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Evolution of Growth in Gulf of St Lawrence Cod?

Mikko Heino (mikko.heino@imr.no)
Loïc Baulier (loic.baulier@imr.no)
David Boukal (david.boukal@imr.no)
Erin Dunlop (erin.dunlop@imr.no)
Sigrunn Eliassen (Sigrunn.Eliassen@bio.uib.no)
Katja Enberg (katja.enberg@bio.uib.no)
Christian Jørgensen (christian.jorgensen@bio.uib.no)
Øystein Varpe (oystein.varpe@bio.uib.no)

Approved by

Ulf Dieckmann
Leader, Evolution and Ecology Program

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Contents

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Mikko Heino[1,2,3†], Loïc Baulier[1,2], David S. Boukal[1,2], Erin S. Dunlop[1,2], Sigrunn Eliassen[2], Katja Enberg[1,2], Christian Jørgensen[2], and Øystein Varpe[2,4]

[1] Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway
[2] Department of Biology, University of Bergen, P. O. Box 7800, N-5020 Bergen, Norway
[3] International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria
[4] The University Centre in Svalbard, P. O. Box 156, N-9171 Longyearbyen, Norway

[†] Author for correspondence. E-mail: mikko.heino@bio.uib.no

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Fishing is often size-selective such that the likelihood of capture increases with body size. It has therefore been postulated that fishing could favour evolution of slower growth because smaller size would reduce exposure to fishing gear (e.g., Ricker 1981). The recent study by Swain et al. (2007; hereafter referred to as SSH) makes a valuable attempt to demonstrate such an effect on length-at-age of the southern Gulf of St Lawrence cod (*Gadus morhua*). The strength of their study lies in an innovative combination of three elements. First, as the evolving trait they used length-at-age 4 years, an age at which cod are representatively sampled but have experienced little fishing mortality. Confounding demographic effects of size-selective fishing were therefore avoided. Second, they had time series of temperature and population density, both possibly affecting length-at-age through phenotypic plasticity. Finally, and as the most innovative element, they linked their approach to quantitative genetics theory. Using a modified breeder's equation, they modelled changes in length-at-age 4 as a function of genetic and environmental components: $\Delta L_4 = h^2 S + \beta \Delta E + \varepsilon$. Here ΔL_4 and ΔE are differences in length-at-age 4 and environment, respectively, between the focal cohort and its parent generation. S is the selection differential (difference in length-at-age 4 between fish observed at age 4 and those observed at reproducing ages). Heritability h^2 and parameter β are regression coefficients, and ε is a normally distributed error term with zero mean. SSH assumed that the environment can be described by changes in population density Δd and temperature Δt. The key point is that a significant effect of S on ΔL_4 would indicate an evolutionary response in length-at-age 4.

SSH's statistically favoured regression model was one including both S and Δd; they concluded that the data suggested an evolutionary response to fishing. Of course, as SSH readily pointed out, one cannot rule out the existence of alternative and untested factors. Here, we comment on some caveats in the analysis by SSH. We do not challenge their novel approach, but question some key assumptions and the strength of their conclusions.

Length-at-age is not the same as growth.
SSH analyzed changes in the mean length of 4-year-old cod, and concluded that their results support the hypothesis of a genetic decline in growth. The transition from length-at-age to growth is, however, non-trivial. An individual's length-at-age depends on the environment

and at least three life-history traits: growth capacity, maturation schedule, and reproductive investment. The *growth capacity* reflects an individual's propensity to forage and the efficiency with which it turns food into body mass. Growth capacity is a quantitative trait under genetic control that can respond to harvest-induced selection (Conover and Munch 2002). Individuals with different growth capacities would have different length-at-age trajectories before maturation even in the same environment. After *maturation*, growth slows down or even stops, because *reproductive investment* channels resources away from growth. Length-at-age measured at or after first reproduction hence depends on all three traits. Only changes in growth capacity equate to what is strictly meant by evolving growth rate. For 1990 to 1995, data on the southern Gulf cod stock reveal that 35-60% of males and 10-50% females were mature at age 4; maturation data outside this 6-year window are unfortunately unreliable and cannot unravel temporal trends (Trippel et al. 1997). To reduce the confounding effects of changes in reproductive investment or the proportion of mature fish, we thus suggest that lengths-at-ages earlier than 4 years be used as the evolving trait; for example, age 3 data is available for the entire time series.

Lack of intercept is not trivial

None of the regression models considered by SSH included an intercept. The logic is that if the environment does not change and the selection differential is zero, ΔL_4 will not change and the intercept should be zero. Hidden assumptions are that all relevant environmental variables are included and that the data are unbiased.

