

# An Explicit Model of the Adaptive Evolution by Mutation of the Coccolithophore *Emiliana huxleyi*

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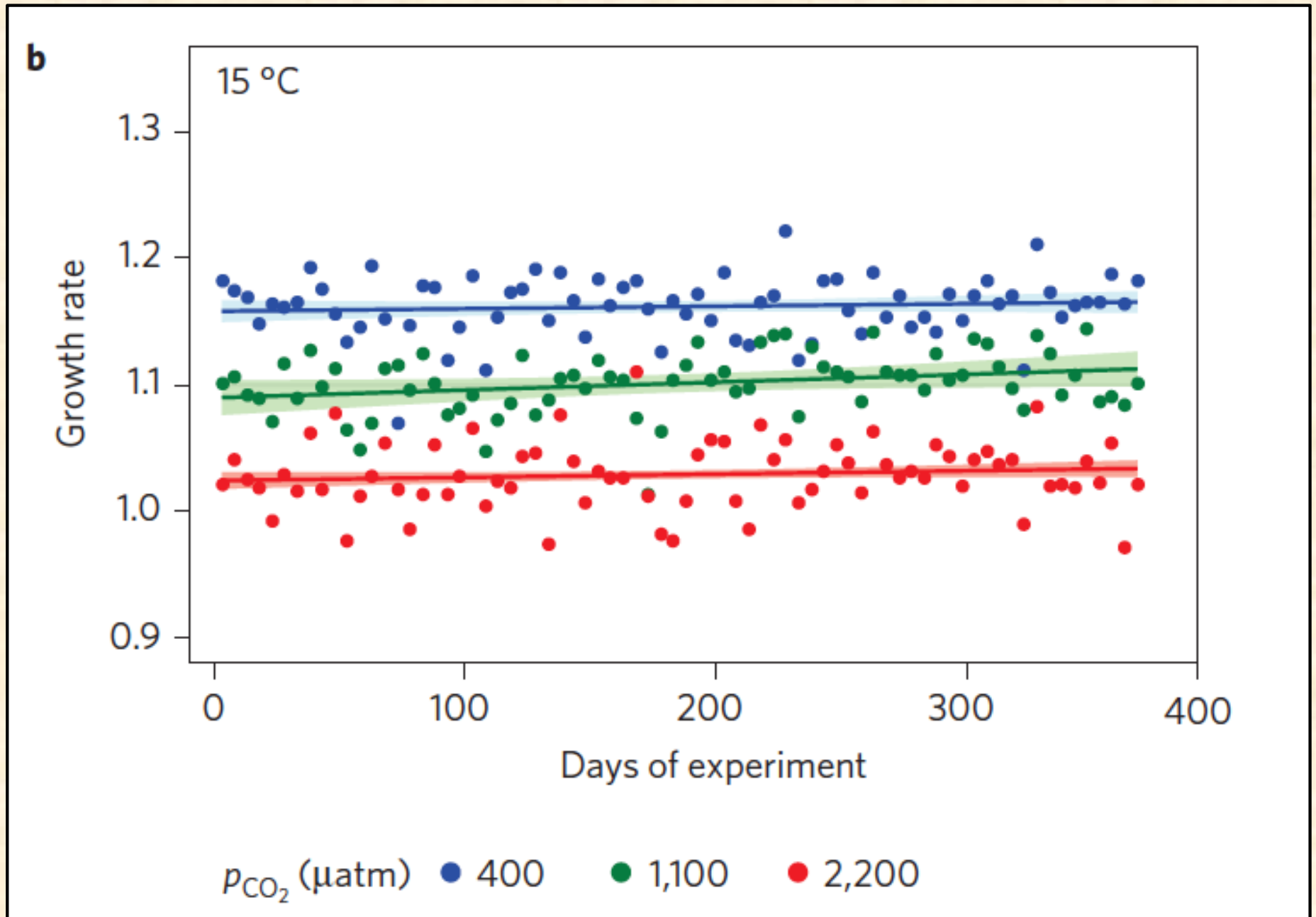


# Based on the Experimental Laboratory Results of:

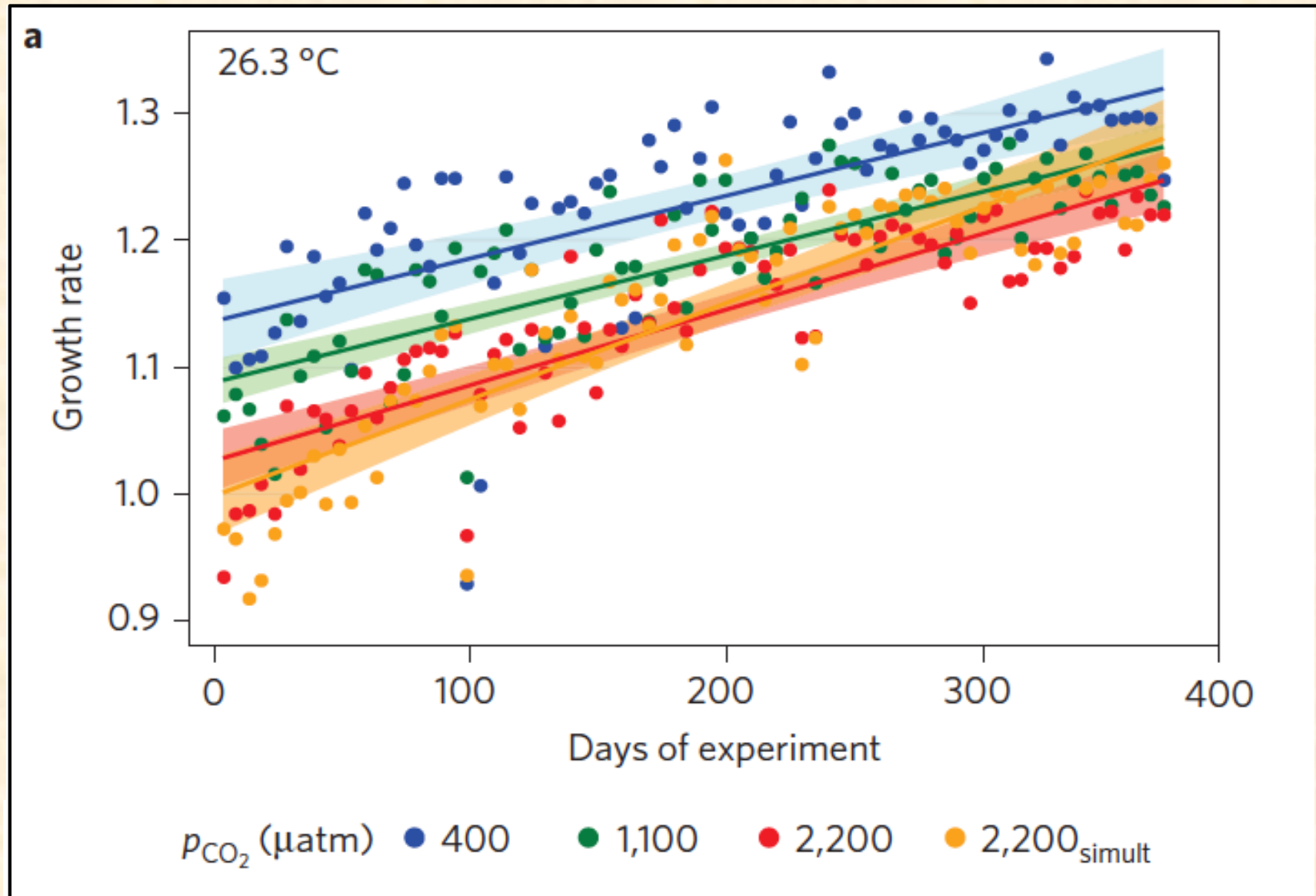
Schlüter et al., 2014. Adaptation of a globally important coccolithophore to ocean warming and acidification, *Nature Climate Change*, DOI: 10.1038/NCLIMATE2379

- started from a single cell isolated from Norwegian coastal waters
- 5 replicates grown in batch cultures at 15°C for 3 years (~1500 generations)
- new cultures started every 5 days with  $10^5$  cells
- after 3 years, temperature raised 1 °C each day to a final temperature of 26.3°C
- 5 replicates grown for 1 year at 26.3°C (~460 gens)

