981, with a lesser peak occurring in 1977 (Fig. 6). The Deriso model provided a very good fit of the historical record (Fig. 6), with the best fit obtained using the parameter estimates of: $k=5$; $l=0.37$; $q=0.33$; $\alpha=4.8$; $\beta=5.5 \times 10^{-5}$; and $m=0.64$. The model did not reflect a minor peak in 1977, nor was this peak suggested by independent population estimates calculated from mark-recapture data available from other studies (Craig and

Haldorson 1981, Griffiths and Galloway 1982) covering the period 1976 through 1981 (Fig. 6). Apart from the 1977 peak, the three population indicators (CPUE, Model, Mark-recapture) reflected a similar trend in population levels for the years to which they could all be applied.

The model was responsive with the five-year lag period between events, as well as with an m value 0.64 indicating an exceptionally low proportion of catchable spawners. The model's performance suggests that the bulk of the catch should consist of fish of ages five to seven, and spawners should comprise a small proportion of the catch as compared to mature non-spawners. Both of these implications from the biological model agree well with the observed age and maturity composition of the actual catch from the fishery, suggesting model validity. The validity of other model parameters remains to be verified. The question of why spawners are largely non-vulnerable to the Colville fishery is addressed below.

The α value of 4.8 estimated by the model suggests a strongly density-dependent stock-recruitment relationship which is reasonable given the pattern of the CPUE data. A strongly density-dependent relationship results in an oscillating population level of spawners because the maximum level of recruitment occurs when the spawner population is low and vice versa. Further, the lag time of five years between spawning and recruitment of fish to the fishery agrees well with the known life history of Arctic cisco. Nevertheless, the value of 4.8 for α is unusually high. We believe that it is likely that the oscillations in catch are due more to regional environmental effects than to recruitment phenomena. That is, we may have the overall dynamics represented correctly, but the appearance of strongly density-dependent recruitment to Alaska could actually be the result of a few environmentally extreme years. For example, 1974 and 1975 were particularly bad ice years (the pack ice remained along the mainland coast throughout summer in the Beaufort Sea) and were followed by a series of relatively good years (the pack ice was up to 100 km offshore during summer) until 1982. If the environmental conditions of 1974 and 1975 affected the transport or survival of age one fish in the nearshore zone during these years, the effects would be seen in the fishery about five years later (1979 and 1980). The question of attributing the stock oscillations to stock-recruitment relationships or to environmental factors could be resolved given several additional years of data from the fishery. It should be noted that while the model fit is good, and the parameters k and m give us some confidence in the results, the data extended over a total of only 15 years. The assumed lag of 5 years to recruitment allowed us only 10 points to fit 5 parameters.

Given either explanation for the stock oscillations, the existing fisheries of the Colville Delta probably have little impact on the population levels of catchable Arctic cisco. Mean fishing mortality (F , calculated from Ricker 1975) was estimated to have been only 0.15. The commercial and subsistence catches

are likely to continue to fluctuate radically over the years due to either environmental conditions or density of spawners. If the latter case is true, lower densities of spawners would result in higher yields of recruits on a 5- to 7-year cycle.

Finally, it is unlikely that the 3.9-km long causeway near Prudhoe Bay, Alaska has contributed much to the observed oscillations in population levels. Results of tagging studies (Craig and Griffiths 1981b, Griffiths and Gallaway 1982) have shown no significant difference in the proportion of large Arctic cisco on the Colville River overwintering grounds between fish that were initially marked during summer on different sides of the causeway. Distributional modeling of small Arctic cisco based upon temperature preference and environmental conditions around the causeway suggest that during conditions of westward transport, small fish would also successfully move around the causeway (Neill et al. 1983). Our understanding of the functional relationship of arctic fishes to environmental factors remains rudimentary despite progress reported here. More observation and experimentation are required to be able to relate environmental perturbations resulting from development activities to impacts on fish stocks with confidence.

Thus, application of the Deriso (1980) model to the CPUE data of the Helmericks' commercial fishery yielded a set of reasonable estimates for biological parameters which gave a predicted sequence of CPUE data closely mimicking the historical record. The model's estimates of survival and lag time parameters appeared particularly good in light of what is known or hypothesized about the biology of Arctic cisco, but the parameter associated with recruitment showing a strong density-dependent stock-recruitment relationship appeared suspect due to its magnitude. A few more years' data should permit an assessment of the validity of this parameter estimate versus the alternative hypothesis that the observed population oscillations result from environmental effects. The current model will be used to project future catches in the Colville fishery. These projections will be compared to actual catches and this "validation" attempt will serve as the subject for a later paper.

A Theory Concerning Stock Origin

The question raised above as to why spawners are largely non-vulnerable to the Colville fishery begs an explanation. One interpretation is that the Arctic cisco overwintering in the Colville River might, for the most part, leave this system soon after becoming sexually mature and return to the Mackenzie River to spawn. We suggest that there may not be two stocks of Arctic cisco—one associated with the Mackenzie and the other with the Colville River—as has been previously postulated (e.g. Alt and Kogl 1973, Craig and Mann 1974), but only the one that is reproductively associated with the Mackenzie system. Sup-

port for this interpretation can be drawn from the following review of Canadian and Alaskan observations.

Spawning migrations and early life histories of Arctic cisco are reasonably well documented for the Mackenzie River system. Spawners leave nearshore brackish waters and enter the Mackenzie system during late June through late July, and undertake spawning migrations to some of the larger tributaries (e.g. Peel, Arctic Red, Great Bear, Mountain and Liard Rivers). The spawning runs in these tributaries occur at different times corresponding to the distance up the Mackenzie River system the fish must move. Hatfield et al. (1972) reported sexually mature Arctic cisco in the Arctic Red River (near the Mackenzie Delta) from late June to the end of August, and at the Great Bear River (approximately halfway up the Mackenzie River) from early August to late September. O'Neil et al. (1981) reported that Arctic cisco spawners first appeared at the mouth of the Liard River (the farthest upstream Arctic cisco tributary reported) by mid-August in 1979, peak numbers occurred in September, and the run was completed by mid-October.

During the spawning run in the Mackenzie River system, Arctic cisco eggs increase in diameter from a range of 0.6 to 1.3 mm, characteristic of presumed mature, green females in brackish nearshore-marine habitats (Griffiths et al. 1975, Griffiths et al. 1977, Craig and Haldorson 1981) to a range of 1.9 to 2.1 mm ($\bar{x} = 2.03$, $SD = 0.08$) for green females and to a range of 2.0 to 2.3 mm ($\bar{x} = 2.13$, $SD = 0.10$) for ripe females caught in the Liard River in October (Gary Ash, RL and L Consultants, Vancouver, British Columbia, pers. comm. 1981).

After spawning in the fall, adult Arctic cisco are thought to undertake a post-spawning migration back down the Mackenzie Delta (Wynne-Edwards 1952). While Mann (1975) caught no Arctic cisco in the inner delta, a few have been caught in brackish waters of the outer delta (Percy 1975, Kendel et al. 1975, Galbraith and Hunter 1979).

Arctic cisco eggs hatch the following spring and the young-of-the-year (age zero) are carried down the Mackenzie River to the delta during spring breakup, where they have been found foraging in the shallow lakes of the delta by early June (Hatfield et al. 1972, McLeod et al. 1979, O'Neil et al. 1981, Taylor et al. 1982). Taylor et al. (1982) reported that between 80 and 90 percent of all Arctic cisco found in the lakes they sampled were young-of-the-year and that most Arctic cisco had left the lakes by mid-September. Some young-of-the-year are undoubtedly carried into nearshore marine habitats during the spring freshet and perhaps during other times of the year.

Our earlier belief that there are two stocks of Arctic cisco was based on a moderate amount of evidence from the Mackenzie drainage (Wynne-Edwards 1952, Hatfield et al. 1972, Stein et al. 1973) and a small amount of evidence from the Colville River area (Alt and Kogl 1973, Kogl and Schell 1974). Over-

wintering Arctic cisco had been reported from both these areas (separated by over 400 km) and, although fish in spawning condition had not been documented in Alaskan waters, young-of-the-year fish had been reported in the Colville Delta (Kogl and Schell 1974). Since 1974, several fisheries investigations have been conducted but have yielded little support for the hypothesis of a separate spawning population of Arctic cisco associated with the Colville River.

The strongest evidence against the hypothesis of two stocks is the lack of fish in spawning condition and the lack of spawned-out fish in the fishery at the Colville Delta. Moreover, spawning runs of Arctic cisco have not been documented for the Colville River despite summer and fall surveys conducted in 1977 and 1978 by Bendock (1979) and ours in 1978, 1979 and 1980 (McElderry and Craig 1981, Craig and Griffiths 1981). On the contrary, these studies have collectively indicated that Arctic cisco probably do not penetrate the Colville River beyond Umiat (about 175 km upstream); they are abundant only as far upstream as the Itkillik River (about 48 km, Fig. 2) and few, if any, of these fish are in spawning condition. We consider it significant that Inupiat residents of Alaska's North Slope can accurately describe local spawning habitats and timing for all anadromous salmonid and coregonid species except the Arctic cisco.

The time-at-large data (years elapsed between marking and recapture) for tagged Arctic cisco as compared to similar data for least cisco provides additional evidence that older (larger) Arctic cisco may leave the area. Least cisco have been documented to spawn in the Colville River system. Specimens in spawning condition have been collected throughout the lower reaches of the river (Kogl 1972, McElderry and Craig 1981) and according to unpublished data (Helmericks) spawned-out individuals are commonly taken in the fall fishery. Least cisco overwinter in the Colville Delta area and disperse into the nearshore, brackish waters of the region for feeding during summer. Through 1981, a total of 409 tagged least cisco had been recaptured, having time-at-large ranging from 0 to 5 years with 63, 18, 10, 5, 0, and 3 percent of these fish recaptured each year, respectively (Craig and Haldorson 1981; unpublished data held by LGL). During this same period, 130 tagged Arctic cisco were recaptured, 86 percent of which were taken during the same year they were marked, 12 percent after one year at large, and 2 percent after two years. These data suggest that most large Arctic cisco are scarce or absent from the Colville River area within one year of being tagged. We believe that these data support the contention that most Arctic cisco leave the Colville Delta region when they approach sexual maturity, and we believe that they return to the Mackenzie River system for spawning.

To our knowledge there have been no recoveries in the Mackenzie River system of Arctic cisco tagged along the central Beaufort Sea coast of

Alaska—information which would strongly support the proposed theory.⁴ The lack of these supporting data may be due to the absence of any large-scale scientific surveys performed in the lower Mackenzie River system during the period corresponding to years when large numbers of Arctic cisco have been tagged and released in Alaska. Moreover, we have received several tag returns from as far east as the Barter Island domestic fishery (Craig and Haldorson 1981, Griffiths and Gallaway 1982) but none from the domestic fishery centered around Barrow to the west. Although limited, these data support the idea of an eastward dispersal of large Arctic cisco. Electrophoretic studies have not been conducted to date, but are needed. Results from such studies would probably clarify the question of stock identity.

