# Understanding the causes of maturation shifts in gadoid populations

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### Summary

This study examined the importance of timing, energetic state and temperature on maturation commitment in haddock and cod. The autumn equinox appears to be an important signal for the activation of the brain-pituitary-gonad axis. Experimental trials in haddock found that temperature and growth in the months preceding this time can substantially promote maturation commitment. The relevance of these factors to explaining maturation change in wild haddock was explored using a stochastic, individual-based simulation model of growth and maturity. Although the model explained some of the intra-annual variation in maturity at age, it could not account for the magnitude of the positive trend. Rather an increasing departure between predicted and observed proportion mature over recent decades suggested a long-term decline in the maturation – state threshold, suggestive of a genetic change. Common environment experiments suggest that differences in maturity at size that have developed between adjacent populations do have a genetic basis.

### Introduction

Although often described in terms of size and age, maturation (i.e. onset of puberty) involves the activation of the brain-pituitary-gonad axis modulated through factors such as growth, adiposity, food intake and temperature at critical periods of the year (Taranger *et al.*, 2010). There is also a heritable component to maturation, as evident from family-level differences in the threshold levels (Gutierrez et al., 2014). In this study we undertook experiments to determine the critical period and the proximate conditions influencing maturation inhibition in haddock and cod. Using this information to parameterise a stochastic individual based model, we considered whether changes in maturation schedules of haddock could be explained by determined relationships between maturity, energetic state and environmental conditions.

## Materials and Methods

Maturation timing was examined from monitoring changes in gonad development, follicle stimulating hormone  $\beta$  transcript expression profile, size and condition (see Tobin et al., 2010). A second experiment considered the effects of temperature (8, 10 and 12°C) on maturation (Tobin and Wright, 2011). A third experiment compared maturation commitment under common conditions in two haddock (Wright and Tobin, 2013) and two cod (Harrald et al., 2010) populations whose field derived size based maturation reaction norms differed. A stochastic, individual-based simulation life history model was used to predict changes in maturation in west North Sea haddock. Model parameters were derived using a Bayesian approach using experimentally and field derived relationships as prior distributions.

### **Results and Discussion**

Maturation commitment was evident from the elevated expression of FSH- $\beta$  in September followed by the appearance of cortical aveoli oocytes in October indicating that the critical period ended by the autumn equinox. Temperature differences during the critical period explained most of the accountable variation in maturation, with the proportion maturing by November in the 12°C treatment being over twice that of the 8°C treatment (Figure 1). The effect of body size and energy accumulation on maturation was greatest early in this critical period.

The life history model predicted that warming would generally have a significant positive effect on the probability of maturing, although the magnitude of change expected from the simulations was substantially lower than the increase in the proportion mature observed (Figure 2). The disparity between the rate of change between the observed and predicted maturity at age suggests there has been a substantial shift in the threshold energetic state linked to maturity commitment, although warming clearly has been an important contributory influence. Population differences in the threshold energetic state determining maturity commitment in haddock (Wright and Tobin, 2013) and cod (Harrald *et al.*, 2010) reared in a common environment can explain present day regional differences in probabilistic maturation reaction norms that have developed following several decades of divergence (Wright *et al.*, 2011a,b).



Figure 1. Estimates of proportion mature haddock predicted by length in June, growth rate June- September and temperature regime (redrawn from Tobin and Wright, 2011)



Figure 2. Linear regression fits for observed (black line) and predicted upper and lower 95% credible intervals (blue lines) for proportions of haddock maturing at age 2 against cohort (redrawn from Wright et al., in press).

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