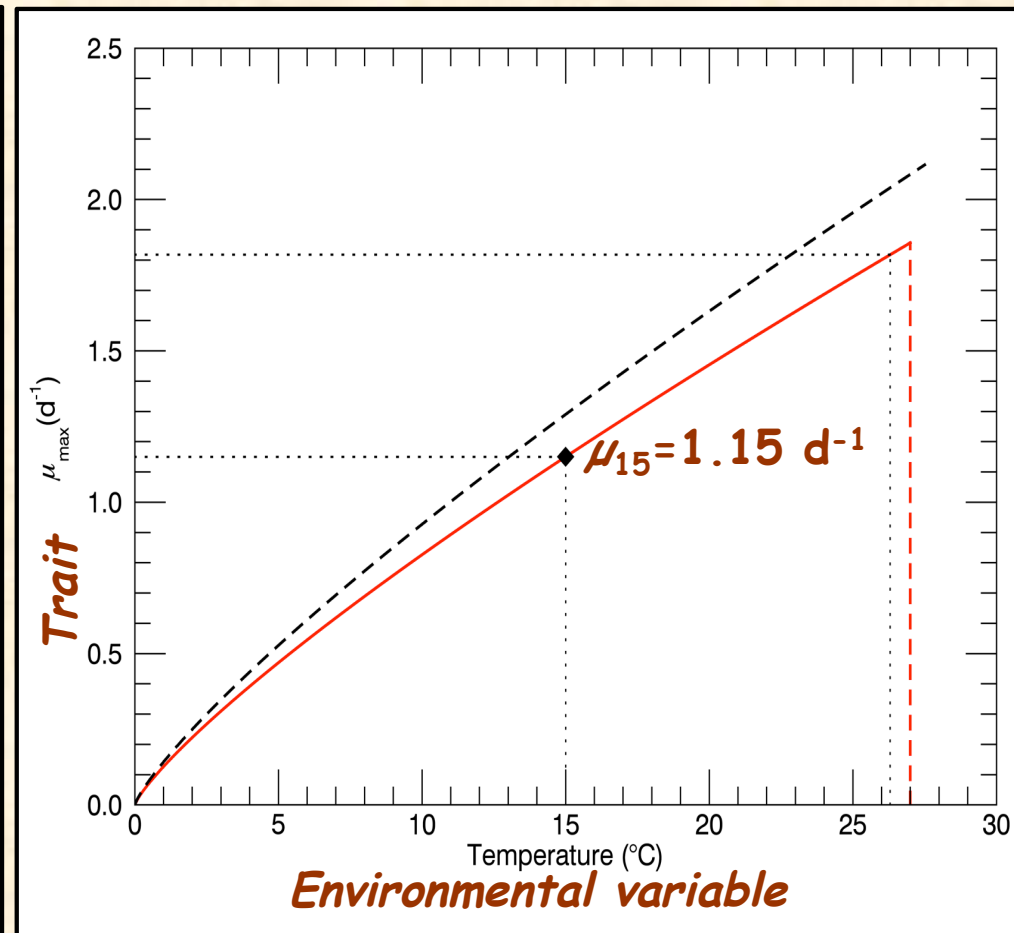
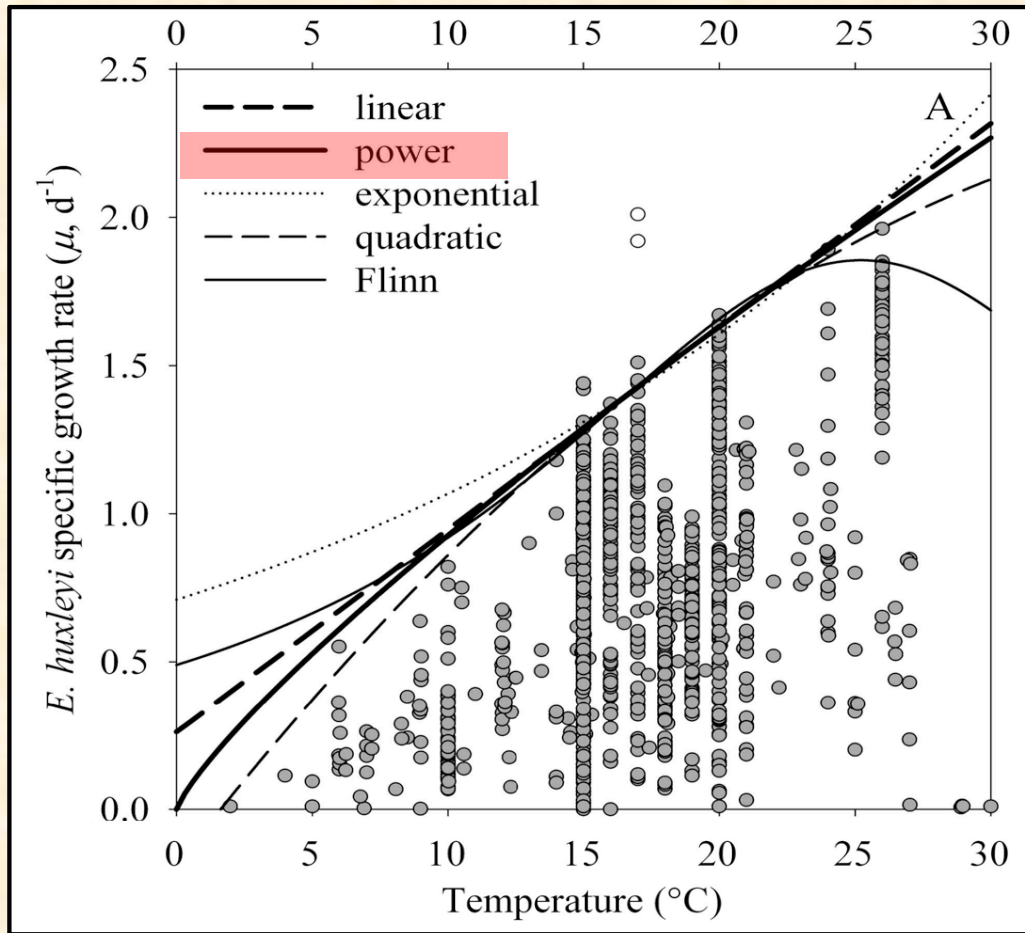
# Fourth Year at 15°C