For the above spawning scenario to be reasonable, a dispersal mechanism is required to account for the presence of young Arctic cisco in Alaska. We suggest that the prevailing east-to-west longshore current along the Beaufort Sea coast represents an adequate dispersal mechanism. These currents generally move parallel to the coast at about 3 to 4 percent of the speed of the wind and in the same direction as the wind. Summer winds are typically from the northeast, and average about 5 m/sec (Mungall 1978). Coastal waters move westward under these conditions at about 15 cm/sec (13 km/day). Under these conditions, a westward drift of small fish (mean lengths of ages zero and one fish are 70 and 110 mm respectively) in the nearshore would be expected. If the transport were passive, movement from the Mackenzie to the Colville region under average conditions would require about 35 days, but could require as little as seven days during occasional extended periods of strong wind.

Overwintering by Arctic cisco has been documented in brackish habitats in the deltaic and estuarine regions of both the Colville and Mackenzie Rivers. If the fish are moving between these two systems as proposed, it would seem logical that similar habitats associated with some of the other large rivers between the Mackenzie and Colville (e.g. the Sagavanirktok River) should also be used for overwintering by the non-spawning segment of the population. Although late winter surveys of overwintering habitats in the Sagavanirktok and Kuparuk River Deltas (Bendock 1979, Dew 1982) have not yielded any Arctic cisco, these surveys have been conducted in upstream freshwater habitats rather than the seaward parts of these deltas.

⁴ (Ed. Note) As this paper went to press, the authors were advised of a tag recovery from an adult Arctic cisco in the Mackenzie River Delta in early September 1983. The fish had been tagged and released on 8 July 1981 west of the Prudhoe Bay Waterflood Causeway. It was estimated from its length (330 mm) to have been age 6-8 in 1981, hence age 8-10 by 1983.

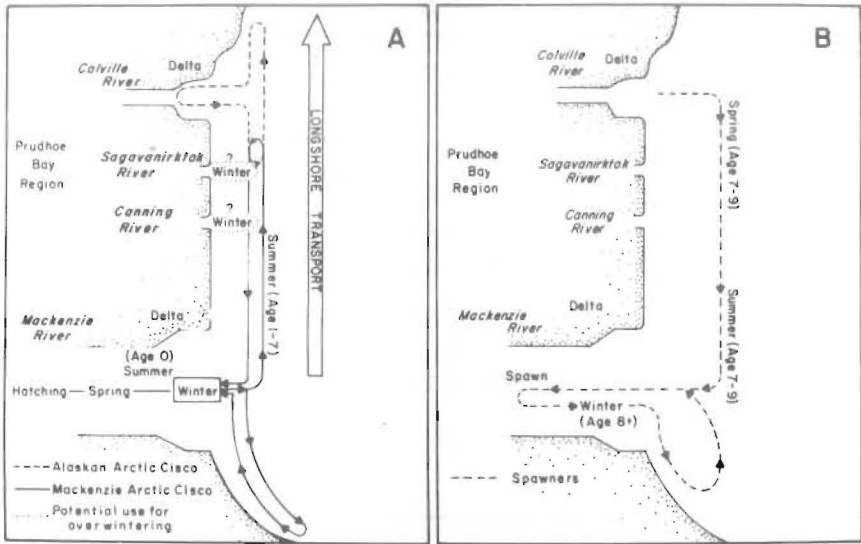


Fig. 7. Conceptual model of Arctic cisco life history cycle in Alaska and Canada. (A): Pre-spawning age fish. (B): Spawning age fish.

A conceptual model of the postulated life history cycle for Arctic cisco is shown by Fig. 7. In this model, spawning occurs in the Mackenzie River in fall, young-of-the-year use the delta as nursery grounds during their first summer, and they overwinter there but in a different habitat. Some young-of-the-year may be carried by the spring freshet into the nearshore region. At age one, the small fish move into the nearshore environment during the summer feeding dispersal along the coast. Some unknown proportion disperses to the west, and at some point are entrained by the strong westward-flowing longshore currents off the Alaskan coast. Upon the approach of freeze-up, the Colville River and perhaps other rivers afford brackish overwintering habitat in the lower delta areas adjacent to the sea. Arctic cisco that have been transported into Alaska use the Colville River and perhaps other suitable river delta habitats on Alaska's North Slope (Fig. 7A), until attaining sexual maturity, as well as a size enabling them to contend with the longshore currents. Thereupon they presumably seek their natal stream in the Mackenzie River system to spawn (Fig. 7B). Such a pattern is consistent with the patterns of seasonal abundance and distribution observed in Arctic cisco, and would account for a high proportion of spawners being non-vulnerable to the Colville fishery.

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TEMPERATURE PREFERENCE OF JUVENILE
ARCTIC CISCO (*Coregonus autumnalis*) FROM THE
ALASKAN BEAUFORT SEA

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ABSTRACT

The temperature preferences of juvenile Arctic cisco, *Coregonus autumnalis*, were tested in a horizontal thermal gradient as a function of both acclimation temperature and salinity. Cisco preferred temperatures ranging from 11.5°C for fish acclimated to 5°C/5 ppt, to 15.4°C for fish acclimated to 15°C/15 ppt. Estimated final temperature preferences 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. Observations of fish in the acclimation tanks suggest that physiologically optimal temperatures of juvenile Arctic cisco genuinely exceed 10°C in the salinity range of 5–30 ppt. These results are consistent with the observed summer distributions of Arctic cisco in the Alaskan Beaufort Sea: fish concentrate near shore in a narrow band of relatively warm, moderately saline water.

KEY WORDS: Temperature preference, Arctic cisco, *Coregonus autumnalis*, Beaufort Sea, salinity, summer distribution, behavior.

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INTRODUCTION

The Arctic cisco, *Coregonus autumnalis*, is one of the most abundant anadromous fishes in the estuarine waters of the central Beaufort Sea. From spawning areas in the Mackenzie River system (Hatfield et al. 1972, O'Neil et al. 1981, Gallaway et al. 1983), and possibly other major river systems (e.g. Colville River) 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 1981). Freshwater runoff and solar heating make these shallow coastal habitats comparatively warmer and less saline than deeper offshore waters (Truett 1981). Nearshore areas also serve as primary summer feeding grounds for Arctic cisco because of current-driven shoreward and longshore transport of zooplankton-rich ocean waters (Griffiths and Dillinger 1981).

The abundance of Arctic cisco and other anadromous species in the warm-water areas during summer has prompted speculation about the effects of temperature on the migration and distribution of these fishes. We therefore conducted a laboratory study of the temperature preference of juvenile Arctic cisco as a function of both acclimation temperature and salinity. Although numerous temperature preference data have been published (Coutant 1977), none are available for this species nor any other high-arctic coregonine. Temperature preferences were measured in a horizontal-thermal-gradient apparatus described in this paper.

MATERIALS AND METHODS

Arctic cisco (total lengths: 83–136 mm) were taken by fyke net from the Beaufort Sea near Prudhoe Bay, Alaska, during July and August 1981. On the day of their capture the fish were flown via commercial airline to the LGL Alaska Research Associates, Inc. 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 the time and place of capture (5–8°C and 10–25 ppt).

Groups of 20–25 fish were held in 450-litre filtered aquaria. Holding tanks were provided with constant overhead lighting to simulate the 24-hour day length (LD24:0) then occurring at latitude 70°N where the fish were collected. Dechlorinated tap water and artificial sea salts were used in all phases of the experiment. Conditions of acclimation were organized in a 3×3 design—salinities of 5, 15, and 30 ppt (± 2 ppt) versus temperatures of 5, 10, and 15°C ($\pm 0.5^\circ\text{C}$). (The 5 ppt/15°C acclimation group was not tested owing to a shortage of fish and time.) Groups were brought to their specific acclimation conditions by incrementally adjusting temperature and salinity at the rates of 2°C per day and

5 ppt per day, respectively, and maintained at their final acclimation levels for a minimum of 10 days prior to testing. During the acclimation period they were fed to satiation 2–3 times daily on a commercial mixture of freeze-dried euphausiid shrimp and brine shrimp. Once testing of a particular group began, fish were fed to satiation 20–30 min before the beginning of each temperature preference trial.

Test Apparatus

Horizontal thermal gradients were formed in an elongate, cylindrical chamber made from a 5-m length of transparent polyvinyl chloride (PVC) Excelon® 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 countercurrent 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 enclosed by the vinyl wrap. This system produced linear to slightly sigmoidal gradients as great as 18°C (Fig. 2), 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 0.2-m intervals, prevented cross-sectional thermal variation and provided aeration. A screen of plastic mesh prevented fish from touching the heat exchangers and aeration pipe.

Each of four such gradient tanks (mounted one above another) was marked off at intervals of 0.5 m to give ten stations. A copper-constantan thermocouple submerged at each station was connected to a Bailey Instruments Inc. digital thermometer (Model BAT-12; display accuracy = 0.1°C) to monitor water temperature. Fluorescent light reflected off a white background provided low-level, uniform backlighting.

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 to 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 into areas of stressful temperature, small blocking nets were placed in the gradient at points equivalent to the acclimation temperature $\pm 3.0^\circ$. The blocking nets were removed after 30 min and the

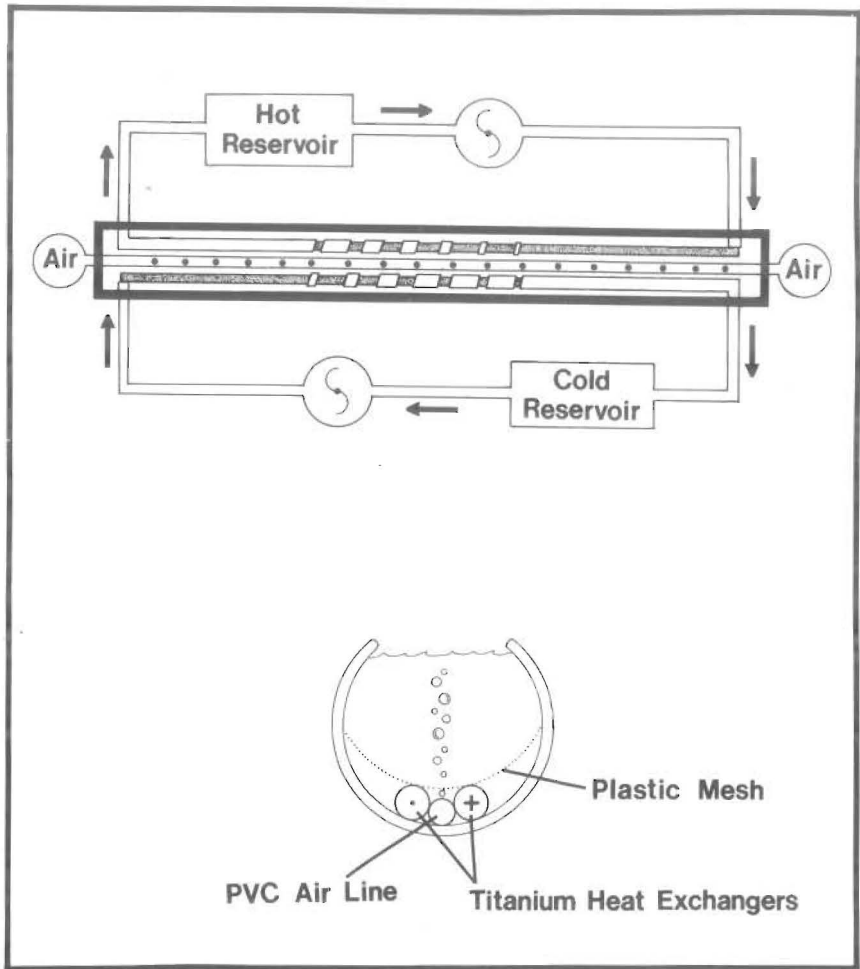


Fig. 1. Schematic representation of one of the thermal gradient systems (above) and a cross-sectional view of a gradient tank (below).

