"Noise" in the Distributional Responses of Fish to Environment: An Exercise in Deterministic Modeling Motivated by the Beaufort Sea Experience

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Abstract. Fishes in unstable habitats may forever seek their environmental preferenda without achieving them. Simulation of temperature-dictated movements of Arctic cisco suggests that lack of apparent correlation between synoptic distributions of these fish and temperature is a natural consequence of the complexity and dynamics of habitat—temperature distribution. More generally, the "noise" in fish-catch data may reflect not so much intractable stochasticity as the failure of empirical models to cope with the space–time dependencies inherent in such data. Because appropriate mechanistic models explicitly accommodate these dependencies, their judicious application could increase greatly the informational yield of fish-monitoring studies like those conducted in the nearshore Beaufort Sea.

INTRODUCTION

No experienced student of fish ecology doubts that fish movements and distribution are strongly influenced by such environmental variables as temperature, dissolved oxygen, currents, and light intensity. Yet, the precise role of these factors is difficult to infer from even the most carefully collected field data of the usual sort. One problem, of course, is that fish respond not to single environmental factors in isolation, but to the totality of environment. Even if the researcher could be sure that all important components of the environment are identified and properly measured, there remains the likelihood of complex interactions among components. Then, too, there are the usual doubts about the adequacy of the fish samples, in terms of size, frequency, and freedom from bias. Invariably, more and bigger samples are needed than reasonably can be obtained. This is because fish-catch data are notoriously "noisy," reflecting the large role of chance in the processes leading to fish distribution and apparent abundance.

There's the real culprit: Chance. If the researcher could measure all important environmental variables and collect truly adequate fish samples, he need only apply conventional multivariate regression analysis to unravel the effects of environment on fish distribution. Right? Before you agree too quickly, please consider our story1 of Arctic cisco (Coregonus autumnalis) distribution in Quliuqtuat Bay on the Beaufort Sea coast.

A FISH STORY

Quliuqtuat Bay is typical of coastal waters along the Beaufort Sea coast of western North America. The Bay represents a seaward extension of the gently sloping coastal plain; the 2-m depth contour is almost 6 km offshore. During the arctic summer, strong winds drive the currents first one way and then another, at intervals of 2 to 4 days. Frigid, saline water from the open Beaufort Sea periodically invades the bay through gaps between the barrier islands and vies with warmer freshwater discharged from the Saglu River to dictate the bay's changeable environment.

In such habitats live several coregonine fishes, including Arctic cisco. Extensive sampling along the Beaufort Sea coast (e.g., Craig and Mann 1974; Craig and Haldorson 1981; Griffiths and Gallaway 1982; Critchlow 1983; Moulton et al. 1985; Envirosphere 1986) suggests that young Arctic cisco live mostly in the coastal band of warmer, less saline water. Temperature-preference experiments in the laboratory (Fechhelm et al. 1983) confirm that this fish prefers temperatures near 14°C (Fig. 1), which in coastal waters of the Beaufort Sea occur only in midsummer and then usually in association with river effluent.

Quliuqtuat Bay seemed an appropriate arena in which to settle, once and for all, the degree to which temperature governs distribution of young Arctic cisco in their natural habitat. To this end, we undertook an exhaustive sampling program. First, 25 stations were established at points 1 km apart on a five-by-five grid in Quliuqtuat Bay (Fig. 2). Then, at each of the 25 stations water temperature was monitored and a fyke net fished daily for 20 consecutive days during midsummer.
The sequence of environmental events is evident from plots of the study area’s isotherms at 2-day intervals (Fig. 3). At the beginning of the sampling period, strong northerly winds had driven cold oceanic water onshore, leaving the entire Bay uniformly at 3°C. Cessation of winds permitted the river discharge to form a typical thermal plume by day 2. The plume was better developed on day 4 but was deflected toward the southern shore by rising northeasterly winds and corresponding current drift. After a brief period of light westerly winds (day 6), the wind returned to the northeast and by day 8 had driven an intrusion of oceanic water through the Bay, cutting off a gyre of relatively warm water. By day 10, southwestward current drift preceding continuing northeasterly winds had compressed the river plume against the southern shore. Winds (and currents) were light and variable on day 12. Strong westerly winds and corresponding current drift then cut off a new “warm ring” and deflected the river plume eastward by day 14; persistent deflection of the plume resulted in marked compression of isotherms against the eastern shore of the bay by day 16. During the final days of the study, winds shifted to the northwest, diminished, and finally were calm by day 20.