# Growth Rate at 26.3°C Gradually Increases over 1 Year Due to Mutation?



# Maximum Growth Curve(s) for *Emiliana huxleyi* (Fielding 2013, L&O)

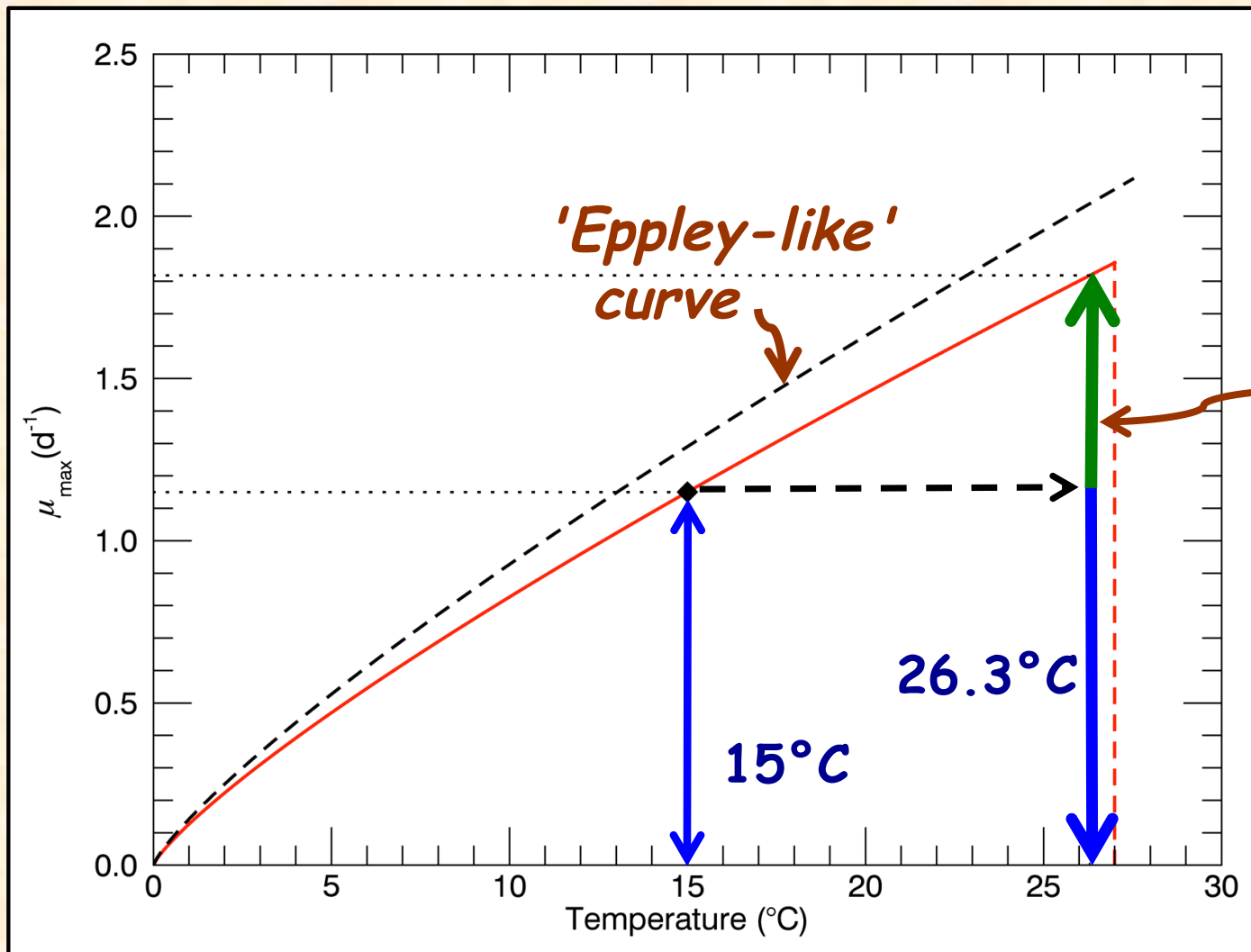


'Eppley-like' curve for single species *E. huxleyi*:  
*Eppley, 1972, Fish. Bull. 70(4)*



# 'Mutation' Experiment: Random Mutation of Growth Rate along Blue Line:

After 3 years, shift from 15°C to 26.3°C:



'Mutants' with higher growth rates (higher 'fitness') should become relatively more abundant

# Model Setup

- The model is a simple exponential growth equation for each genotype  $i$ :

$$\frac{dB_i}{dt} = \mu_i N_i$$

- The 'fitness' of a mutant genotype  $m$  relative to the ancestor genotype  $j$  can be expressed as

$$S_{ma} = (\mu_m - \mu_a) / \mu_a *$$

*\* Lenski et al. 1991, Am. Nat. 138*

'Normalized' to  $10^5$  cells every time step:  
5 per day vs every 5 days in Schlüter et al.

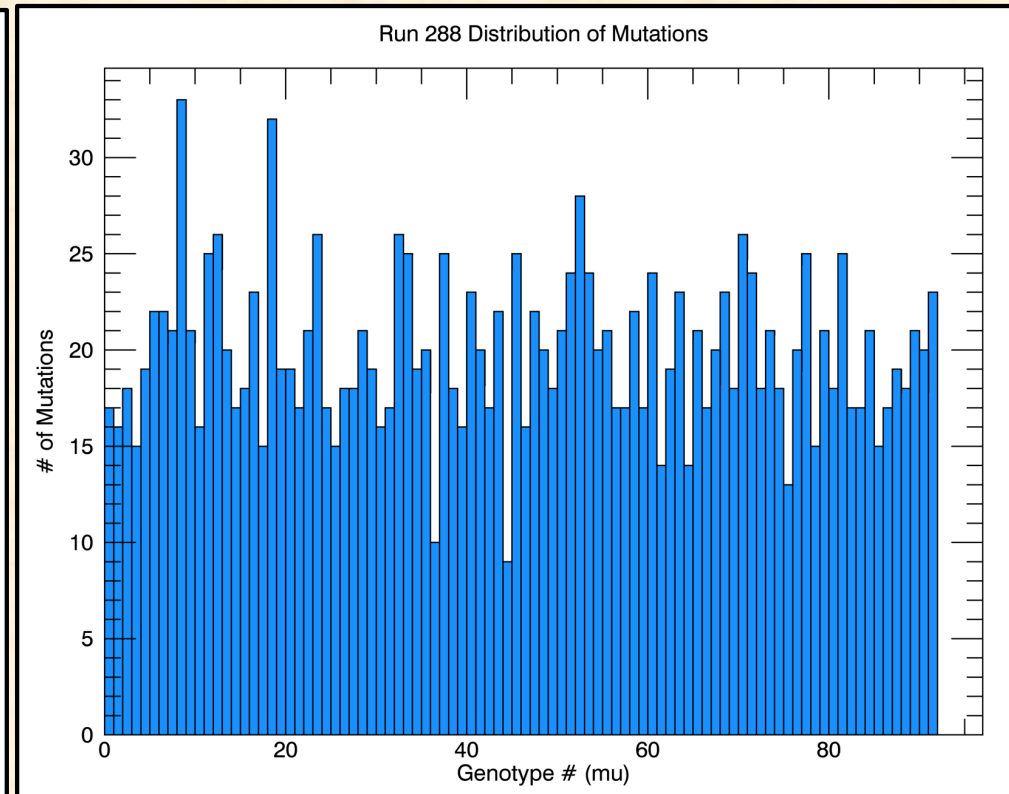
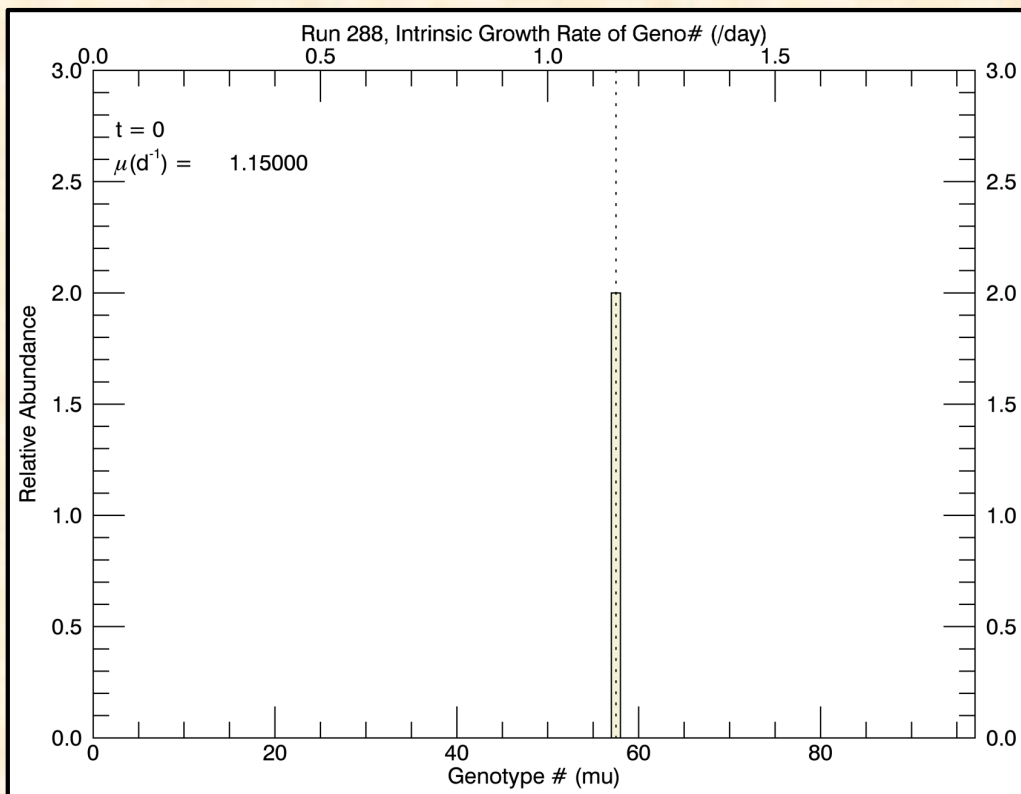
# Magnitude and Rate of Mutations