fish was given an additional 90 min to habituate to the test apparatus. The position of the fish 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 interpolated (if between thermocouples) for each positional observation were

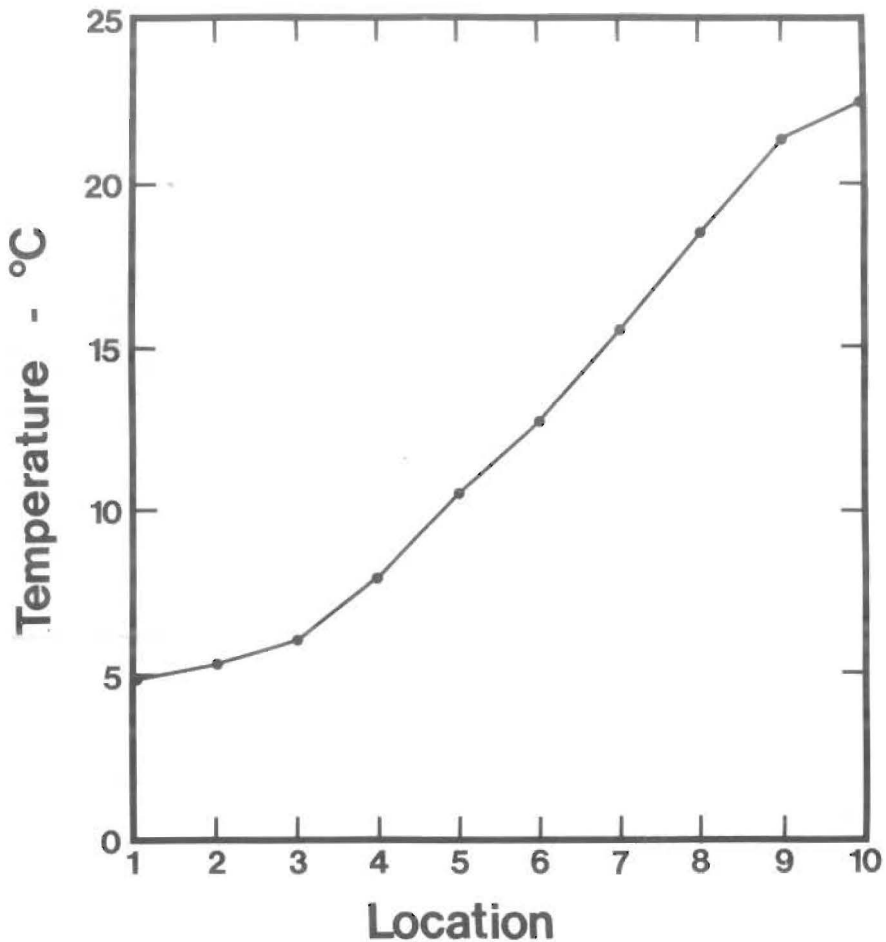


Fig. 2. Water temperature versus location (at 0.5-m intervals) for a typical horizontal thermal gradient.

tabulated and the median taken as the preferred temperature for that particular trial. Absolute frequency distributions based on temperature (1°C increments) and position (0.5-m increments) were also calculated. Fish from a particular acclimation group were tested in a minimum of two different test tanks whose gradients 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 among acclimation groups.

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

Acclimation Salinity (ppt)	Acclimation Temperature ($^{\circ}$ C)		
	5	10	15
5	11.5 \pm 0.7 (12)	12.8 \pm 0.6 (15)	no data
15	13.7 \pm 0.5 (10)	13.8 \pm 0.4 (14)	15.4 \pm 0.4 (16)
30	12.8 \pm 0.7 (11)	12.7 \pm 0.6 (12)	14.1 \pm 0.9 (10)

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 percent 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 from 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 acute temperature preference ranged from a high of 15.4 $^{\circ}$ C for fish acclimated to 15 $^{\circ}$ C/15 ppt to a low of 11.5 $^{\circ}$ C for the 5 $^{\circ}$ C/5-ppt acclimation group (Table 1, Fig. 3). Arctic cisco acclimated to 15 $^{\circ}$ C preferred temperatures higher ($P < 0.05$) than those preferred by the 5 $^{\circ}$ C or 10 $^{\circ}$ C acclimation groups;

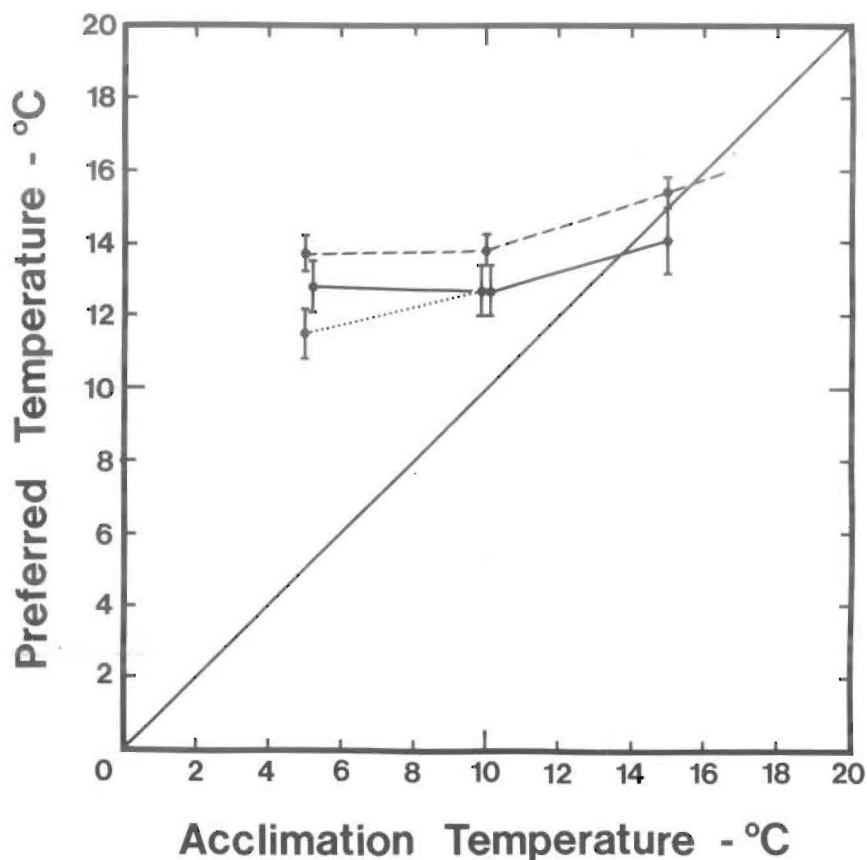


Fig. 3. Preferred temperature (± 1 SE) versus acclimation temperature for acclimation-test salinities of 5 ppt (dotted line), 15 ppt (dashed line) and 30 ppt (solid line).

however, there was no significant ($P > 0.05$) difference in thermal preference between fish acclimated to 5 and 10°C. The mean acute temperature preferendum was significantly ($P < 0.05$) higher than the temperature of acclimation in all groups except 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).

Behaviorial Observations

The behavior of fish in the acclimation tanks suggested that physiologically optimal temperatures exceed 10°C. Fish acclimated to 15°C appeared alert, perceptive and were extremely elusive. When slowly pursued about the holding

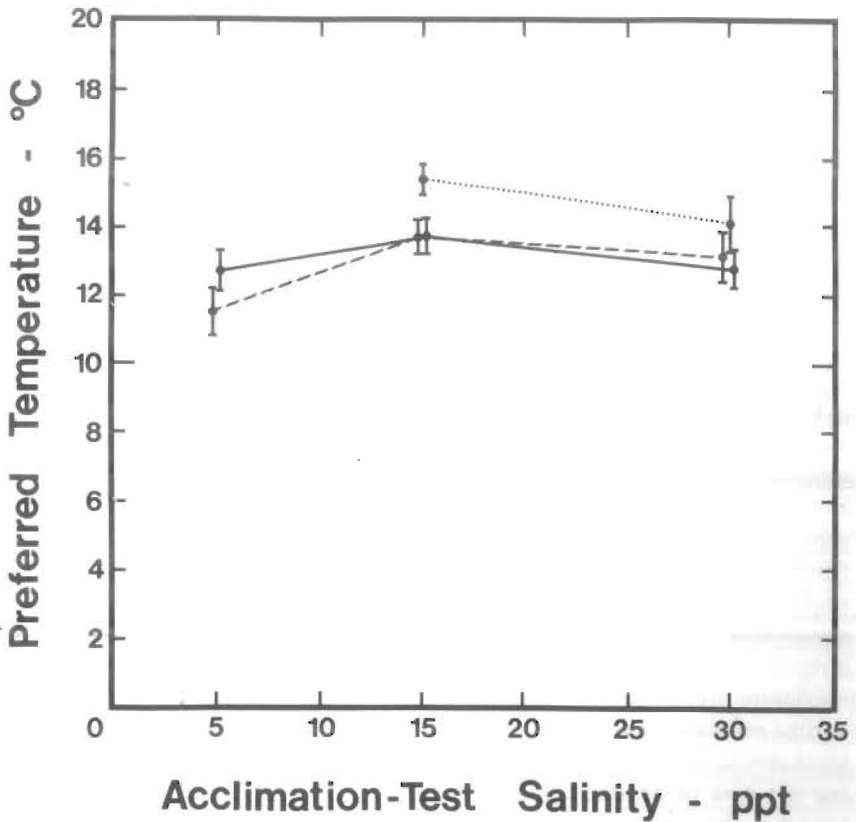


Fig. 4. Preferred temperature (± 1 SE) versus acclimation-test salinity for acclimation temperatures of 5°C (dashed line), 10°C (solid line) and 15°C (dotted line).

tank the majority of individuals tended to form cohesive, well-organized schools. Such characteristics reflect a high degree of both muscular and neurological capability consistent with poikilotherms 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 2 hours) were undoubtedly linked to elevated metabolic rates induced by the high temperature. There were no fatalities among fish kept in the 15°C acclimation holding tanks.

By contrast, Arctic cisco acclimated to 5°C appeared lethargic and lacked the locomotory agility noted in their 15°C counterparts. Tenuous schools, consisting of loose aggregations 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 per 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 in schooling behavior, which was 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

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. For fish in general, there appears to be a strong relationship between preferred temperature and the optimum for physiological performance (Brett 1971) in such parameters as maximum potential for growth (Jobling 1981), maximum sustainable swimming speed (Fry and Hart 1949), maximum distance moved as a result of electrical stimulation (Fisher and Elson 1950) and, most important, maximum metabolic scope for activity (Brett 1964, Beamish 1970a). Thermal optima reflect a 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 locomotory performance noted in Arctic cisco acclimated to 10 and 15°C support the determinations of thermal preferenda (11.5–15.4°C) in the gradient experiments.

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. Seasonality and maturity could induce shifts in biochemical mechanisms which lower the temperature of optimum physiological capability, thus lowering thermal preferenda.

