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 distributions. 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. Sall 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 change in fish density in the ith sector attributable to movement of fish from the ith sector to a contiguous jth sector \(\frac{dC_i}{dt} = \frac{p_j}{P_i + p_j} \cdot X_{ij} \cdot C_i\) was taken as

\[\frac{dC_i}{dt} = - \frac{p_j}{P_i + p_j} \cdot X_{ij} \cdot C_i\]  

(1)

where

- \(P_i\) and \(P_j\) are the relative preference values of temperatures at the centers of the ith and jth sectors;
- \(X_{ij}\) is the distance between centers of the ith and jth 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 ith sector.

\(\text{In the absence of information to the contrary, we assumed from the outset that Arctic cisco, confronted with simultaneous gradients of temperature and salinity, orient to the temperature component only, but do so in a way that depends on salinity as well as temperature. In the coastal Beaufort during summer, temperature and salinity tend to be inversely related.}\)
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 \( (\frac{dC_{i\rightarrow j}}{dt}) \) was

\[
\frac{dC_{i\rightarrow j}}{dt} = \frac{p_i}{p_i + p_j} \cdot \frac{s}{X_{ij}} \cdot C_j. \tag{2}
\]

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

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

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

\[
\frac{p_i C_i + p_i C_j - p_j C_i - p_j C_j}{p_i + p_j}
\]

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

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

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

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

which, upon integration, gives the negative exponential equation

\[
C_i(t) = C_i(\infty) - (C_i(\infty) - C_i(0)) \cdot \exp \left( -\frac{s}{X_{ij}} \cdot t \right)
\]

\[
= C_i(0) + (C_i(\infty) - C_i(0)) \cdot (1 - \exp \left( -\frac{s}{X_{ij}} \cdot t \right)). \tag{6}
\]

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

\[
C_i(t) = C_i(t-\Delta t) + (C_i(\infty) - C_i(t-\Delta t)) \cdot (1 - \exp \left( -\frac{s}{X_{ij}} \cdot \Delta t \right)),
\]

or

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

Equation (9) states that fish density in the \( i \)-th sector at time \( t \) is the density at time \( t - \Delta t \), 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 \( \Delta t \).

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:

\[
C_i(t) = C_i(t-\Delta t) + \sum_j \left[ \frac{p_j \cdot (C_i + C_j)}{p_i + p_j} - C_i(t-\Delta t) \right] \cdot (1 - \exp \left( -\frac{s}{X_{ij}} \cdot \Delta t \right)). \tag{10}
\]
Evaluation of net transfer rates was facilitated in that

\[ \Delta C_{ij} \cdot i = -\Delta C_{i} \cdot j \]  

(11)

(where \( \Delta C_{ij} \) is one of the elements in the summation indicated in equation 10) and also in that \( \Delta C_{ij} \) 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 \( \overline{T_{ij}}, \overline{S_{ij}} \) 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 \( T_{ij} \) and \( S_{ij} \). 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

\[ \text{BLS} = 0.06 \cdot \exp (0.145 \cdot T) . \]  

(12)

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

\[ V = (\text{BLS} \cdot \text{length} \cdot \text{sec}^{-1}) \cdot (\text{SL} \cdot \text{cm} \cdot \text{length}^{-1}) \cdot (3600 \cdot \text{sec} \cdot \text{h}^{-1}) \]

\[ \times (1 \cdot \text{km} \cdot (100,000 \text{ cm})^{-1}) = 0.036 \cdot \text{BLS} \cdot \text{SL} \cdot \text{km} \cdot \text{h}^{-1} . \]  

(13)

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

\[ g = \frac{p_i - p_j}{p_i + p_j} . \]  

(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:

\[ e = 1.0 \text{ if } g > 0.1 \text{ km}^{-1} ; \]  

(15)

\[ e = 0.2 \text{ if } g < 0.1 \text{ km}^{-1} . \]  

(16)

The dispersal rate coefficient \( s \), then, was defined as

\[ s = e \cdot V . \]  

(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.
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 actual 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.

<table>
<thead>
<tr>
<th>Model Scenario</th>
<th>Sector 2</th>
<th>Sector 17</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Kendall's tau</td>
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<tr>
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</table>

(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 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 a 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; $\bar{X}_g$ is the grand geometric mean over all dates and sectors.

<table>
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<th>Sector</th>
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<th>7</th>
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<th>11</th>
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August conditions were strongly weighted by net density shifts during 14-15 August. Net transit during these dates was on the west side and increased by 41.5%. Temperature-salinity heterogeneity caused relative concentration in all other sectors.
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

\[
C_i' = C_i - (C_i - C_{i-1}') \cdot \exp \left(-k \cdot \Delta t \right)
\]  

(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
- \(\Delta t\) = 1 day = the time interval between data values.

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

\[
C_1' = C_1.
\]  

(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).
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); \(\tau\) 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 Waterfall 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 Waterfall Causeway should lessen the rate at which migrating Arctic cisco (and other anadromous fishes) will be entrained or impinged at the 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.
ACKNOWLEDGMENTS

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LITERATURE CITED