- Evolutionary theorists recently favor large magnitude mutations [e.g. H.A. Orr, 1998, 2005]: - hence first try a 'flat' PDF for random mutations of growth rate
- *"Experimental measures of mutation rates in phytoplankton range from  $10^{-5}$  to  $10^{-7}$  mutations per cell per generation"* [Huertas et al., 2011, *Proc. Roy. Soc. B*].
  - Schlüter et al. (2014) maintained batch cultures for 5 days, starting a new batch from  $10^5$  cells then reaching concentrations of  $\sim 10^7$  cells after 5 days

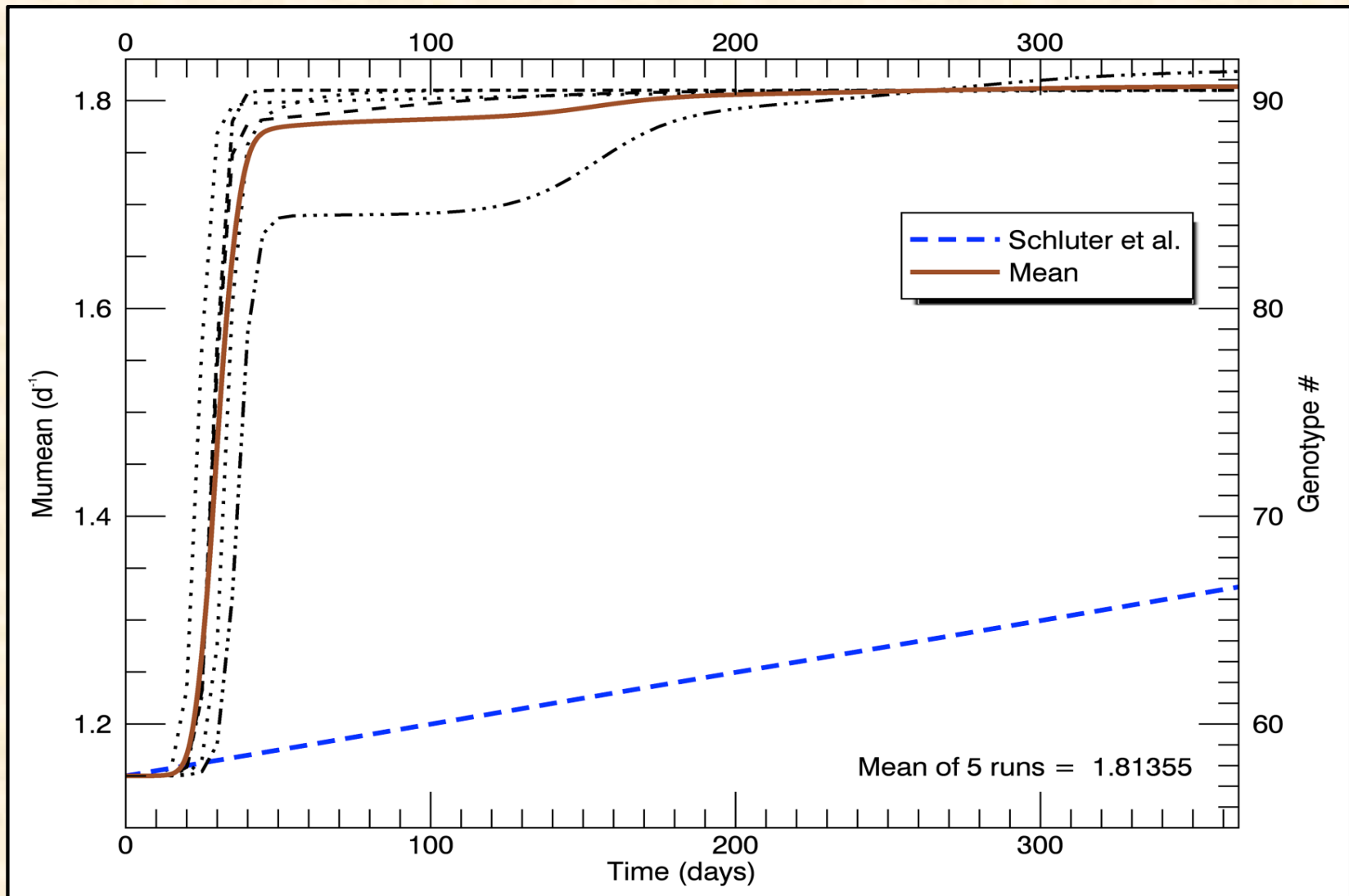


# First Experiment of 1 Year at 26.3°C

- 'flat' pdf of random mutations across 93 genotypes #0 to #92 (each 0.02 d<sup>-1</sup> wide) spanning the range of  $\mu$  from 0 to 1.84 d<sup>-1</sup>, the value for 26.3°C
- initial genotype #57 with  $\mu = 1.15$  d<sup>-1</sup>  
the genotype after 3 years at 15°C



# Mutation that Occurred to Highest Genotype Quickly Dominates, After a Lag



5 simulations, each with different random number 'seed'

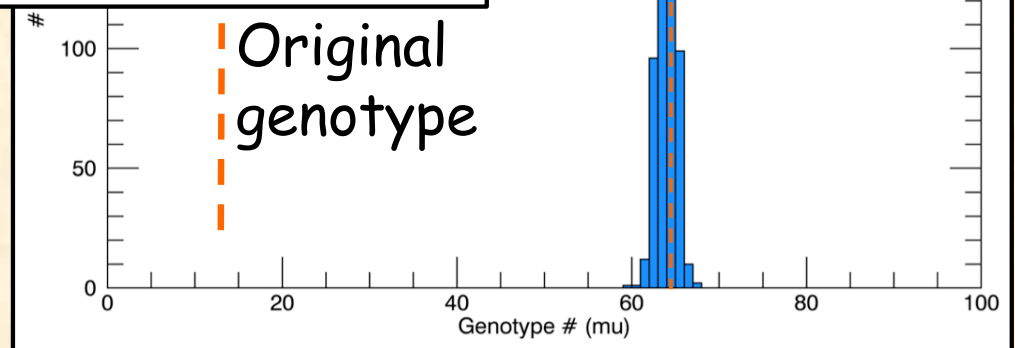
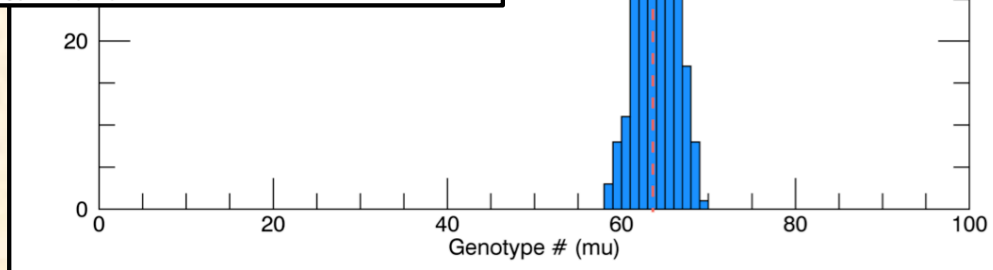
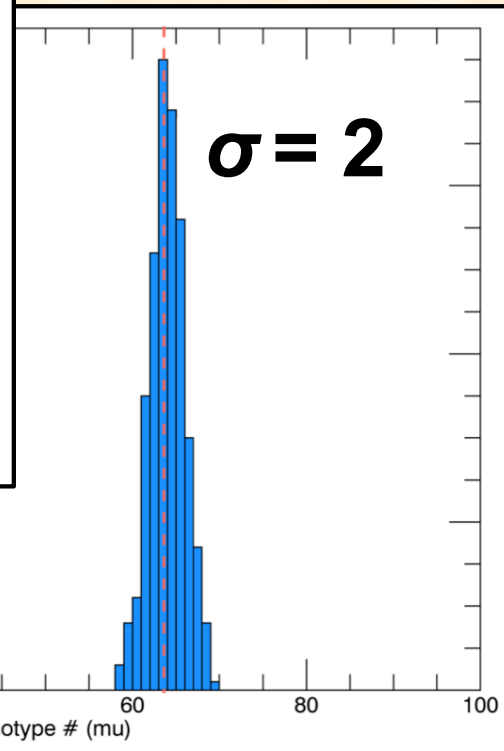
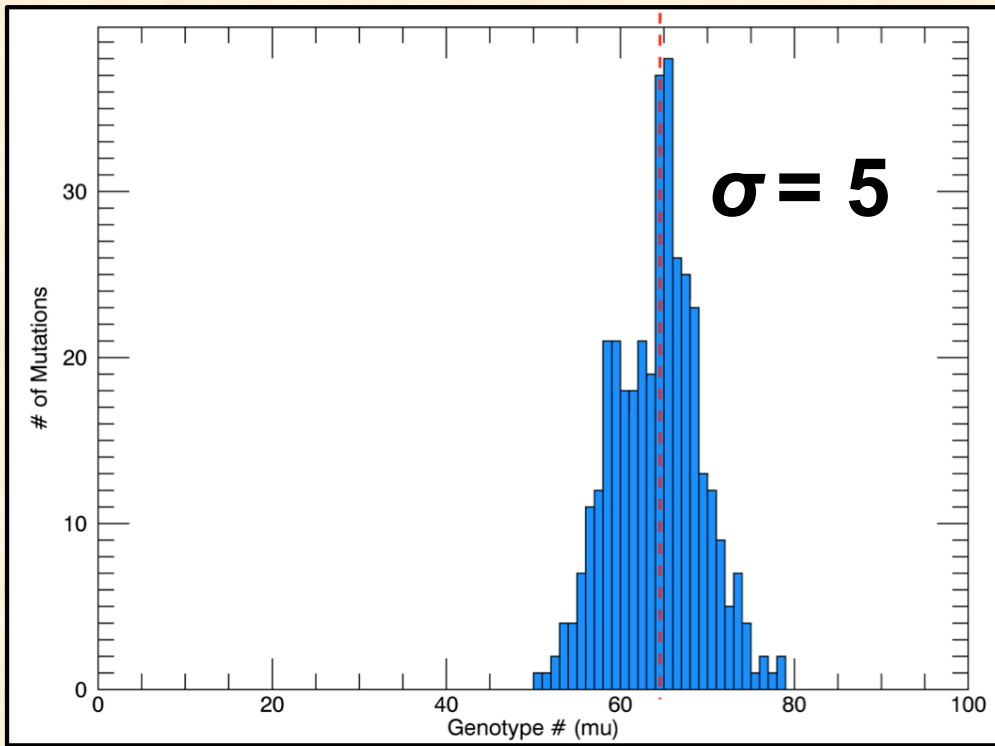
# Try 'Micromutationism' with Gaussian Normal PDF for Mutation Magnitude

