Invited reply

Evolution of growth in Gulf of St Lawrence cod: reply to Heino *et al.*

1. INTRODUCTION

In a recent paper (Swain *et al.* 2007), we examined the evidence for a genetic response to size-selective mortality in southern Gulf of St Lawrence cod, using data on back-calculated length at age and a quantitative genetics model. We used the model

$$\Delta L_4 = h^2 S + \beta \Delta E + \varepsilon, \quad (1.1)$$

where ΔL_4 and ΔE are the differences in length-at-age 4 years and in environment (Δd , density and/or Δt , ambient temperature at ages up to 4 years) between an offspring cohort and its parents, S is the selection differential experienced by parents between 4 years of age and spawning, h^2 (heritability) and β are regression coefficients, and ε is random error (assumed to be normally distributed with a mean of zero). We observed a significant ($p < 0.05$) positive effect of S on ΔL_4 , supporting the hypothesis that there has been a genetic response in this population to size-selective fishing. Heino *et al.* (2008) commented on our paper and questioned our conclusions. In this reply, we address their criticisms and, following their suggestions, provide further support for our conclusions.

2. MODEL INTERCEPT

The main criticism raised by Heino *et al.* is that our models did not include an intercept. Our rationale for not including an intercept is that if there is no difference in environment between offspring and their parents and the selection differential is zero, then ΔL_4 should be zero. An intercept would imply a steady change in length between offspring and their parents in the absence of selection for L_4 or changes in the environmental factors considered in the model. One way to examine the adequacy of the no-intercept model is to regress the observed ΔL_4 against those predicted by the model. We did this for the two models in Swain *et al.* (2007) that were ranked as the best models based on Akaike's information criterion. The best model included terms for S , Δd and Δt (model 1), and the second-best model included terms for S and Δd (model 2). In both cases, the intercept of the regression of observed values on predicted values did not differ significantly from 0 ($p = 0.28$ and 0.09 , respectively). This supports the exclusion of an intercept from these models, as expected on theoretical grounds.

Heino *et al.* note that in our data, S and an intercept will have similar effects because for much of the time-series ' S varies little and is always negative'. Controlling for differences in density and temperature between offspring and their parents, there is a tendency in our data for offspring to be shorter than their parents at an age of 4 years.

The accompanying comment can be viewed on page 1111 or at <http://dx.doi.org/10.1098/rspb.2007.1429>.

This tendency can be accounted for by including an intercept in our models or by replacing the intercept with S . The first approach leaves this tendency unexplained. The alternative approach demonstrates that a genetic response to selection can account for much of the tendency for offspring to be shorter than their parents. In our view, this latter approach is clearly a step forward in understanding the causes of changes in length-at-age of southern Gulf cod.

Heino *et al.* note that this difficulty in distinguishing between an S -term and an intercept may be common in studies of directional selection. A significant intercept term identifies a tendency for steady change between offspring and parental phenotypes but provides no explanation for this change. An explanation is provided if the intercept can be replaced by an S -term. A significant positive relationship between S and the change in length between offspring and parents supports the hypothesis of a genetic response to selection, even if the effect of S cannot be distinguished from that of an intercept term because S varies little from a constant value.

3. DATA SUBSETTING

Heino *et al.* fit models to our data in sliding 10-year windows. They note that no models are significant when restricted to 10-year windows in the second half of the time-series, when there are no strong trends in ΔL_4 . They appear to attribute this to some fundamental change in the influences on ΔL_4 . However, the lack of significance in models restricted to the second half of the time-series can be accounted for by confounding between the factors affecting ΔL_4 . Δd is negative from the mid-1980s to the early 1990s. Since the parameter for this effect is negative, the effect of Δd on ΔL_4 is positive during this period, while the effect of S is negative. Thus, the two effects tend to cancel each other and ΔL_4 fluctuates around a value near 0. This illustrates the difficulty in disentangling effects of partially confounded factors with limited data. Potential explanatory factors are frequently confounded in natural systems, and it is important to use as much data as possible to disentangle their effects.