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 observations of Rao (1968): in terms of oxygen consumption, the cost of osmoregulation for rainbow trout (*Salmo gairdneri*) reached 20–27 percent of total metabolic demand as environmental salinity diverged from the isosmotic condition. 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 an elevated metabolism resulting from higher salinities. Our experimental temperature gradients were accompanied by relatively linear dissolved oxygen gradients ranging from approximately 9 mg O₂ per litre at 20°C to 15 mg O₂ per litre 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 temperatures, the thermal preferences of juvenile Arctic cisco exceed temperatures that are typically available to them during the summer season. Nearshore waters of the Alaskan Beaufort Sea reach an annual maximum of 10–12°C (Craig and Haldorson 1981), although temperatures as high as 15°C have been measured (D. Schmidt, LGL Alaska Research Associates, Inc., pers. comm.). Average temperatures are much lower, ranging between 0 and 8°C. If the thermoregulatory responses observed in our laboratory experiments are consistent with those occurring in the field then Arctic cisco should be biased toward the warmest waters locally available during most of the open-water season. The idea of “locally warmest water” is an important ecological concept. If thermoregulatory behavior were a totally viable biological mechanism, fish would still be limited by highest temperatures in the field which in some cases could be considered very low (i.e. 0–5°C). 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 Bothnia, Finland.

During the summer, arctic coastal waters not only provide the highest temperatures locally available, but also generate intense trophic support for resident fish species. This simultaneous occurrence 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 temperature that promotes maximum growth. If this relationship 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 725 km up-river (Stein et al. 1973, Griffiths et al. 1975). 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 and August temperatures ranging from 11–18°C, decreasing to 7–9°C by the end of September (P. Craig, LGL Ltd. pers. comm.). It is likely that such temperatures occur in the more southerly upstream reaches of the river system. If the seasonal temperature decline upstream lags behind that of the delta 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 the life cycles of fish, could again correspond with seasonally high temperatures.

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, depth 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 a variety of biotic and abiotic factors (Reynolds and Casterlin 1979).

Understanding the potential of such complex interactions and the dynamics of the environment is critical when analyzing field data. Although thermoregulatory behavior may act as a directive mechanism, site- and time-specific field observations may not reflect this fact. For example, fish in the process of migrating from a colder to a warmer environment could be sampled en route. Prevailing currents might also delay or prevent fish from reaching their thermal objective. In a continuously and rapidly varying environment, fish could be in a perpetual transient state. Synoptic surveys which may not distinguish the temporal and spatial dynamics of the system might thus fail to identify the mechanisms controlling fish distribution.

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 merits con-

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

In a companion and follow-up study to this one, Neill et al. (1983) evaluated the predictive power of water temperature and other factors in assessing Arctic cisco responses to changes of water mass characteristics around a man-made coastal modification near Prudhoe Bay.

ACKNOWLEDGMENTS

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MODELING MOVEMENTS AND DISTRIBUTION OF
ARCTIC CISCO (*Coregonus autumnalis*) RELATIVE TO
TEMPERATURE - SALINITY REGIMES OF THE
BEAUFORT SEA NEAR THE WATERFLOOD
CAUSEWAY, PRUDHOE BAY, ALASKA

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ABSTRACT

A mechanistic model was developed to evaluate the movement patterns of small Arctic cisco relative to environmental heterogeneity associated with the Waterflood Causeway, a gravel pier that projects 3.9 km into the Beaufort Sea from the Alaskan coast near Prudhoe Bay. Fish movement and resultant changes in density were treated as a donor-controlled drift process biased by experimentally determined temperature preferences (given temperature and salinity acclimation) of the fish. Simulated fish density was significantly rank-correlated with actual catch. Goodness-of-fit was improved when observed data were filtered to remove the effects of presumed high-frequency changes in fish catchability.

Under the assumption of model validity, small Arctic cisco make appropriate use of the causeway's breach as a passageway. Causeway-induced variation in water quality during August 1981 directed fish movement in a manner that should reduce entrainment and impingement potential of planned water-intake structures, although these same water quality differences resulted in an estimated 7 percent reduction in fish density that would have been present in the area had environmental heterogeneity provided no directional bias in fish movements.

KEY WORDS: Fish movements, behavioral thermoregulation, ecological modeling, Arctic cisco, *Coregonus autumnalis*, Beaufort Sea.

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INTRODUCTION

Enhanced oil recovery from the Prudhoe Bay Reservoir is the responsibility of a consortium of petroleum companies. These companies chose a method of secondary recovery known as "waterflooding," whereby Beaufort Sea water will be injected year-round into wells at the perimeter of the Prudhoe Bay field to displace the reservoir's remaining crude oil toward producing wells. The water-intake structures must be located offshore in water at least 4.3 m deep, to exceed the combined vertical dimensions of the sea-ice layer during winter (2 m) and the structures themselves (2.3 m). To provide access to water of sufficient depth and to clad the piping that will bring the water ashore to the sites of injection, an existing causeway from the western shore of Prudhoe Bay was extended to a total length of 3.9 km in 1981. The causeway is a solid-fill gravel pier, 30–50 m wide. Through the causeway—at a point of 1,125 m from its tip—is a 30-m wide breach to provide a channel for fish passage.

In response to concerns expressed by resource agencies and the public over the influence of the Waterflood Project on local ecological dynamics, a Waterflood Monitoring Program was initiated in 1980–81. In part, this program was designed to measure responses of migrating anadromous fish to the causeway and its breach, and to assess the likelihood that passing fish will be able to avoid being drawn into the water-intake structures when these become operational.

During the arctic summer, the causeway deflects longshore currents and their entrained plumes of relatively warm, low salinity water discharged from several rivers of Alaska's North Slope. As a result, the shallow (<5 m deep) waters in the vicinity of the causeway frequently develop heterogeneities in temperature and salinity; differences of 10°C and 30 ppt across the causeway were recorded in July 1981.

Anadromous fishes of the North Slope spend their summers moving through nearshore waters like those in which the causeway has been built. Fyke net and gill net sampling near the causeway during summer 1981 suggested that the distributions of ciscoes (*Coregonus* spp.) and other anadromous fishes could be influenced by the causeway and the environmental heterogeneities resulting from its presence. These fishes appeared in the sampling area in rather discrete pulses, however, making interpretation of the catch data difficult.

Concurrent with the fish sampling near the causeway as part of the Waterflood Monitoring Program, a relevant experimental study was underway at the LGL laboratory in Fairbanks under the auspices of the National Oceanic and Atmospheric Administration/Outer Continental Shelf Environmental Assessment Program (NOAA/OCSEAP). This study measured temperature preference as a function of temperature and salinity acclimation in one of the North Slope's most abundant and important anadromous fishes, the Arctic

cisco (*Coregonus autumnalis*). Specimens used in the experiments were taken from fyke nets in the causeway area. Results indicated that young Arctic cisco prefer temperatures between 11.5 and 15.4°C, depending on temperature (5-15°C) and salinity (5-30 ppt) acclimation (Fechhelm et al. 1983).

This paper describes our preliminary attempts to integrate field data and experimental results by mathematically modeling the movements of young Arctic cisco near the Prudhoe Bay causeway. The objective of the modeling effort was both to gain insight into the causeway's influence on the dynamics of Arctic cisco distribution and to develop a practical approach for modeling fish movements in two-dimensional space relative to environmental heterogeneity.

METHODS

Theory and Structure of the Model

We sought a conceptually adequate model that would reasonably represent shifts in the distribution of young Arctic cisco near the causeway (as reflected in fyke net catch per unit effort, CPUE) that might result both from density-dependent dispersive processes and from the responses by fish to varying temperature and salinity distributions⁴. The requisite model had to be consistent with the preference behavior of young Arctic cisco in experimental temperature gradients (Fechhelm et al. 1983) and had to accommodate both the local geography of the causeway area and apparent "pulsing" of the fish through the area. The model further had to be tolerant of a relative lack of information on the area's fine-scale environmental structure over long spans of time and space.

The approach that seemed most appropriate was to treat fish movement and resultant changes in fish density as a donor-controlled drift process biased by experimentally determined temperature preferences (Fig. 1). Development of a more mechanistic model that would stochastically simulate fish movement as a biased random walk (e.g. Saila and Shappy 1963, DeAngelis 1978, Neill 1979) was considered, but rejected because such models are extremely costly in computer time and demand data of higher resolution on environmental structure than were available for the causeway area. Our deterministic model was built "from scratch" but is generally consistent with the mathematical model described by Balchen (1979).

For a two-dimensional space partitioned into n sectors, the time-rate of

⁴In the absence of information to the contrary, we assumed from the outset that Arctic cisco, confronted with simultaneous gradients of temperature and salinity, orient to the temperature component only, but do so in a way that depends on salinity as well as temperature. In the coastal Beaufort during summer, temperature and salinity tend to be inversely related.

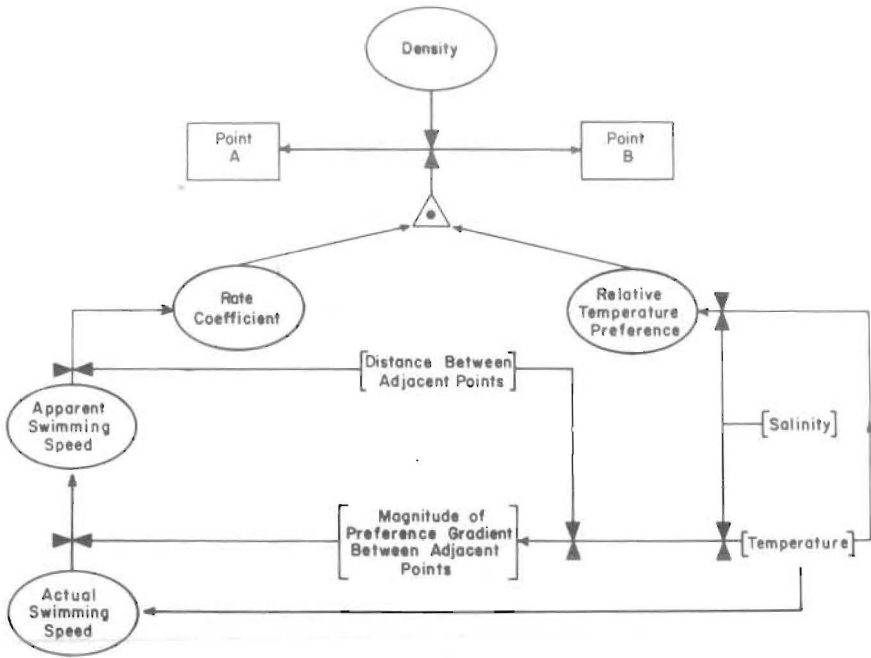


Fig.1. Conceptual model of fish movement between adjacent points and the relationships with environmental (brackets) and species (ovals) variables.

change in fish density in the i th sector attributable to movement of fish from the i th sector to a contiguous j th sector ($dC_{i \rightarrow j}/dt$) was taken as

$$\frac{dC_{i \rightarrow j}}{dt} = - \frac{p_j}{p_i + p_j} \cdot \frac{s}{X_{ij}} \cdot C_i, \quad (1)$$

where

- P_i and P_j are the relative preference values of temperatures at the centers of the i th and j th sectors;
- X_{ij} is the distance between centers of the i th and j th sectors; measured through the mid-point of the common boundary;
- s is the dispersal rate coefficient, based on the swimming speeds of young Arctic cisco estimated in the laboratory temperature gradient experiments, together with assumed directedness (see below) of the swimming path; and,
- C_i is the density of fish in the i th sector.