- to have higher probability of small mutations about the dominant genotype, for continuous increase in  $\mu$
- to reduce initial lag?

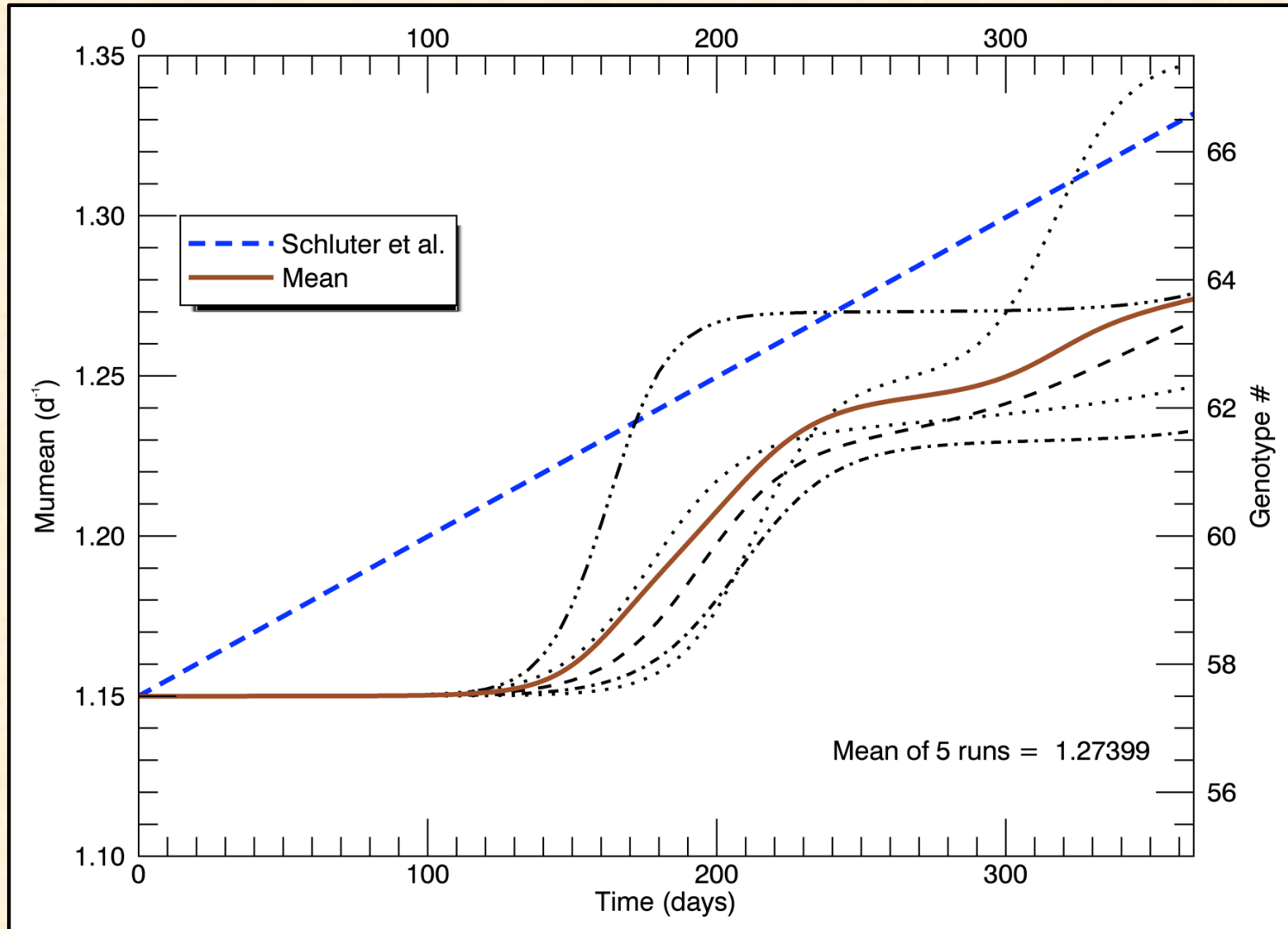
Gaussian Normal pdf,  $N(\mu_{\text{peak}}, \sigma)$

- centered on  $\mu_{\text{peak}}$ , the genotype with the highest biomass
- with a width  $\sigma$  (in genotype intervals)

