



REPLY TO ENBERG AND JØRGENSEN:

Ecology and evolution both matter for explaining stock dynamics

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Enberg and Jørgensen (1) state that the “conclusion that fishing-induced evolution is negligible follows from model assumptions”. First, it goes without saying that results of model-based studies all follow from model assumptions. Second, we conclude that evolution has not been negligible (2). In fact, fisheries-induced evolution appears to have been required to prevent stock collapse. Furthermore, it is the interactions between ecological and evolutionary dynamics that are critical for explaining observed trends in Northeast Arctic (NEA) cod. Below, we address Enberg and Jørgensen’s other points in turn.

Emergent Heritabilities

Emergent heritabilities for the four directly evolving traits remain close to their initial values (0.20 ± 0.01). For age at maturation, emergent heritabilities are also far from small, with ranges 0.28–0.31 and 0.12–0.21 among five replicate model runs for the historical and contemporary density-dependent growth models, respectively (Fig. 1). These values are well in line with existing literature, including citations in ref. 1, and are much higher than what Enberg and Jørgensen estimate from a model not parameterized for NEA cod.

Maturation Evolution

Our model shows that observed trends in NEA cod’s age and length at maturation can be explained with less growth evolution when growth is strongly density dependent than when growth is weakly density dependent. The statistical analysis of maturation evolution reported in ref. 3 used neither of these assumptions. We agree with Enberg and Jørgensen that this highlights an important opportunity for investigating whether assumptions underlying the dynamical

analysis in ref. 2 or the statistical analysis in ref. 3 are more realistic.

Maturation Variation

As described in our article (ref. 2, discussion, p. 15033, and sections S7 and S8), an interesting direction for future research involves exploring alternative approaches to the joint scaling of individual-level probabilistic maturation reaction norm (PMRN) widths, population-level PMRN widths, and population-level genetic variances of PMRN traits. We appreciate Enberg and Jørgensen’s agreement with this prospect.

Density-Dependent Growth

Fig. 2 shows estimates of contemporary density-dependent growth resulting when temporal variations in environmental factors are only partly accounted for. Contrary to what Enberg and Jørgensen hypothesize, this mostly leads to stronger density dependence, which makes the contemporary growth model in our study conservative. Fig. 2 also shows that, contrary to Enberg and Jørgensen’s implied claim, the growth model estimated for 1978–2009 provides a reasonable description of growth throughout 1932–2009, that is, also for the early years when the stock’s biomass was much higher.

Conclusions

In the end, our conclusions are straightforward and remain unchanged: for weakly density-dependent growth, explaining the observed stock dynamics requires evolution of faster growth and earlier maturation, whereas for more strongly density-dependent growth, less evolution is inferred. Although we commend Enberg and Jørgensen’s complementary efforts based on a “cod-like” model, understanding the eco-evolutionary dynamics of an

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actual stock (in this case NEA cod), requires integrating the available stock-specific data on fishing pressures, life history, density dependence, and phenotypic plasticity with a quantitative

analysis of fisheries-induced evolution. Our study steps up to this challenge and will hopefully stimulate further scientific investigation.

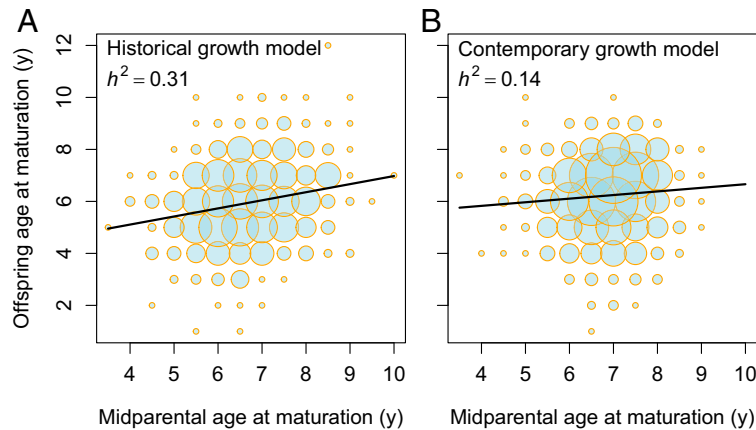


Fig. 1. Heritabilities of age at maturation in our model for (A) the historical growth model and (B) the contemporary growth model. Emergent heritabilities (h^2) are estimated for the two growth models by regressing the age at maturation of offspring individuals on the mean age at maturation of their parents. The median of five replicate model runs is shown for each model, with circle sizes being proportional to counts of values for 1995–2005. The lines indicate the resultant linear parent–offspring regressions, with their slopes equaling h^2 .

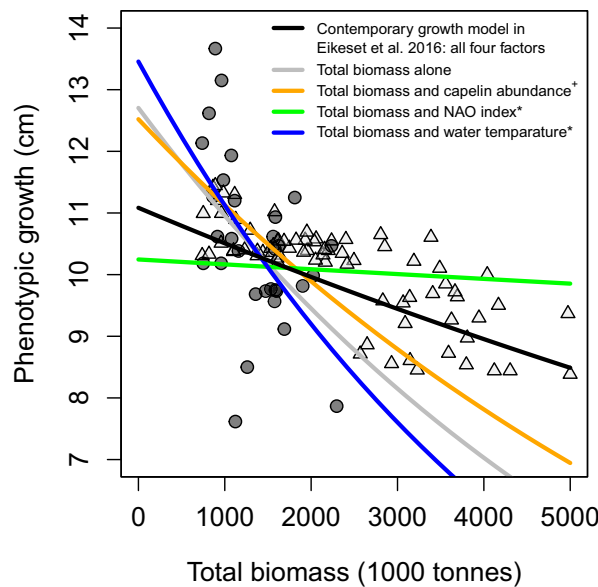


Fig. 2. Alternative density-dependent growth models. The contemporary growth model used in ref. 2 (black line), accounting for three environmental factors [North Atlantic Oscillation (NAO) index, water temperature, and log-transformed capelin abundance] in addition to the total biomass of NEA cod at ages 3 y and older (horizontal axis), is compared with four simpler models accounting for at most one additional environmental factor. Models are estimated based on growth data from the contemporary period (1978–2009; circles); growth data from the remaining period (1932–1977) are shown for reference (triangles). Interactions among factors are included when significant (*) and excluded otherwise (+). Model predictions are depicted for zero NAO index and for the means of water temperature and capelin abundance during 1978–2009.

1 Enberg K, Jørgensen C (2017) Conclusion that fishing-induced evolution is negligible follows from model assumptions. *Proc Natl Acad Sci USA* 114:E4321.
 2 Eikeset AM, et al. (2016) Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. *Proc Natl Acad Sci USA* 113:15030–15035.
 3 Heino M, Dieckmann U, Godø OR (2002) Reaction norm analysis of fisheries-induced adaptive change and the case of the Northeast Arctic cod. Working paper ICES Document CM 2002/Y:14 (ICES, Copenhagen). Available at hdl.handle.net/11250/100545.