Reply: Spatial implications of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada[1]

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Sinclair and Swain (1996) have discussed in considerable detail their belief that temperature is of only modest consequence to the growth of cod, and that alternative factors are more influential in explaining the spatial and temporal trends that have been observed on the eastern coast of Canada. We welcome their interest in this subject, and fully support their plea for further research on the factors influencing growth rate. As was stated on numerous occasions in our paper, temperature alone cannot explain the observed growth patterns; other variables are almost certainly at play. Nevertheless, we were surprised and concerned by the emphasis that Sinclair and Swain placed on these possible alternatives, and by the extent to which they downplayed the influence of temperature. Indeed, in one of their opening comments, they stated that "while there is a clear spatial correlation between cod size at age and temperature in this area, their analysis does not reveal a convincing causal relationship between the two." Presumably, Sinclair and Swain did not intend to suggest that there is no causal relationship between temperature and growth rate in fish. Indeed, we believed that all those familiar with the subject of fish growth would accept the causal link as a given. In a review of the field of fish growth, Brett (1979) referred to temperature as the "controlling factor" of fish growth, through its direct effect on metabolic rate, oxygen consumption, feeding rate, digestive rate, activity, and scope for growth. He went on to indicate that the effects of temperature, first and foremost, must be accounted for before the effects of other "limiting" factors can be quantified. These sentiments were later echoed by Ricker (1979), and supported by the 2719 other papers (number based on a computerized literature search) published since 1978 that document a relationship between temperature and fish growth. Accordingly, we must disagree with Sinclair and Swain on the emphasis that should be placed on further research. The question is not whether temperature has a major influence on cod growth in space and time; the question is how large will its effect be?

To determine the expected magnitude of the temperature effect on cod growth, we must turn to the literature reporting the results of controlled experiments. There are surprisingly few papers that quantify and compare cod growth under controlled conditions of temperature, and most of those deal with juveniles. Nevertheless, the different sets of results are very consistent. Brown et al. (1989) reported a 40% increase in growth rate at length for cod reared at 8.3°C compared with 4.5°C. This value was similar to that of Otterlei et al. (1994), who reported a growth rate increase of about 50% with each 4°C increase in temperature between 6 and 14°C, and that of Waiwood (1978), who reported 33–50% higher growth rates for cod reared at 8°C compared with 4°C. Compare these experimental results with the 32% increase predicted by our growth model over the same temperature range (4–8°C). Clearly, our predicted effect of temperature is, if anything, somewhat smaller than that which is observed experimentally. While we do not suggest that temperature accounts for all of the observed growth rate variation in cod, both the experimental results and basic physiological theory indicate that it could (and should) account for a major proportion of it.

In attempting to build a case for alternative modifiers of cod growth, Sinclair and Swain questioned the accuracy and care with which our growth model was developed. These arguments were not well founded. In particular, their reconstruction of our predictive growth model for eastern Scotian Shelf cod was in error and was not that used or described in our paper. Their error appears to stem from their definition of $I_{i,j}$, which is not the same as that in Campana et al. (1995). The annual growth increment (I) along a cohort in year j was calculated in Campana et al. (1995) as

$$I_j = a + b \times \text{temperature}_j$$

where a and b are the age and (age × temperature) coefficients presented in the lower panel of Table 1 in Campana et al. (1995). Length at age i was then calculated as

$$L_{i,j} = L_{2,j-6} + \sum_{j-3}^{j} I_j$$

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Fig. 1. Relationship between observed and predicted lengths of age-8 cod (centimetres) on the eastern Scotian Shelf between 1971 and 1992. The slope of the regression is statistically significant ($p < 0.05$) both for the whole time series and for the period from 1980 onwards.
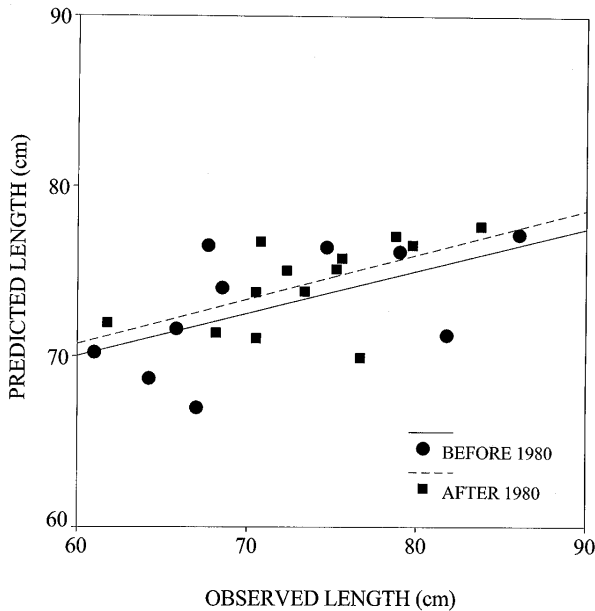
Therefore, for an 8-year-old cod in year j, the calculation would be

$$L_{8,j} = L_{2,j-6} + I_{j-5} + I_{j-4} + I_{j-3} + I_{j-2} + I_{j-1} + I_j$$
$$= L_{2,j-6} + (a + b \times \text{temp}_{j-5}) + (a + b \times \text{temp}_{j-4})$$
$$+ (a + b \times \text{temp}_{j-3}) + ... + (a + b \times \text{temp}_j)$$
$$= L_{2,j-6} + 6a + b(\text{temp}_{j-5} + \text{temp}_{j-4} + ... + \text{temp}_j)$$

Contrary to the assertion of Sinclair and Swain, there is no cancellation of annual temperature terms in this calculation, and no undue effect of the temperature in the year of collection compared with earlier years.