# 365 Gaussian Normal Mutations

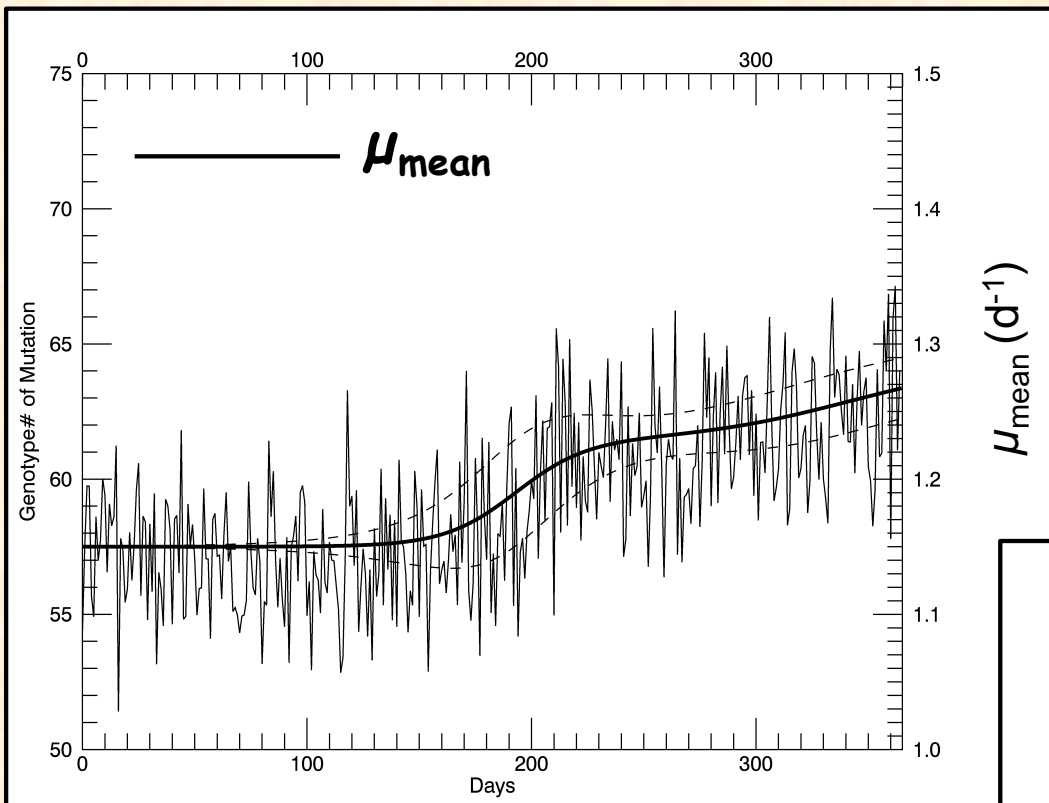


# 5-Member Ensemble at 26.3° with $\sigma = 2$



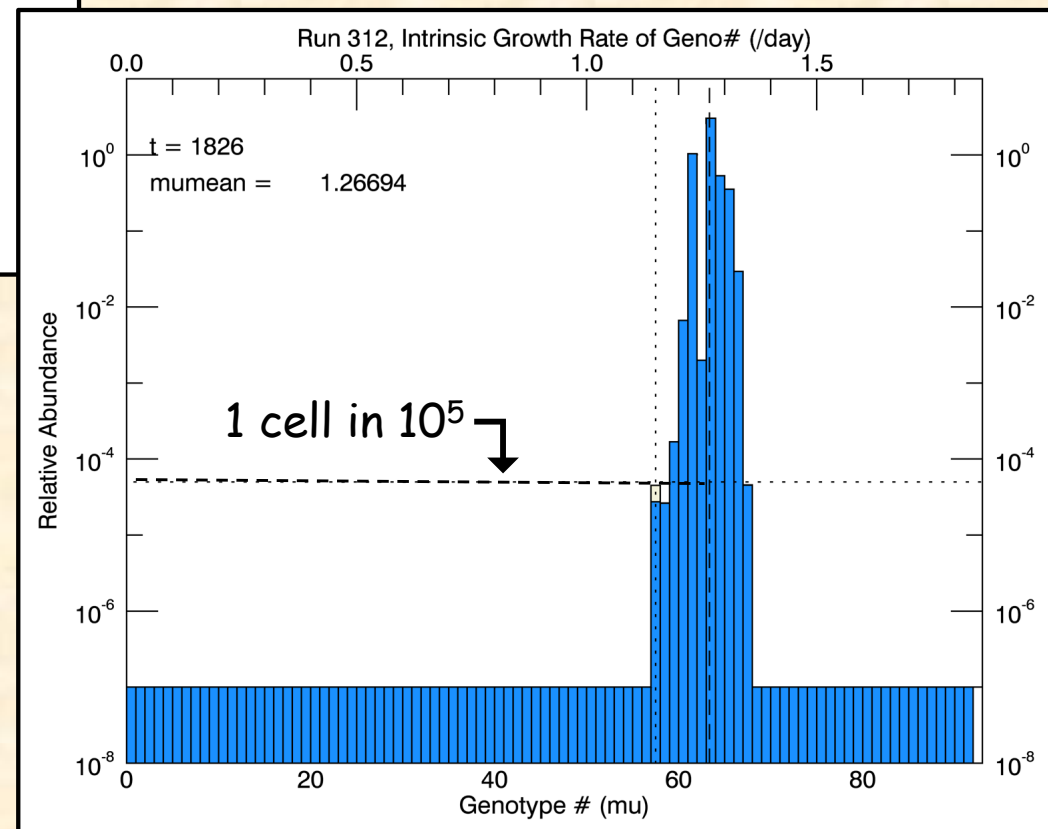
- 1 year increase in  $\mu_{\text{mean}}$  too small
- initial lag of ~110 days not realistic

# Simulation at 26.3° with $\mu_n = 2$



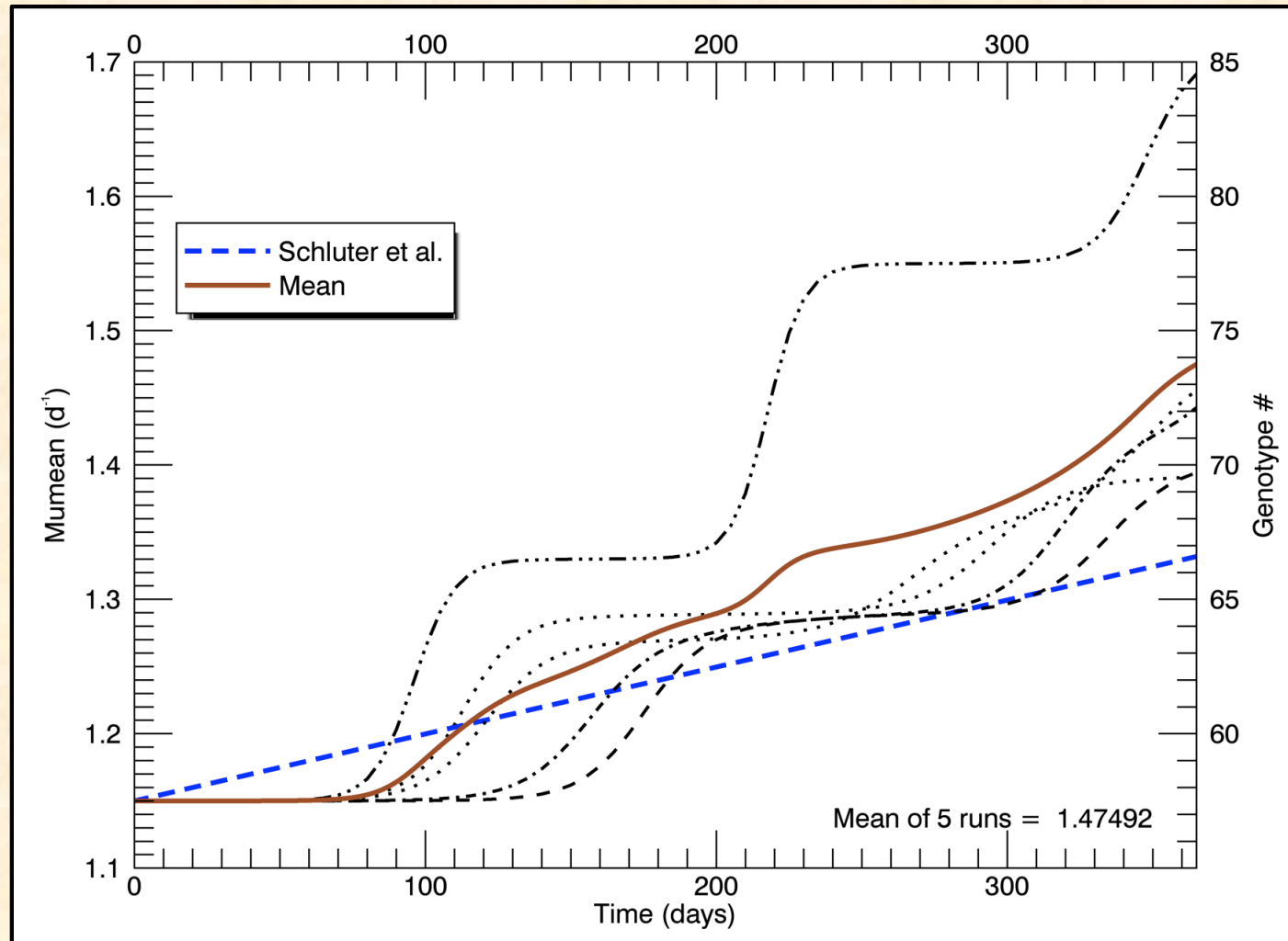
← 1 random mutation per day (light jagged line)

Distribution of biomass across genotypes after → 1 year ( $\log_{10}$  scale)