What did young Arctic cisco do during this period of shifting thermal regimes? The pattern is made evident by considering events only at the central station, number 13. Temperature and catch of 10-cm-long Arctic cisco fluctuated drastically, but not in synchrony (Fig. 4). In fact, a plot of catch rate against temperature reveals the familiar lack of apparent correlation (Fig. 5). Only 10 percent of the variation in catch rate is attributable to variation in temperature, under the model presented in Figure 1.

From this result we must conclude that temperature had little demonstrable influence on the distribution of small Arctic cisco in Quliuqtuat Bay. Temperature’s undoubted effects on physiology and behavior of the fish must have been overridden or masked by the operation of other variables or obscured by errors in sampling temperature, fish density, or both. Right? Wrong! — Variation in fish-catch rate was dictated entirely by variation in temperature.

THE “STORY” REVEALED

How can we be so confident, in the face of a straightforward regression analysis to the contrary, that temperature and temperature alone accounted for variation in our catch data? Our confidence derives from the knowledge that the story related above is just that—a “story.” There were no catch data, because there was no field study in Quliuqtuat Bay. In fact, there is no Quliuqtuat Bay on North America’s Beaufort Sea coast (to the best of our knowledge).

What we have described is a hypothetical study conducted via computer simulation. To be sure, the computer program incorporated as much realism and reason as we could muster. The temperature data are reminiscent of real observations in Alaskan coastal waters (e.g., Moulton et al. 1985). The model of Arctic cisco responses to temperature is that published in this journal 5 years ago (Neill et al. 1983); the published model produced results reasonably consistent with actual field data collected near the Waterflood Causeway (Prudhoe Bay) during summer 1981.

The model (Fig. 6) treats fish movement as a donor-
controlled drift process biased by the fish's temperature preference (which, for juvenile Arctic cisco, was measured experimentally by Fechhelm et al. [1983]). Considering two adjacent spatial locations \((i\) and \(j)\), the fish continually move toward the location having the higher value of the ratio \(p:C\), where \(p\) is the relative preference for the temperature (Fig. 1) and \(C\) the density of fish at that location; net rate of change in fish density (eq. 4 in Neill et al. 1983) is

\[
\frac{dC_i}{dt} = \frac{s}{X_{ij}} \left[ \frac{p_i (C_i + C_j)}{p_i + p_j} - C_j \right],
\]

where \(s\) is a temperature-dependent dispersal rate (maximal, the swimming speed observed experimentally by Fechhelm et al. [1983]) and \(X_{ij}\) is distance between locations \(i\) and \(j\). At steady state, density of fish is directly proportional to \(p\) and, therefore, must be related to temperature in the same way as \(p\).

The present implementation of the model involved 2,500 units of hypothetical fish density, initially distributed at 100 units per station. The computer program linearly interpolated station temperature between days (noon to noon) and evaluated fish-density flux on an hourly basis. The hourly values of density, averaged over the day, were output as daily "catch."

Plainly, catch of Arctic cisco vs. temperature at Quiliuqtuat Bay's Station 13 (Fig. 5) bore little resemblance to the temperature-preference function (Fig. 1) driving the model! What explains the seemingly "sloppy" performance of our simulated fish? The explanation is not that other factors of environment interfered with or masked responses to temperature: The only environmental factor at work in Quiliuqtuat Bay was temperature. Nor is the explanation a faulty sampling program: Samples both of fish density and temperature were flawless. Finally, chance was not the culprit: The model is deterministic, not stochastic.
Figure 3. Thermal structure of study area at 2-day intervals over the 20-day study period.

The explanation is that all temperatures were not equally available and freely accessible to fish in Quiluqquat Bay, and that small Arctic cisco simply could not swim fast enough to keep pace with the shifting thermal regime. Then, too, the relatively inferior thermal status of Station 13 caused the total number of fish “caught” there to underestimate the average density of fish in the Bay.

The explanation is made more explicit by erecting a model of conventional expectation. We began by specifying a model of conventional expectation. We decided that most of us, when confronted by a graph like that presented in Figure 4, casually compare the catch series with an intuitive model of the form

$$E(C) = CE = \frac{p}{\Sigma p(t)} \cdot \Sigma C(t),$$

where $C$ is fish density at the station on a particular day, $E(C)$ is the expectation of $C$, $p$ is the station's environmental value (from a graph like that in Fig. 1) on that
all 25 stations on each day; and CSS is steady-state density, computed by running the simulation to steady state for each day's temperature distribution, having begun with the distribution of CSIM on that day. The representation of distributional hysteresis as CSS-CSIM is obvious, but the interpretation of CEADJ-CSS as a measure

\[ CE - CSIM = (CE - CETOT) + (CETOT - CEADJ) + (CEADJ - CSS) + (CSS - CSIM), \]

where CE is the conventional expectation of density as defined above; CSIM is simulated density; CETOT = \( \sum p(t) \cdot 2,100 \), 2,100 being the total (over all 21 days—days 0–20) “catch” expected at Station 13 had fish density at this site been average for the system; CEADJ = \( \sum p(s) \cdot 2,500 \), 2,500 being the total density of fish in the system on each day and the summation of \( p \) being over
day, and the summations are over all days in the series. Underlying this model are the implicit assumptions that (1) the sampling station occupied a changing position in an array of environments equally available and freely accessible to the fish, and (2) the rate of change in environmental distribution was much slower than the fish could swim.