Similarly, the rate of change in fish density in the i th sector attributable to movement from the j th to the i th sector ($dC_{i \leftarrow j}/dt$) was

$$\frac{dC_{i \leftarrow j}}{dt} = \frac{p_i}{p_i + p_j} \cdot \frac{s}{X_{ij}} \cdot C_j \quad (2)$$

The rate of net transfer of fish density between the two sectors ($dC_{i \cdot j}/dt$) was then

$$\frac{dC_{i \cdot j}}{dt} = \frac{s}{X_{ij}} \cdot \left[\frac{p_i C_j - p_j C_i}{p_i + p_j} \right] \quad (3)$$

The bracketed quantity in (3) is the instantaneous potential for net transfer of fish density between the i th and j th sectors. Addition of $p_i C_i$ to, and its subtraction from, the numerator of the quantity gives

$$\frac{p_i C_i + p_i C_j - p_i C_i - p_j C_i}{p_i + p_j}$$

which, upon rearrangement, yields

$$\frac{p_i \cdot (C_i + C_j)}{p_i + p_j} - C_i$$

The two terms of the above expression are, first, the steady-state density of fish in the i th sector (considering only transfer between the i th and j th sectors) and, second, the existing density of fish in the i th sector. Substitution of the expression for the bracketed quantity in (3) yields

$$\frac{dC_{i \cdot j}}{dt} = \frac{s}{X_{ij}} \cdot \left[\frac{p_i \cdot (C_i + C_j)}{p_i + p_j} - C_i \right] \quad (4)$$

Considering only transfer between *i*th and *j*th sectors, $C_i + C_j$ must be a constant and $dC_{i,j}$ must be dC_i . Thus, equation (4) may be rewritten

$$\frac{dC_i}{dt} = \frac{s}{X_{ij}} \cdot (C_i(t \rightarrow \infty) - C_i), \quad (5)$$

which, upon integration, gives the negative exponential equation

$$C_i(t) = C_i(\infty) - (C_i(\infty) - C_i(0)) \cdot \exp\left(-\frac{s}{X_{ij}} \cdot t\right) \quad (6)$$

$$= C_i(0) + (C_i(\infty) - C_i(0)) \cdot (1 - \exp\left(-\frac{s}{X_{ij}} \cdot t\right)) \quad (7)$$

Taking advantage of the recursive property of the negative exponential relation, we may rewrite equation (7)

$$C_i(t) = C_i(t - \Delta t) + (C_i(\infty) - C_i(t - \Delta t)) \cdot (1 - \exp\left(-\frac{s}{X_{ij}} \cdot \Delta t\right)) \quad (8)$$

or

$$C_i(t) = C_i(t - \Delta t) + \left[\frac{p_i \cdot (C_i + C_j)}{p_i + p_j} - C_i(t - \Delta t) \right] \cdot (1 - \exp\left(-\frac{s}{X_{ij}} \cdot \Delta t\right)) \quad (9)$$

Equation (9) states that fish density in the *i*th sector at time *t* is the density at time *t* - Δt , plus the net transfer between the *i*th and *j*th sectors (a positive quantity if the transfer is from *j* to *i*, negative if from *i* to *j*) during the time interval Δt .

Computer implementation of the model made direct use of equation (9), except that computation for a sector exchanging fish density with more than one other sector required summation of net transfers between itself and each of the other sectors:

$$C_i(t) = C_i(t - \Delta t) + \sum_j \left[\frac{p_i \cdot (C_i + C_j)}{p_i + p_j} - C_i(t - \Delta t) \right] \cdot (1 - \exp\left(-\frac{s}{X_{ij}} \cdot \Delta t\right)) \quad (10)$$

Evaluation of net transfer rates was facilitated in that

$$\Delta C_{j \cdot i} = -\Delta C_{i \cdot j} \quad (11)$$

(where $\Delta C_{i \cdot j}$ is one of the elements in the summation indicated in equation 10) and also in that $\Delta C_{i \cdot j}$ could be set equal to zero, without the necessity of calculation, for all pairs of sectors not sharing a boundary of finite length and for the trivial pairs in which $i=j$.

Driving variables estimated from the laboratory experiments were p_i , p_j , and s . Fish moving between the i th and j th sectors were represented as being fully acclimated to temperature and salinity levels equivalent to the average $(\bar{T}_{ij}, \bar{S}_{ij})$ of those at the centers of the two sectors $(T_i, T_j; S_i, S_j)$. The values of p_i and p_j then were set equal to the frequency-densities of fish at T_i and T_j , respectively, measured in temperature preference experiments (Fechhelm et al. 1983) involving subjects acclimated to the temperature (5, 10 or 15°C) and salinity (5, 15, or 30 ppt) combination algebraically nearest \bar{T}_{ij} and \bar{S}_{ij} . Because the temperature preference curves were bell-shaped, the value of p_i exceeded p_j for any T_i that was nearer the preferred temperature than was T_j .

Computation of the dispersal rate coefficient s first required the calculation of voluntary swimming speed in fish body lengths per second (BLS). For young Arctic cisco acclimated and tested in the laboratory (Fechhelm et al. 1983), we observed that BLS was related to temperature (T) by the function

$$\text{BLS} = 0.06 \cdot \exp(0.145 \cdot T) \quad (12)$$

For simulation, BLS was computed by replacing T in the above equation with \bar{T}_{ij} . Multiplication by standard length of fish (SL, set to 10 cm in all simulations) and by appropriate constants converted BLS to speed V in $\text{km} \cdot \text{h}^{-1}$:

$$\begin{aligned} V &= (\text{BLS} \cdot \text{length} \cdot \text{sec}^{-1}) \cdot (\text{SL} \cdot \text{cm} \cdot \text{length}^{-1}) \cdot (3600 \cdot \text{sec} \cdot \text{h}^{-1}) \\ &\cdot (1 \cdot \text{km} \cdot (100,000 \text{ cm})^{-1}) = 0.036 \cdot \text{BLS} \cdot \text{SL} \cdot \text{km} \cdot \text{h}^{-1} \quad (13) \end{aligned}$$

The dispersal rate should depend on the swimming speed of fish and on the directedness of their movement. Thus, we included a second component in the dispersal coefficient. We reasoned that directedness of fish movement should be a function of the environmental preference gradient (g), which we defined as

$$g = \frac{\left| \frac{P_i - P_j}{P_i + P_j} \right|}{X_{ij}} \quad (14)$$

In the absence of empirical information, we arbitrarily defined the relation between path directedness (e) and magnitude of the preference gradient (g) as follows:

$$e = 1.0 \text{ if } g \geq 0.1 \text{ km}^{-1} ; \quad (15)$$

$$e = 0.2 \text{ if } g < 0.1 \text{ km}^{-1} . \quad (16)$$

The dispersal rate coefficient s , then, was defined as

$$s = e \cdot V . \quad (17)$$

Thus, fish density was assumed to shift between sectors at a rate equivalent to observed swimming speed if the preference gradient were sufficiently steep; otherwise, the shift in fish density occurred at a rate only one-fifth as great. In the latter case, directed dispersal was reduced to near-diffusion along the fish density gradient.

Implementation of the Model

The simulation model, in general form, was written in BASIC and developed on a 48K Apple II Plus® microcomputer. The model then was adapted for application in the causeway situation, translated into the Hewlett Packard (HP) version of BASIC, and executed on a HP 9845 microcomputer.

Implementation of the model mainly involved appropriate sectoring of the causeway area and deciding the more difficult issue of how peripheral sectors should be treated. Waters near the causeway were partitioned into 17 sectors (Fig. 2). Sectors were made to conform with stations at which either LGL or Woodward-Clyde, Inc. teams sampled water quality and fish density during summer 1981 as part of the Waterflood Monitoring Program. Of particular importance were sectors 1, 2, 17, and 14; in these sectors were located LGL fyke net stations 6, 5, 4, and 3, respectively, which were the sole source of data on the actual densities of young Arctic cisco (Griffiths and Gallaway 1982).

Catch per day (24 h) at fyke net stations 3 and 6 (sectors 14 and 1) during the period from 30 July to 28 August 1981 was the input used to drive the model.

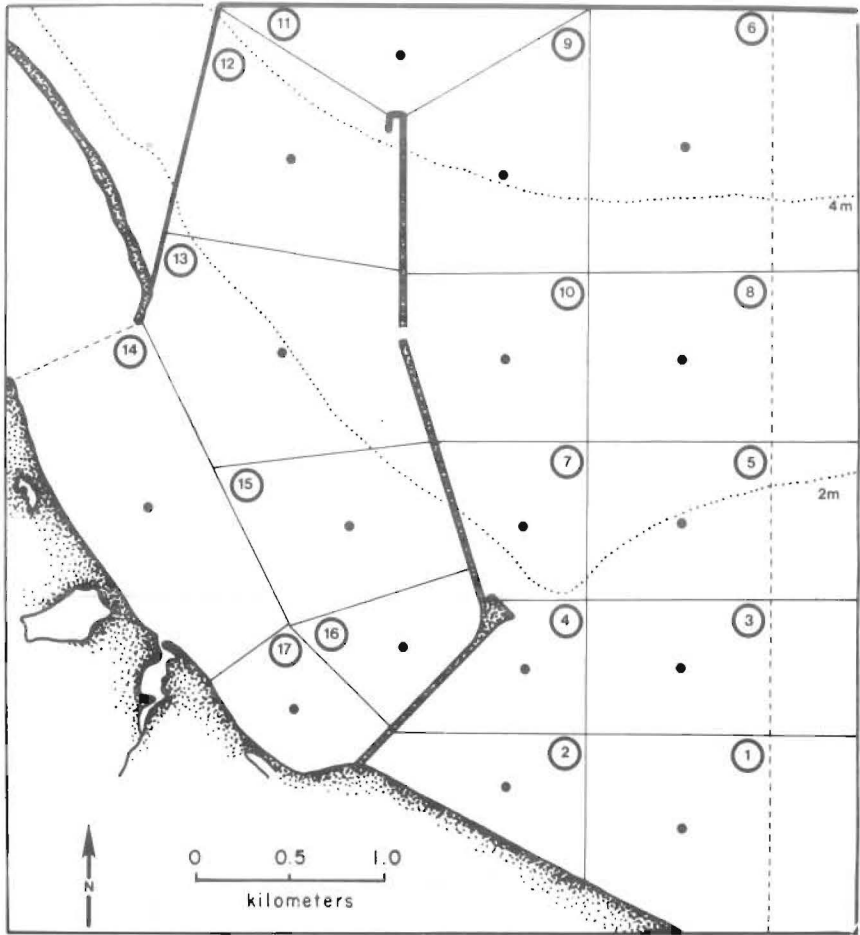


Fig. 2. Map of the causeway area, showing the boundaries and centers of the 17 sectors used in simulation. Location of the breach, intended as a fish passage structure, is indicated as a break in the causeway.