# 5-Member Ensemble at 26.3°C, $\sigma = 3$

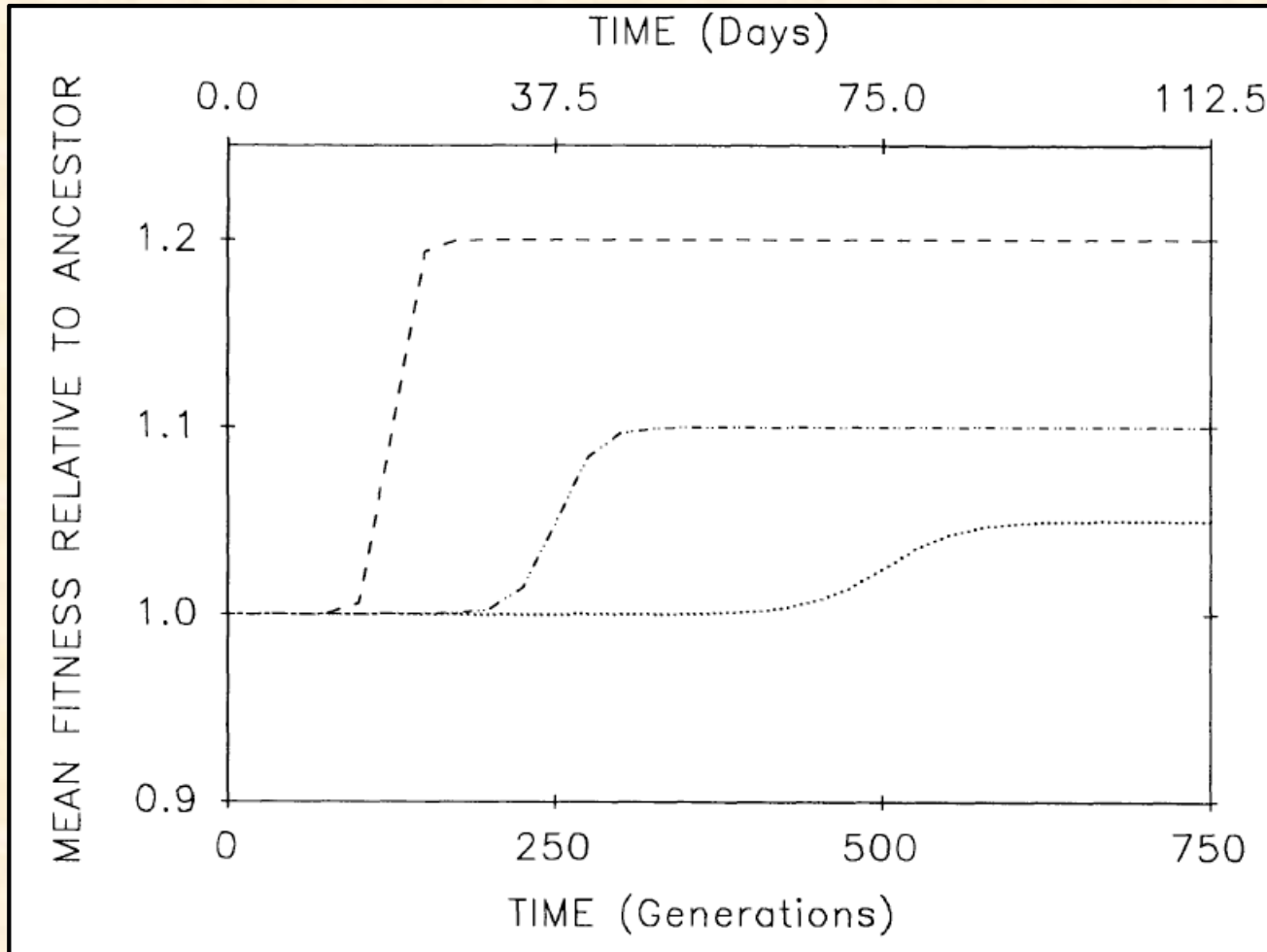


- 1 year increase in  $\mu_{\text{mean}}$  too large
- initial lag of ~70-120 days before increase not realistic
- thereafter ~linear increase in ensemble mean growth rate

# All Simulations Have a Lag Before $\mu_{\text{mean}}$ Begins Increasing

- Tried up to 10 mutations per day and also many fewer, but cannot replicate the approximately linear increase in  $\mu_{\text{mean}}$  without any lag, as observed in the laboratory culture experiments
- Lag was longer and subsequent increase was more gradual for micromutations

# Length of Lag Depends on Relative Fitness of 'Mutant' versus 'Ancestor'



- Single mutant initially 1 cell in  $3 \times 10^{-7}$  cells
- 'Mean relative fitness':

$$S_{ma} = (\mu_m - \mu_a) / \mu_a$$

R.E. Lenski *et al.*, 1991. Long-term experimental evolution in *E. coli*. *Am. Nat.* 138, 1315-1341.

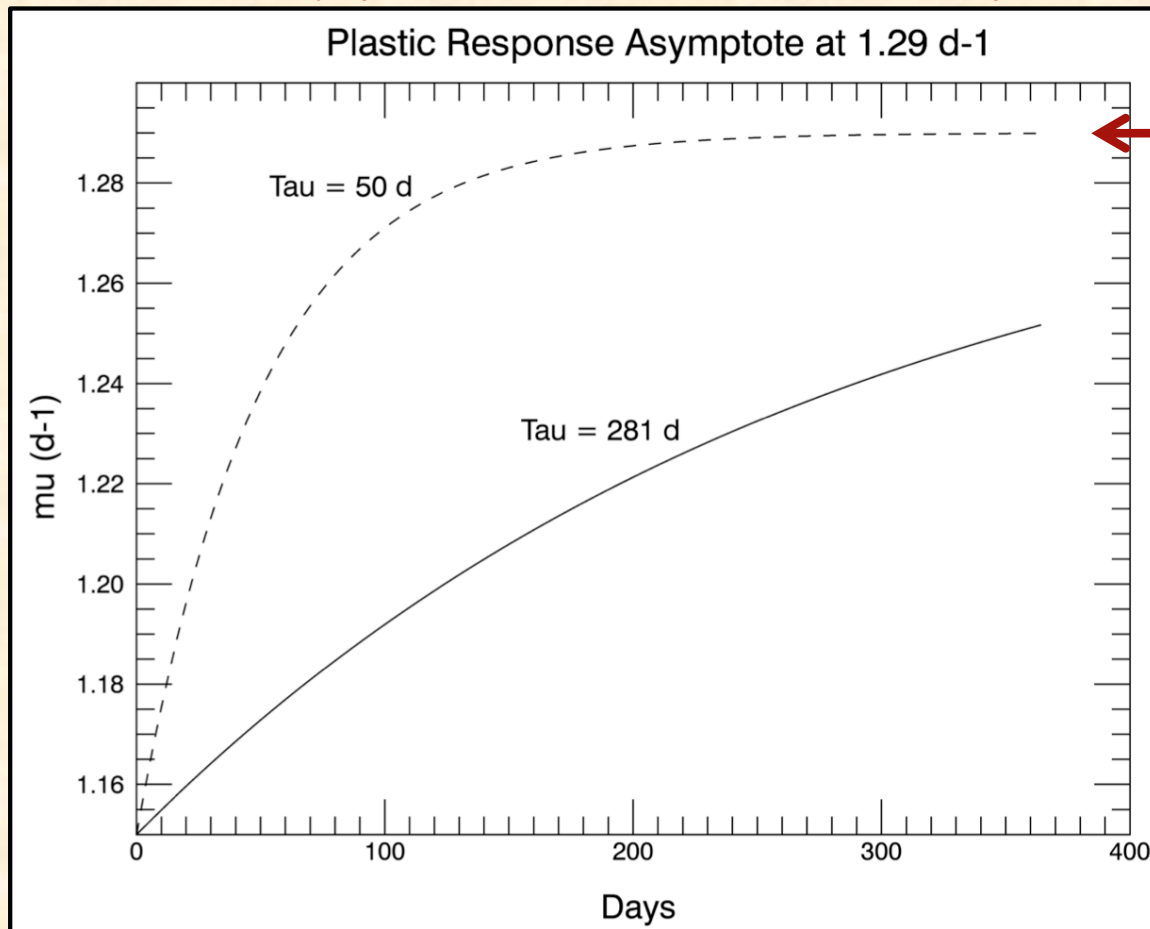
# Perhaps There Was Also a 'Plastic' Response

*"Phenotypic plasticity broadly defines the adjustment of phenotypic values of genotypes depending on the environment, without genetic changes" [Reusch, 2014. *Evol. Appl.* 7]*

The lag period can be considered a 'bottleneck' in evolutionary adaptation, and plasticity can maintain a population from approaching extinction until adaptation via a favorable mutation can become significant.