To test whether these assumptions hold, we added an intercept to SSH's favoured model ($\Delta d + S$); it was significantly different from zero (–0.98; p=0.03) and, at the same time, S became insignificant (p=0.34). A model with Δd and an intercept C also has a lower AIC value than SSH's favoured model, and S is not significant for any other combination of variables. A significant C suggests a negative component to change in length that cannot be statistically ascribed to any of the three explanatory variables.

Low contrast makes results fragile

The first and second half of the time-series of S and ΔL_4 differ qualitatively (Fig. 1a). To check robustness of the results presented by SSH, we estimated a range of alternative models for sliding windows of 10 successive cohorts (Fig. 1b; Δd and Δt are strongly correlated and we present only Δd as the results are similar). In the first sliding windows, a range of models can explain the data well (Fig. 1b). Ranked with AIC, SSH's favoured model is among the two best models, but only for the first window does it outperform the model where S is replaced by C. From the window beginning with cohort 1984, all models become non-significant and the observed change in length can best be interpreted as noise. At the same time, the estimated heritability dropped from between 0.5 and 0.7 to ~0 (Fig. 1c), which could be due to the erosion of additive genetic variance. However, it seems unlikely that such high levels of heritability could be purged in 1-2 cohorts and it does not explain why explanatory variables other than S loose significance at the same time (Fig. 1b).

These patterns illustrate two problems. The first and well-known problem is the difficulty of partitioning statistical effects between correlated variables. The second problem

is more specific to the present study, but may pose similar challenges to other studies of directional selection. In a model without C, any patterns in the data must be ascribed to the explanatory variables of the model, and here it happens that the pattern is absorbed by S. For much of the time series, S varies little and is always negative (Fig. 1a); S or C will therefore have similar effects. One would wish S to show more pronounced patterns, but as this is not the case, the problem appears statistically unresolvable.

In conclusion, the new approach of Swain et al. (2007) holds promise because it simultaneously accounts for the effects of the environment and selection on length-at-age. We look forward to seeing their methodology applied to other fish populations. However, it remains inconclusive as to whether fisheries have induced evolution of reduced growth capacity in the Gulf of St. Lawrence cod. Nevertheless, there are changes in length-at-age that cannot be explained by the considered environmental variables. To determine the role of S, one would have to assess and control for other factors, such as observation error or unaccounted environmental trends. Neither S nor ΔL_4 are directly observable, but are based on model-derived quantities and merge many sources of information. At the same time, the Gulf of St. Lawrence has undergone large environmental changes, the effects of which might not be captured by density and temperature alone.
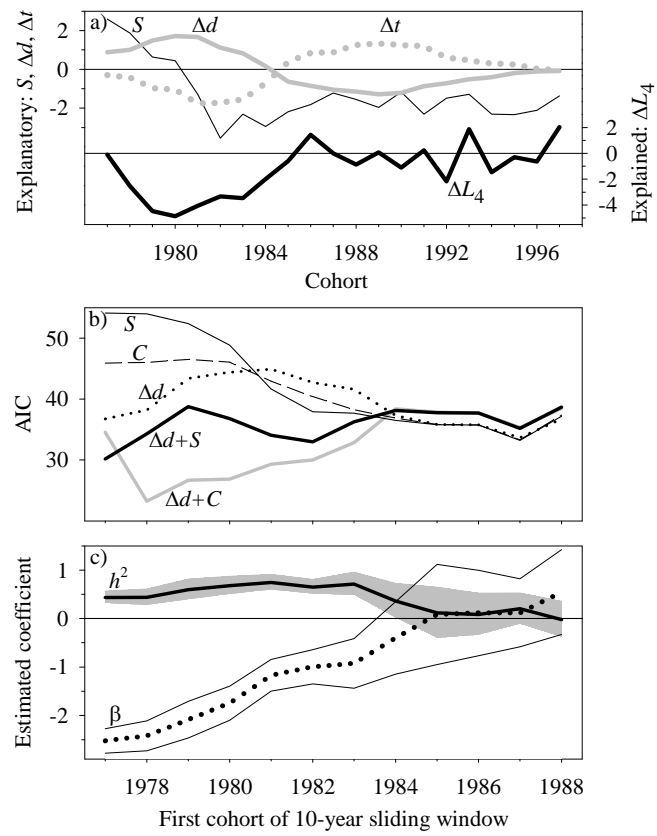
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1 **Figure 1.**

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