Sinclair and Swain then asserted that there was no correlation between the growth model's predictions of length at age 8 and those that were actually observed in eastern Scotian Shelf cod. This statement is incorrect. Predicted and observed lengths at age 8 were significantly correlated ($p < 0.05$) throughout the time series (Fig. 1); they were also significantly correlated ($p < 0.05$) for the period from 1980 onwards, which is the period to which they pointed as showing no correlation (Fig. 1). Given the fact that temperature in this area has declined significantly ($p < 0.05$) since the mid-1980s (Page et al. 1994; Fig. 10 of Campana et al. 1995), and in light of the accepted causal relationship between growth rate and temperature, we infer that falling temperature contributed to the decline in growth rates. We agree with Sinclair and Swain that temperature alone cannot explain all of this decline, a point that we made in our original paper. However, we are at a loss to suggest an additional cause. While Sinclair and Swain suggested that density-dependent effects might be responsible, such effects were examined and later rejected by the stock assessment working group responsible for the area, owing largely to the fact that both growth rates and stock biomass

have declined in concert in the past 10 years (Department of Fisheries and Oceans 1996).

Sinclair and Swain reported that they had difficulty reproducing our growth calculations for European cod stocks, and in some cases, were unable to locate the cited references. We are at a loss to explain their difficulty, as we have rechecked the accuracy of both our calculations and our references. All were correct as originally presented. Perhaps their problem stemmed from the error in their growth increment calculations noted above. As for their statement that we selected for presentation only those ages that matched our model predictions, we would be pleased to provide the growth comparisons for all age groups in each stock to any interested reader: such an examination would show that in each of the stocks we selected for presentation the oldest available age group was well represented within the age–frequency distribution.

We agree with Sinclair and Swain that what were termed "stock" effects in Table 2 of Campana et al. (1995) contributed significantly to the growth model. However, ambiguous terminology on our part has confused the issue. While they mistakenly attributed the term stock effects to genetic differences in growth rate, the intended meaning of the term was stock area effects, defined as the difference in growing days (loosely defined here as the number of degree-days over the temperature range in which the stock can be found) among stock areas. Such differences can be very large. For example, Swain and Kramer (1995) reported that 95% of the Gulf of St. Lawrence cod stock was found in temperatures of –0.25 to 9.7°C, a range that excludes temperatures present in the surface waters of the Gulf for 6 of the 12 months (Petrie 1990). On the other hand, 90% of the cod in the Bay of Fundy were found at temperatures between 4 and 12°C (Page et al. 1994), a range that excludes only one monthly average temperature in the environment (Petrie et al. 1996). Because temperatures tend to be highest during the summer (when the temperatures for the growth model were collected), and because the Bay of Fundy has the highest year-round temperatures, it follows that the research vessel temperature index would underestimate the growing period in the Bay of Fundy relative to the Gulf and other areas. Thus, it is not at all surprising that the model residuals were positive in the Bay of Fundy, and it is completely unnecessary to invoke hypothetical genetic differences. We would also note the results of two studies reporting the results of rearing genetically and environmentally distinct cod stocks together under identical environmental conditions. In both instances, the differences in growth rate were significant but small (<10%) (Naevdal et al. 1992; Svasand et al. 1996). Genetically induced differences in growth rate would have to be much larger (~300%) to be able to explain the observed growth rate variation in Scotian Shelf cod stocks.

Sinclair and Swain were critical of our decision to exclude stations at depths of less than 50 m in the Gulf of St. Lawrence, but do not appear to have considered the consequences of their proposal. The following data were drawn from Petrie (1990) and Petrie et al. (1996): at depths of 0, 50, and 100 m, summer temperatures were 13.0, 0.6, and 0.7°C, respectively, in the southern Gulf, and 10.4, 8.0, and 7.3°C, respectively, in the Bay of Fundy. Because the median temperature of association for cod in the Gulf in summer is 0.85°C (Swain and Kramer 1995), it is clear that surface water temperatures of 13°C are not an appropriate index of living temperature for southern

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Gulf cod. It is for that reason that Gulf cod captured at such shallow depths were not included in the growth model, despite the fact that their length at age was not significantly different from that of cod captured below 50 m. On the other hand, temperatures throughout the water column were much more similar in the Bay of Fundy, reflecting the fact that the waters in that area were much less stratified, and suitable for growth all year round. Thus we felt, and still feel, that elimination of depths of less than 50 m from the entire Scotian Shelf would have very little impact on most areas, but their exclusion makes the temperature index for the southern Gulf far more realistic.

Despite our disagreement with many of the points raised by Sinclair and Swain, we continue to support the general premise that factors other than temperature must be contributing to the observed spatial and temporal patterns in cod size at age. Yet the search for these alternative factors has, to this point, been disappointing. Sinclair and Swain suggested three potentially important modifiers of cod growth: density dependence, genetics, and fishing. Of these, evidence of density-dependent growth has been noted only in the southern Gulf of St. Lawrence cod stock, but even there, growth rates have remained low despite very low stock abundance (Sinclair et al. 1996). There has been no inverse relationship reported between growth rate and stock biomass in the other cod stocks of the Scotian Shelf; indeed, the opposite correlation is now present on the eastern Scotian Shelf. As for genetic effects, the two studies on cod reported only small (<10%) growth differences between genetically distinct stocks reared together under identical environmental conditions (Naevdal et al. 1992; Svasand et al. 1996). The final possibility, fishing effects, is much more difficult to evaluate, as it involves long-term genetic selection. However, it seems reasonable to acknowledge its existence, even if we are not yet able to quantify its impact.

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