*[e.g. Lande, 2009; Chevin et al. 2010; Kopp and Matuszewski, 2014, *Evol. App.* 7]*

# A Plausible Plastic Response for 15°C Genotype after Abrupt Increase to 26.3°C



$$\mu_{\max}(15^{\circ}\text{C}) = 1.29 \text{ d}^{-1}$$

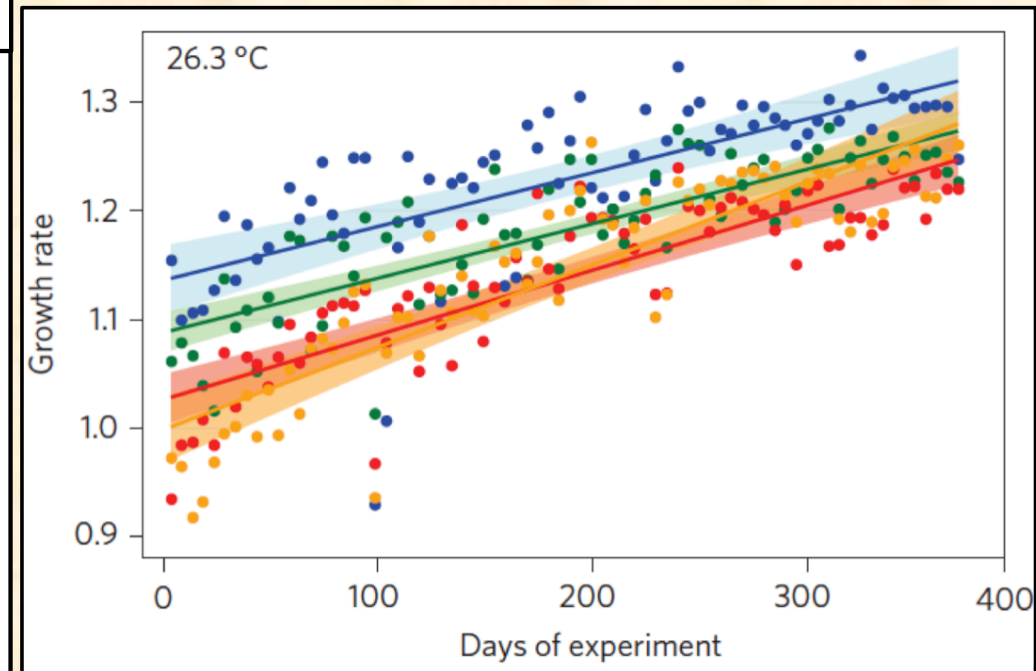
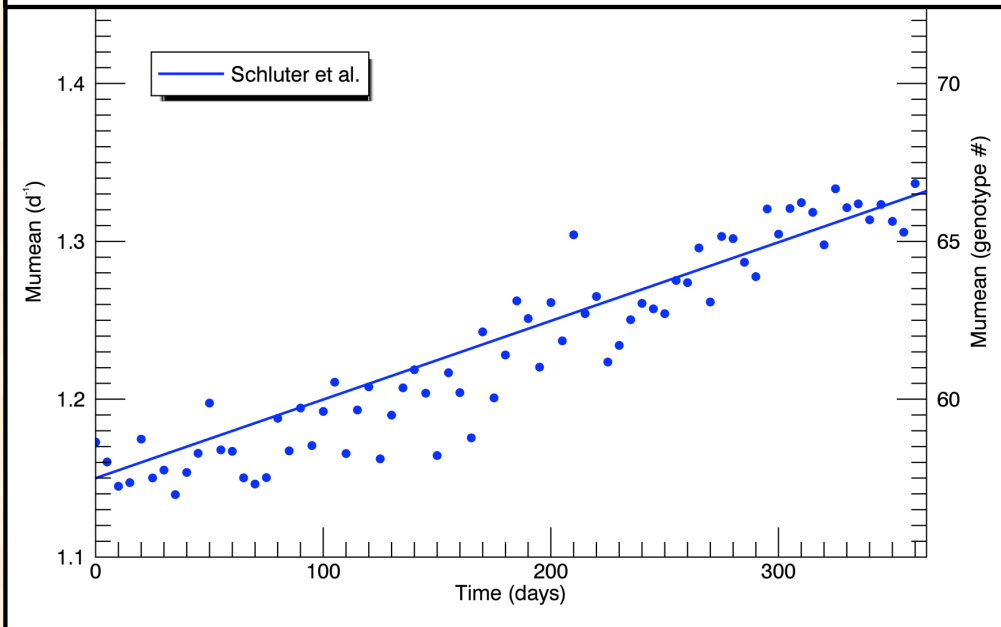
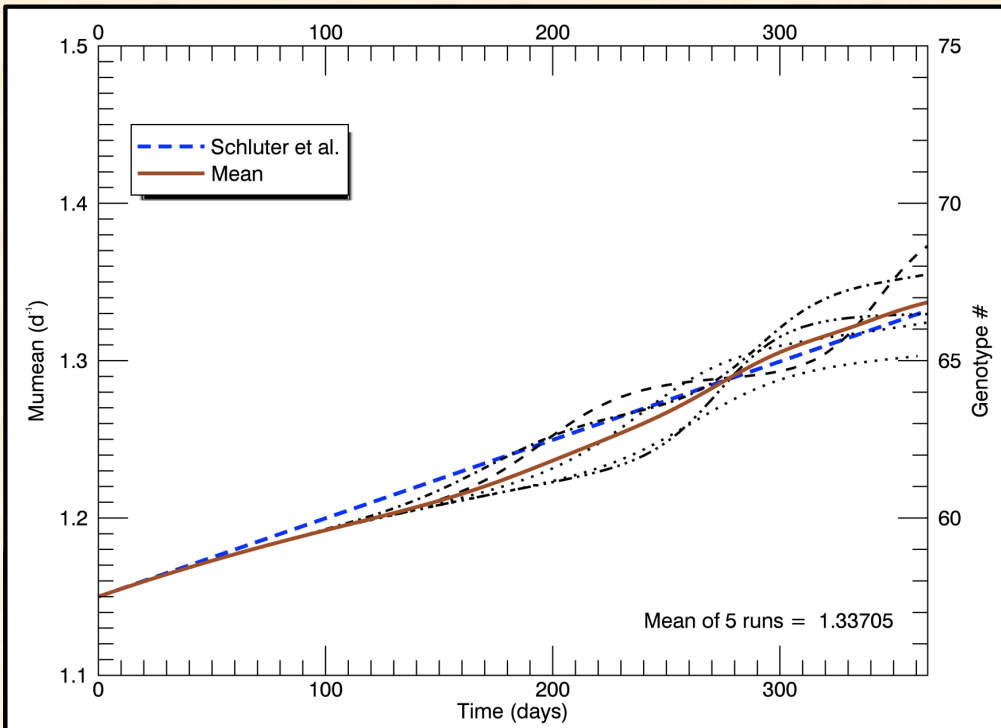
First order kinetic response:

$$\frac{d\mu_i(t)}{dt} = (\mu_{\max}(i) - \mu_i(t)) / T$$

*Must be "transgenerational", (Philip Munday's talk)*

- Rate inversely proportional to distance from limit
- Limit is  $\mu_{\max}(15^{\circ}\text{C})$
- $T = 281$  days  $\rightarrow$  initial slope matches fitted slope in *Schlüter et al.*

# 5-Member Ensemble at 26.3° with Plastic Response and $\sigma = 2.5$





**If** this representation of evolutionary adaptation by genetic mutation in culture has some validity, then:

- *mutation alone cannot explain the results of Schlüter et al. - because of the lag in response to abrupt warming of ~ 100 generations for all simulation experiments*
- *a plausible plastic response to the warming can remove that lag and 'buy' time for favorable mutations to multiply to significant numbers*
- *genetic information and energy budget are required for further progress - especially on plasticity*
- *simplest case - 1 trait + 1 environmental variable*

# Thanks

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## Reference:

Denman, K. L. (2017). A model simulation of the adaptive evolution through mutation of the coccolithophore *Emiliana huxleyi* based on a published laboratory study. *Frontiers in Marine Science* 3, 286. doi:10.3389/fmars.2016.00286.