At noon on each simulated day, densities of fish in sectors 1 and 14 were updated to the values of catch per net per day recorded at stations 6 and 3 on the succeeding day. Because nets generally were fished for 24 h at a time, we assumed that catch reflected the density of fish in the sector averaged over a day. Density in sector 1 was propagated to east side peripheral sectors 3, 5, 8, and 6. For the succeeding day of simulation, fish density in sectors 1, 3, 5, 8, 6, and 14 was held constant. Thus, the model was made to treat these sectors as

infinite fish sources and sinks. Whereas fish could transit the boundaries between peripheral and adjacent sectors, fish densities in the peripheral sectors were unaffected. Net exchange of fish density was permitted neither across the northern boundaries of sectors 6 and 11, nor across the northwestern boundaries of sectors 12 and 13. This constraint was equivalent to assuming that young Arctic cisco either do not venture north and northwest of the heavy line bounding these sectors (Fig. 2) or if they do, fish densities and environmental conditions on either side of the boundary are equivalent. Neither of these assumptions is particularly attractive, but the lack of data from the area beyond this boundary permitted no more realistic alternative. Transit across the causeway was not permitted, of course, except via the 30-m wide breach that exists between sectors 10 and 13. All 22 other possible transits between the 17 sectors were permitted, giving a total of 23.

Environmental data limited our resolution in defining the simulation milieu. A description of the surface temperature and salinity regime over the simulation area was provided by Woodward-Clyde, Inc. surveys (Mangarella et al. 1982) for only 12 dates during 1981: 30 July and 3, 5, 7, 10, 12, 14, 19, 22, 23, 26, and 28 August. Even for these dates, we had to interpolate among and extrapolate from the existing data to provide estimates for some sectors, particularly 3, 5, 8, and 6. The simulation program linearly interpolated surface temperature and salinity between consecutive sampling dates to generate an hourly series of values for each of the 17 sectors.

Execution of the simulation program provided hourly predictions of fish density (in units of catch per fyke net per 24 h) for each sector from 1300 h on 30 July through 1200 h on 28 August. Apparently, few young Arctic cisco were in the causeway area at the beginning of the simulation period, because only three individuals were taken in the fyke net at station 3 (sector 14) and none at station 6 (sector 1) during the 24-h period ending on 31 July. Therefore, initial density values were set at 3.0 in all the western sectors (12–17) and 0.0 in all the eastern sectors (1–10); starting density in sector 11 (at the end of the causeway) was set at 2.0.

The program computed averages of predicted fish density at noon on each day for the preceding 24-h period. Also, the net density change across each sector boundary was tallied for each 24-h period.

To separate the modeled effects of environmentally directed movements from those of simple diffusion from areas of high to low fish density, we ran the simulation both with and without incorporating the supposed directional bias associated with heterogeneity of temperature and salinity. The environmentally directed version of the model was reduced to the environmentally undirected version by setting $p_i = p_j$ for transit between all pairs of sectors; i.e., movement between sectors was a simple function of density differences. Because of its dependence upon ambient temperature, however, swimming speed still varied

between sectors and from hour to hour as in the environmentally directed version. Owing to the lack of directional bias, path directedness e was held constant at its minimum value, 0.2. Consequently the dispersal rate coefficient s , being the product of swimming speed and e (equation 17), had a value under the undirected scenario that tended to be less than that under the directed scenario.

Because we believed that the constraint on s may have disproportionately weakened the environmentally undirected model's performance, we ran a third version with the values of p_i and p_j reversed. This reverse-directed version required fish to move down their preference gradient, or opposite the expected direction based upon quantitative laboratory investigations.

RESULTS AND DISCUSSION

The environmentally directed version of the model produced reasonable simulations of fyke net catch (CPUE) in each of the two reference sectors. Predicted catch rates in sectors 2 and 17, when ranked among dates, generally mimicked the rankings of observed catch rates in those sectors (Fig. 3). Both test variants of the model performed well also in sector 17, but neither did nearly as well as the environmentally directed scenario in sector 2 (Fig. 3). Relative performances of the three model versions in each reference sector are made more evident quantitatively by comparing the magnitudes of Kendall's rank-correlation coefficient tau (Siegel 1956) and its associated probability (P) under the null hypothesis of no correlation between predicted and observed series of ranks (Table 1).

Why did the environmentally directed model perform so much better in sector 17 than in sector 2? And how were the other two versions of the model able to do so well in sector 17? The answers to these questions are interrelated and set the stage for later discussion of our attempts at further refinements in modeling strategy.

First, the directed model's lack of fit in sector 2 came primarily from failure to mimic behavior of the system during a single brief period (14–17 August) when observed catches in sector 2 declined precipitously to near zero. We postulate that the decline in CPUE values actually represented a reduction in fish catchability rather than in fish density. Our idea is that catchability (but not necessarily density) was reduced by an abrupt movement of cold, saline water into the causeway area. Temperatures dropped from values near 7°C on 10 August to a mean of 1.5°C in sectors west of the causeway on 12 August; by 14 August, the cold water had spread throughout the causeway area. Whether or not observed catches in sector 2 during 14–17 August were representative of ac-

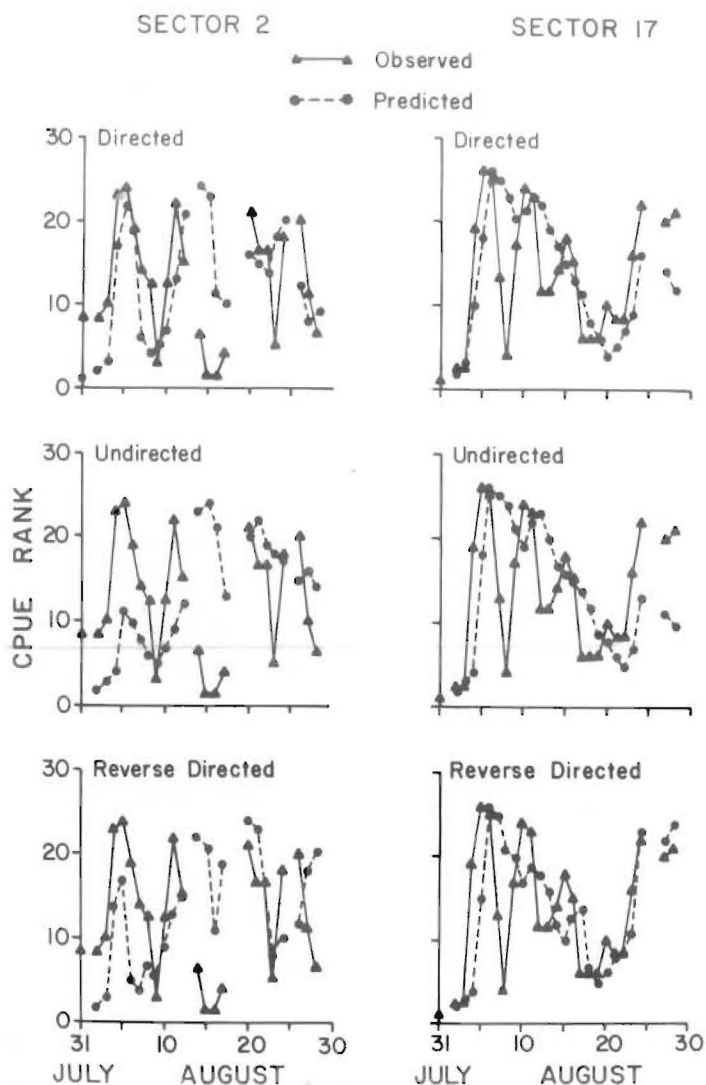


Fig. 3. Ranks of fish density (CPUE) observed versus that predicted under three models in sectors 2 and 17 on each date during the period 31 July to 28 August, 1981, for which observed values were available.

tual fish density, elimination of this subset from the data series greatly improved correlation between observed and predicted values of ranked CPUE under the environmentally directed model (Fig. 4), not only in sector 2 (tau increased from 0.21 to 0.45; P decreased from 0.08 to 0.003) but also in sector 17

Table 1. Coefficients of rank correlation, and their associated probabilities, between fish density (CPUE) observed versus that predicted under three models in sectors 2 and 17.

Model Scenario	Sector 2		Sector 17	
	Kendall's tau	<i>P</i>	Kendall's tau	<i>P</i>
Directed	0.21	0.08	0.44	0.001
Undirected	-0.05	0.35	0.33	0.01
Reverse-directed	0.11	0.23	0.46	<0.001

(tau increased from 0.46 to 0.54; *P* decreased from 0.001 to <0.00003).

A second facet of the answer seems to be that CPUE fluctuations in sector 17, compared with those in sector 2, were driven more by fish density differentials than by gradients of environmental preference, especially during the early part of the simulation period. The average absolute difference between temperatures in the drive and reference sectors during the first 6 days was 0.51°C for sectors 2 versus 1, but only 0.25°C for sectors 17 versus 14. Consequently, hypothetical fish that behaved according to the environmentally directed model had less directive information on the west (sector 17) side of the causeway than on the east (sector 2) side. For the same reason, even the 2

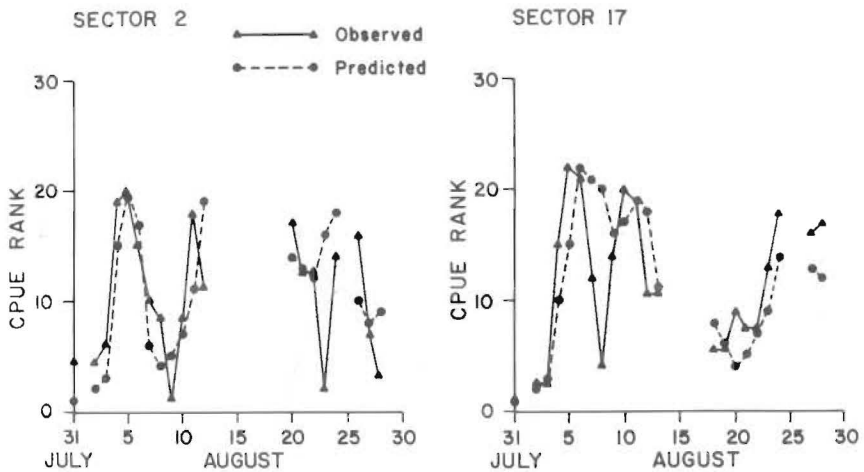


Fig. 4. Ranks of fish density (CPUE) observed versus that predicted under the environmentally directed model in sectors 2 and 17 after the removal of catch data for 14–17 August, 1981.

degraded variants of the model were able to perform creditably in sector 17, but not in sector 2.

Finally, the better performance of all 3 versions of the model in sector 17 than in sector 2 may have resulted partly from more realistic boundary definition on the west side of the causeway. Every east side sector was contiguous with a drive sector in which supposed fish density was constant over each day at the level measured only in sector 1. In contrast, simulated fish moved into and out of west side sectors through only one drive sector, sector 14. As a test of the influence of our conservative boundary conditions, we restricted the drive sectors for the east side of the causeway to sector 1 alone, removing any fish-density flows to and from the offshore sectors 3, 5, 8, and 6. Results for the directed model under this scenario were identical to the original outputs in sector 17 (Kendall's tau = 0.44; $P = 0.001$), but correlation improved for sector 2 (Kendall's tau and P were 0.254 and 0.042, respectively, as compared to the original values of 0.21 and 0.08). These results support the notion that young Arctic cisco have an affinity for waters very near the shoreline (Griffiths and Gallaway 1982).