One or both of these assumptions was false for our simulated catch series at Station 13 in Quliuqtuat Bay: Fish density under the model of conventional expectation differed drastically from simulated density (Fig. 7). We evaluated the discrepancy by partitioning total “error” (CE-CSIM) into components due to (1) Station 13’s misrepresentation of fish density in the system (CE-CETOT), (2) Station 13’s misrepresentation of temperature availability in the system (CETOT-CEADJ), (3) restricted accessibility of temperature (CEADJ-CSS), and (4) inability of the fish to keep pace with temporal changes in the temperature distribution (distributional hysteresis, CSS-CSIM):
of restricted accessibility of temperature needs explanation. CEADJ is the expected density of fish at a particular station on a particular day, given that the thermal value of that station is adjusted for the availability of thermal values throughout the system. But movement of fish between two locations of equal value may be restricted by the existence of lower values at intervening locations. In the extreme, this leads to what Neill (1979) called environmental "trapping"—fish in habitat "oases" of relatively high environmental value (e.g., the warm gyres present in Quliuqtuat Bay on days 8 and 14) are trapped by surrounding habitat with lower values; similarly, high-value oases that appear de novo in low-value parts of the habitat may not be occupied because they are inaccessible. CEADJ is unaffected by these considerations; CSS reflects them. Thus, CEADJ-CSS is the appropriate measure of "error" associated with restricted accessibility of temperature.

How important, in our simulation, were the various "errors"? The "error" due to Station 13's misrepresentation of fish density in the system (CE-CETOT, Fig. 8A) was persistent, of course (being independent of temporal variation in the system), and amounted to 42 percent of average CSIM (=average CE). By far the dominant "error" was that due to Station 13's misrepresentation of temperature availability in the system (CETOT-CEADJ, Fig. 8B); average absolute magnitude of CETOT-CEADJ was 98 percent of average CSIM. Major discrepancies occurred during days 0–2, when higher temperatures were relatively rare, and during days 5–7 and 20, when higher temperatures were overrepresented. Absolute magnitudes of "errors" due to restricted accessibility of temperature (CEADJ-CSS, Fig. 9A) and distributional hysteresis (CSS-CSIM, Fig. 9B) averaged 13.5 and 26 percent, respectively, of average CSIM. We are reluctant to make more of these results because they reflect details of the specific thermal regime, which, after all, was only hypothetical.

THE MORAL

Our point in relating this exercise is not to argue that temperature is the sole factor influencing the distribution of Arctic cisco or any other fish; on the contrary, we are confident that fish do respond to the totality of environment, of which temperature is only one component—albeit, often an important one. Nor do we mean to belittle or discourage monitoring programs; such studies provide raw material useful for generating and essential for testing hypotheses about how fish–environment systems work in nature.

Our story's moral is this: Where a fish is located today depends partly on where it was yesterday and partly on environmental "lay of the land" between times and places. If environment is continually rearranged in space, as is so often the case in the Arctic, fish distribution is always in a transient state that may bear little relation to the fish's steady-state preferences. Therefore, a time-series of catch data, no matter how well attended by synoptic environmental data, may have little information content—unless a valid mechanistic model is available for interpreting those data. Unfortunately for all of us, distributional ecology is relatively long on data but short on models.

CONCLUSION

We who seek to understand the variation in fish distribution should set aside the familiar lack-of-effect scapegoats (e.g., effects of unknown variables, sampling error, and stochasticity of fish behavior) until we have considered that (1) the value (to the fish) of environment "here" depends on the value of environment "there;" (2) a fish can't always get from "there" to "here;" and (3) even when it can, the trip takes time. Proper consideration of these axioms requires both good data and good models.
Figure 8. “Error” in simulated catch attributable to (A) Station 13’s misrepresentation of fish density in the study area (CE-CETOT; see text), and (B) Station 13’s misrepresentation of temperature availability in the study area (CETOT-CEADJ; see text).

Figure 9. “Error” in simulated catch attributable to (A) restricted accessibility of temperature (CEADJ-CSS; see text), and (B) distributional hysteresis (CSS-CSIM; see text).
LITERATURE CITED


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