4. REPRODUCTION AND GROWTH

We analysed variation in length at an age of 4 years because this is the earliest age at which southern Gulf cod are representatively sampled with respect to length. During our study period, a substantial portion of 4-year-old cod was mature. Thus, their length will be affected by their maturation schedule and reproductive investment as well as their growth capacity, as noted by Heino *et al.* The important point here is that effects that we

Figure 1. The difference in mean length at age (a) 3 years or (b) 4 years (Swain *et al.* 2007) between offspring cohorts and their parental cohorts, for fish observed as 4-year-olds. Circles, observed values; lines, values predicted by model 2 in the text.

attribute to a genetic response to size selection may instead reflect confounded changes in maturation schedule or reproductive investment, factors not considered in our analysis. In southern Gulf cod, age at 50% maturity declined sharply in the 1960s and early 1970s, from values near 6–7 years to values near 4 years for females, but has shown no strong trend since then, fluctuating around values near 4–4.5 years (D. P. Swain 2006, unpublished analyses). Our analyses are restricted to offspring cohorts produced since 1977. Thus, declines in length that we attributed to a genetic response to size selection do not appear, instead, to be attributable to a trend in maturation schedule. However, we have little data on trends in reproductive investment in this population. Heino *et al.* suggested using length at age 3 years, when few fish are mature, as the evolving trait in order to reduce potential confounding effects of reproduction. We have followed their suggestion, using as the dependent variable the change in mean back-calculated length at 3 years in fish observed as 4-year-olds. The results were very similar to those in the original analysis (figure 1). For model 2, there was a significant positive effect of S ($p=0.0001$) and a negative effect of Δd ($p=0.0017$). Comparisons between observed and predicted values again did not indicate a need to add an intercept to the model ($p=0.16$). These results indicate that changes in maturation schedule and reproductive investment do not appear to be important confounding effects in this analysis, consistent with the lack of trend in age at maturity over the study period.

5. CONCLUDING REMARKS

Heino *et al.* conclude that in order ‘to determine the role of S , one would have to assess and control for... unaccounted environmental trends’. As noted in our paper, it will never be possible to exclude the possibility of ‘unaccounted environmental trends’ in any study on populations in the wild. We have controlled for population density and ambient temperature, the environmental factors demonstrated to affect length-at-age in this population in

previous studies (Sinclair *et al.* 2002; Swain *et al.* 2003). It would also be desirable to incorporate variation in prey availability in our analysis (e.g. Edeline *et al.* 2007), but the required index is not available. Nonetheless, the effect attributed to S (or an intercept) does not appear to be attributable to variation in prey availability. Most of the preys of southern Gulf cod (Hanson & Chouinard 2002) have increased in biomass over our study period (Benoît *et al.* 2003; D. P. Swain, unpublished analyses). Thus, the observed trend in prey availability should cause offspring to grow faster, not slower, than their parents.

In conclusion, we have shown that changes in the length of southern Gulf cod between offspring cohorts and their parents are positively correlated with the selection differential experienced by parents, controlling for differences in density and/or ambient temperature between offspring and parents. In our view, this is strong support for the hypothesis that there has been a genetic response to length selection in this population (i.e. it is the result predicted by the hypothesis). These results do not ‘prove’ the hypothesis, but proof will never be possible. We will continue to seek alternate hypotheses to explain the continued slow growth of southern Gulf cod despite warm ambient temperatures, low cod density and high prey availability. However, the hypothesis supported by the data that are currently available is that this slow growth reflects a genetic response to size-selective fishing. In our original paper, this was demonstrated for length at an age of 4 years. Following the suggestion by Heino *et al.*, we have now demonstrated that this is also true for the length at an age of 3 years, when the potential for confounding effects of reproduction is largely eliminated.

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