The better overall performance of the environmentally directed version of the model can only be attributed to its provision for appropriate responses by the fish to heterogeneities in temperature and salinity. These responses were not permitted under the environmentally undirected variant and were intentionally subverted under the environmentally reverse-directed variant. The modeling exercise suggests that fluctuating densities of young Arctic cisco near the causeway reflect significant regulatory responses to temperature-salinity structure, despite the large influence of immigration and emigration, and that comparison of model predictions under the directed and undirected versions provides a method for rational separation of the two sources of variation.

Encouraged by the environmentally directed model's performance in the two sectors from which independent data were available for comparison, we examined predictions for the entire causeway area (excluding the drive sectors 1, 3, 5, 6, 8, and 14). To minimize the problem of dependence among sample observations, the analysis was restricted to only those 10 dates on which environmental surveys were conducted 3, 5, 7, 10, 12, 14, 19, 23, 26, and 28 August). Predicted densities (24 h average) under the directed and undirected scenarios were compared, as ratios, for each of the 11 sectors contiguous with the causeway on each of the 10 dates (Table 2). The grand geometric mean ratio of directed density to undirected density over all 11 sectors on all 10 dates was 0.93. This result implies that temperature-salinity heterogeneity associated with the causeway during August 1981 caused young Arctic cisco to be about 7 percent less abundant in the area than they would have been had temperature and salinity provided no directional bias. Over all sectors, temperature-salinity heterogeneity resulted in elevated abundance of young Arctic cisco before 12

Table 2. The ratio of simulated fish density under the environmentally directed scenario to that under the environmentally undirected scenario, by date and sector. \bar{X}_g is the geometric mean for each date or sector; $\bar{\bar{X}}_g$ is the grand geometric mean over all dates and sectors.

Date	Sector											\bar{X}_g
	2	4	7	10	9	11	12	13	15	16	17	
3 Aug 1981	2.68	1.64	0.96	1.13	1.36	0.83	0.71	1.45	1.24	1.05	1.10	1.21
5	1.36	1.32	0.99	1.21	1.01	1.07	1.84	2.09	1.96	2.22	1.05	1.40
7	0.66	1.07	0.97	1.26	1.10	1.24	1.50	1.38	1.43	1.49	1.47	1.20
10	0.85	0.80	1.02	1.21	1.40	1.14	1.22	1.20	0.82	1.01	1.40	1.08
12	0.95	1.02	1.07	1.57	1.48	0.64	1.09	0.63	0.83	1.07	1.40	1.03
14	1.47	0.92	0.74	1.07	1.45	0.93	0.46	0.42	0.38	0.83	0.90	0.79
19	0.61	0.47	0.43	0.58	0.95	1.29	0.49	0.37	0.23	0.40	0.26	0.49
23	0.82	0.71	0.82	0.90	0.93	0.93	0.73	0.92	0.75	0.40	0.40	0.73
26	0.67	1.19	0.92	0.94	0.93	0.90	0.81	0.93	0.90	0.69	0.77	0.87
28	<u>0.57</u>	<u>1.01</u>	<u>1.20</u>	<u>1.00</u>	<u>0.87</u>	<u>0.93</u>	<u>0.85</u>	<u>1.10</u>	<u>1.02</u>	<u>0.91</u>	<u>0.62</u>	<u>0.90</u>
$\bar{\bar{X}}_g$	0.94	0.96	0.88	1.06	1.12	0.97	0.89	0.93	0.82	0.89	0.83	$\bar{\bar{X}}_g = 0.93$

August and markedly reduced abundance thereafter. Over all dates, temperature-salinity heterogeneity caused relative concentration of young Arctic cisco only in sectors 9 and 10, and reduced abundance in all other sectors, especially those on the west side of the causeway.

The above summary of results is made more emphatic and environmentally interpretable by plots of the geometric mean of predicted catch ratio and average temperature against time (Fig. 5). Under the model, the decline in temperature between 10 and 14 August occurred in such a way as to direct young Arctic cisco out of the entire area, particularly out of the sectors on the west side. Fish operating under the environmentally undirected version of the model were essentially trapped by low dispersal rates associated with the reduction in temperature.

The temporal sequence of differences between ratios of predicted catch on east and west sides of the causeway suggested that substantial shifts of fish density should have occurred around the causeway's end and through its breach. Therefore, daily net transit rates between sectors 9 and 11 and between sectors 10 and 13 were examined (for the environmentally directed version of the model) as measures of movement around the causeway's end and through the breach, respectively (Fig. 6). With the general exception of 4-7, 17-19, and 22-23 August, the net transit of fish around the tip of the causeway was in the same direction, although not necessarily of the same magnitude, as that through the causeway breach. During the 4-7, 17-19 and 22-23 August periods, the combined flows of fish tended to form a gyre, giving either an eastward density shift around the end of the causeway corresponding with a westward shift through the breach or vice versa. Such situations existed because of the specific heterogeneous thermal structure and fish density of the waters surrounding the causeway during those brief periods.

Overall, net movement was predominantly eastward during 31 July to 13 August, on 18 August and during 23-24 August (Fig. 7). Over the entire simulation period on a per-day basis, 104.5 net units of fish density moved eastward and 85.4 net units moved westward, yielding a total net eastward shift for the 29-day period of only 19.1 units of fish density, which is about half that typically present in the involved sectors (10, 11, and 13). The trend in net movement can be partly attributed to the thermal structure of the causeway area. During the 31 July to 13 August period, when net transit was eastward, the average temperature (the average of sectors 1 through 9, during 3, 5, 7, 10, and 12 August) on the east side of the causeway was 8.1°C as compared with 6.4°C (average of sectors 11 through 17 during the same dates) on the west side. After 13 August, average temperatures on east and west sides of the causeway were nearly identical—4.73°C on the west side versus 4.68°C on the east side. The predominantly westward movement that occurred after 13 August was strongly weighted by net density shifts during 14-15 August. Net transit during

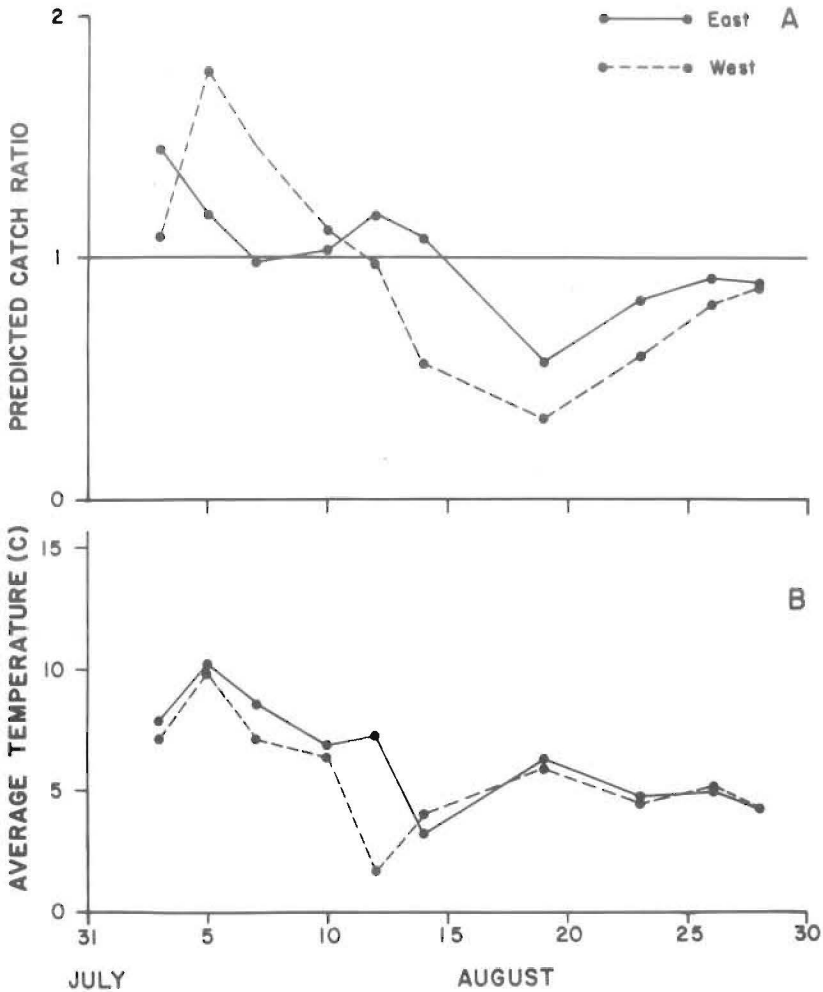


Fig. 5. A) Geometric mean ratio of catch predicted under the directed model to that predicted under the undirected model by date for east (sectors 2, 4, 7, 9, 10) and west (sectors 12, 13, 15, 16, 17) sides of the causeway. B) Average daily temperature for east and west sides of the causeway.

these two days, when thermal structure was highly aberrant, accounted for 70 percent of the total westward shift that occurred during 14–28 August. Excluding 14–15 August, the net movement of fish westward under more homogeneous thermal conditions was only 20 percent of that eastward which occurred during the period of greater thermal heterogeneity, 31 July to 13 August.

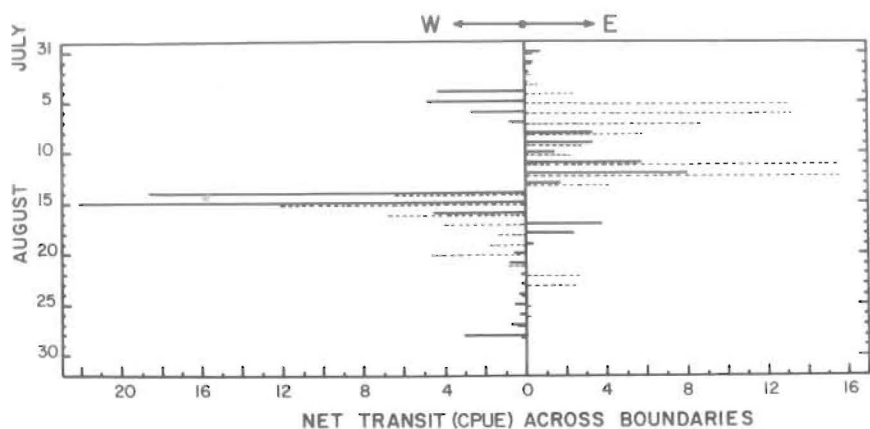


Fig. 6. Net shifts in fish density across the boundaries between sectors 9 and 11 (solid line) and between sectors 10 and 13 (dashed line) during 31 July to 28 August, 1981, under the directed model.

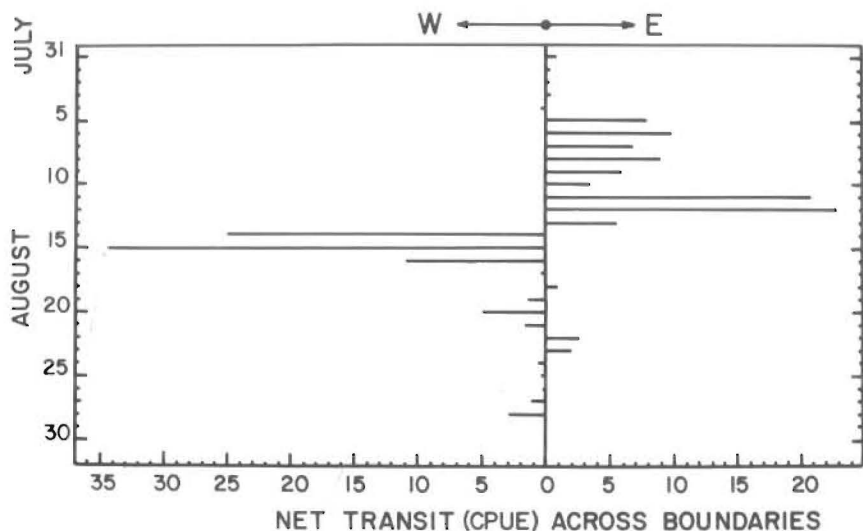


Fig. 7. Combined net shifts in fish density across the boundaries between sectors 9 and 11 and between sectors 10 and 13 during 31 July to 28 August, 1981, under the directed model.

These results suggest that the area's temperature and salinity structure could encourage migrations of young Arctic cisco from one side of the causeway to the other, and likely in a pulsed fashion. Griffiths and Gallaway (1982) noted that abundance of small Arctic cisco often differed greatly between sides of the causeway, especially when temperature-salinity differences were pronounced.

Refinements of the Model

As our thinking about the modeling problem matured, it became apparent that our mechanistic model was not equipped to account for many of the high frequency shifts in fish catch rate that were observed in sectors 2 and 17. Small Arctic cisco simply could not have swum rapidly enough over the distances involved to adjust their densities at the required rates. Either they were moved by currents, or the high frequency fluctuations in catch rate reflected high frequency changes in catchability superimposed on more gradual changes in the density of fish available for capture. Strong currents existed in the causeway area during the simulation period (Mangarella et al. 1982), but the data on currents in the vicinity of the causeway were insufficient to incorporate into the model the effects of passive drift of fish with currents. We therefore turned to the other possibility: high frequency changes in catch resulted from variation in fish catchability, not from changes in density. If the hypothesis were true, each predicted catch series should be more highly correlated with an appropriately filtered version of the observed series than with the observed series itself. To test this hypothesis, we exponentially filtered the observed series for sectors 2 and 17, trying rate coefficients ranging from 0.1 to 10 days⁻¹. Each filtered series was computed by recursive application of the equation

$$C'_i = C_i - (C_i - C'_{i-1}) \cdot \exp(-k \cdot \Delta t) \quad (18)$$

where

- C'_i = filtered catch on *i*th day,
- C_i = actual catch on *i*th day,
- C'_{i-1} = filtered catch on (*i*-1)th day,
- k = the rate coefficient, and
- Δt = 1 day = the time interval between data values.

We assumed that observed catch was at steady-state on the first day; i.e.,

$$C'_1 = C_1 \quad (19)$$

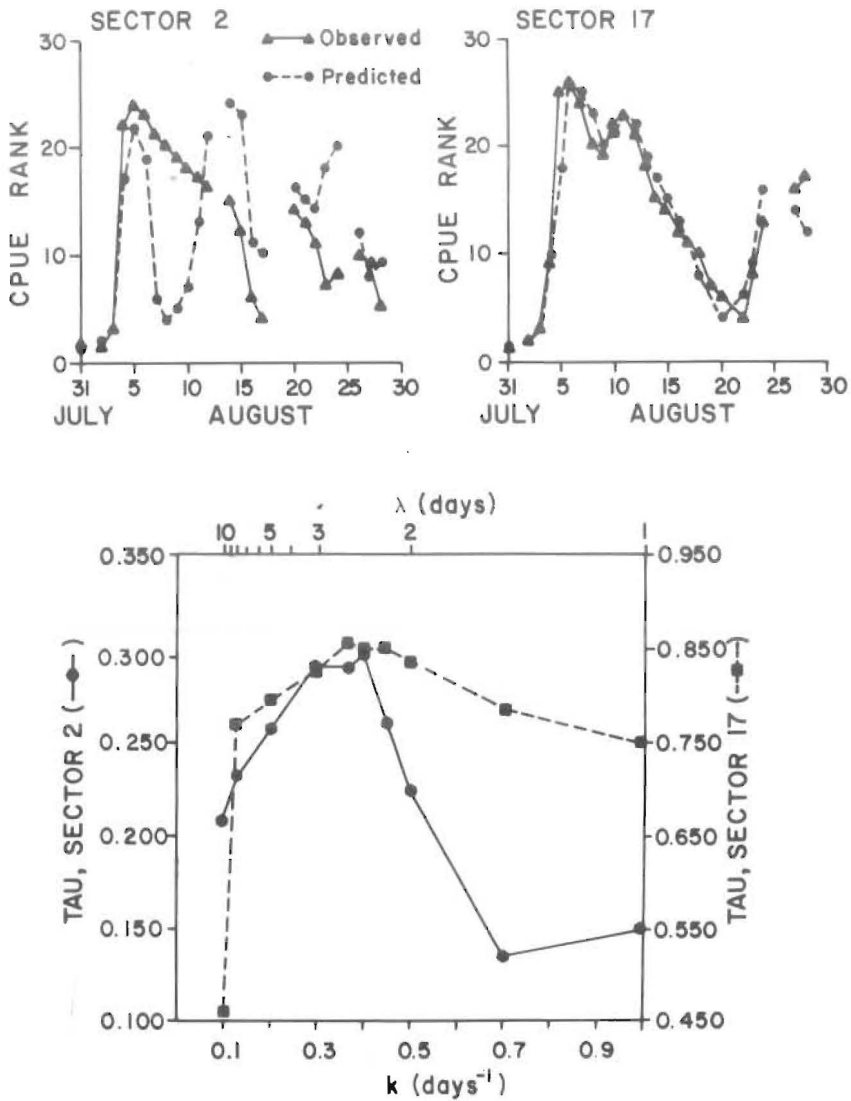


Fig. 8. Ranks of observed versus predicted catch rates after smoothing the observed series with an exponential filter employing a rate constant k of 0.4 days^{-1} (upper panels), the optimum value as measured by magnitude of Kendall's rank correlation coefficient tau (lower panel).

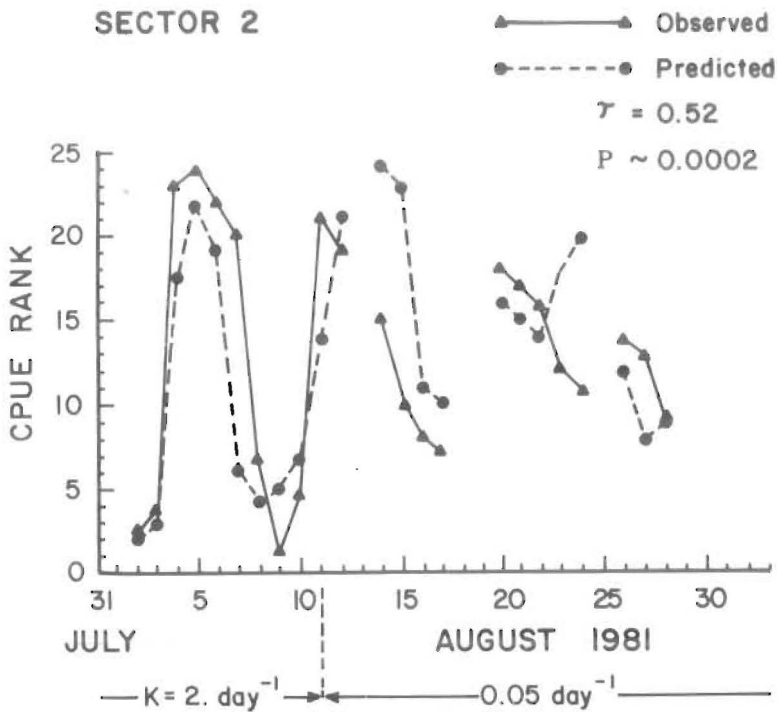


Fig. 9. Ranks of observed versus predicted catch rates after smoothing the observed series for 31 July to 11 August, 1981, with an exponential filter having a rate constant k of 2 days⁻¹ and for the period 12 August onward using a rate constant k of 0.05 days⁻¹.

For both sectors 2 and 17, the optimum filter had a rate coefficient near 0.4 days⁻¹; that is, filtering the observed series with the rate coefficient set equal to 0.4 days⁻¹ produced maximum correlation between predicted and observed catches in each sector (Fig. 8). Improvement of correlation over that for the unfiltered series was modest for sector 2 (tau increased from 0.21 to 0.30; P decreased from 0.08 to 0.02), but was dramatic for sector 17 (tau increased from 0.44 to 0.85; P decreased from 0.001 to 0.00001; Fig. 8). We infer from the exercise that a substantial part of the variation in daily catch rate of the fyke nets, particularly that in sector 17, was associated with factors other than fluctuations in fish density. We suspect that environmentally related changes in catchability were principally responsible. The time constant of the optimum filter, about 2.5 days ($= 1/k$), is consistent with the typical periods of barometric pressure, wind direction, and current direction in the causeway area (Mangarella et al. 1982).

Still not satisfied with the fit in sector 2, we tried a filter with two rate coefficients, one for the early part and the other for the remainder of the simulation period. The best filter (found by trial and error) had a rate coefficient of 2 days^{-1} until 11 August and 0.05 days^{-1} thereafter (Fig. 9); τ and P were 0.52 and 0.0002, respectively. This result suggests that in sector 2 the fluctuations in catch prior to 11 August (when causeway area temperature began its abrupt decline) were consistent with actual changes in fish density, whereas subsequent catch fluctuations reflected a large component of density-independent noise.

Assessment Implications

The present application of the model suggests that "pulsing" of Arctic cisco numbers in coastal waters of the Beaufort Sea reflects distributional responses by the fish to shifting winds and currents that alter nearshore patterns of temperature and salinity. Effects are most dramatic near peninsulas like the Waterflood Causeway. The fish are temporarily delayed in their longshore migrations and concentrated on the warmer, less saline side of such a peninsula until a reversal in prevailing winds alters the temperature-salinity regime, whereupon the migration resumes as a pulse.

The breach in the Waterflood Causeway should lessen the rate at which migrating Arctic cisco (and other anadromous fishes) will be entrained or impinged at the water-intake structures. When winds and currents are east-to-west—the prevailing situation during summer—the warm-water plume from the Sagavanirktok River sweeps around the causeway, providing a broad corridor for migration. Under these conditions, however, cold Beaufort Sea water is upwelled on the causeway's west side thereby reducing use by Arctic cisco. Fish present on the west side will leave the area and may be directed by the temperature gradient through the breach rather than move along the causeway to its end where the water-intake structures will be located. (It is possible, however, that certain conditions lead to formation of a migration "gyre," whereby fish move in one direction through the breach and in the opposite direction around the causeway's end; this could result in multiple exposure of some fish to the risk of entrainment or impingement.)

We must caution that our model, as presently conceived, is totally insensitive to possible social interactions among fish and to any width-of-path effect. Thus, such questions as adequacy of the breach's width (30 m) could not be addressed. The implications of the previous paragraph therefore must be taken as merely suggestive.

We are enthusiastic about our model's potential as a cost-effective tool for interpreting the dynamics of fish distribution. Because the model is mechanistic, it is generic; i.e., it should be equally applicable at other times and places. Moreover, the model's structure and parameters can be adjusted to accommodate a broad spectrum of related applications.

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