

1. Based on the model output and observed data points (Figure 1) from Riley et al. 1946, a mean percentage error (MPE) of -12% was calculated.

$$MPE = \frac{100\%}{n} \sum_{i=1}^n \frac{observation_i - model_i}{observation_i}$$

The sign of this error indicates that the observation was generally lower than the model cast. This method for calculating error allows for balance between overshoot/undershoot of the model relative to the data, however error can also be calculated using the absolute value of the difference between observation and model (this yields a 42% error).

Sensitivity tests were used to determine how the model was influenced by various parameters (Table 1, Figure 2). The model responded most strongly to a +20% change in photosynthetic constant (p) or a +20% change in the correction factor for nutrient depletion (1-N), resulting in phytoplankton population levels in excess of 1000 g*C*m² by the conclusion of the run. These two parameters (p and 1-N) yielded identical results when perturbed. While other parameter perturbations somewhat mirror the rise and fall of the original model, perturbing p or 1-N leads to phytoplankton population values that are maximized at the end of the run. The model was least sensitive to perturbations in rate of change of respiration (r), and in fact increasing r by +20% actually yielded a model with a lower MPE (+7%) than the base case. Compared to the other parameters, the model was moderately sensitive to changes in R0, with a 20% decrease leading to increased phytoplankton population with -127% error from the observations; the model was less sensitive to an increase in this parameter (31% error). The parameter for grazing rate (g) also showed more sensitivity when decreased, with phytoplankton population diverging from the base case around the 100-day mark and peaking over 200 g*C*m² before dropping back down towards the end of the run.

Based on these findings, I would add a caveat to Riley's conclusion that the behavior and accuracy of this model is highly dependent upon the parameters, particularly those which define the "P" box of the model, and that natural fluctuations in these parameters could yield poor prediction of phytoplankton populations. Changes in grazing rate (which can naturally be highly variable depending upon the dominate species of grazer and the life stage) will also have a large impact on the model fit.

Parameter	-20%	+20%
p	62%	-2246%
R0	-127%	31%
r	-47%	7%
g	-465%	44%
1-N	62%	-2246%

Table 1. MPE calculated for each model output (relative to observations) when listed parameters were perturbed by ±20%.

2. For P to be periodic, the final value of P (on an annual cycle) needs to match the initial value of P. Under the base model, a grazing rate (g) value of 0.0074 results in a periodic P. Table 2 (below) shows how this value changes as other variables are perturbed by $\pm 20\%$.

Parameter	-20%	+20%
p	0.0049 (-)	0.01 (+)
R0	0.0085 (+)	0.0064 (-)
r	0.0081 (+)	0.0066 (-)
1-N	0.0049 (-)	0.01 (+)

Table 2. Listing of g-values necessary for phytoplankton population to remain periodic when other listed parameters are varied by $\pm 20\%$.

3. See Figure 3 for plotted 10-year time series with randomly varying g-values. The model was run three different times with varying g, with each run resulting in a distinctly different outcome.
 - Run 1 – Peak production remains relatively constant year-to-year, although steadily decreasing over the last four years
 - Run 2 – Peak production dips in the middle of the run before climbing back up in the final year
 - Run 3 – Peak production steadily decreases over the course of the run, dwindling nearly entirely by year 10

These results confirm conclusions drawn during the sensitivity tests, which indicated that the model is very sensitive to changes in rate of phytoplankton production per grazing unit. It is apparent that variability in g translates to high interannual variability in the model, and also that phytoplankton production in one year has lasting effects on subsequent annual cycles (for example the distinct reduction in population seen over the last five years of Run 3). Variability in grazers should be expected in the real environment, as dominant species and life-stages shift over time. Models building from this set of equations should take this variability into account, perhaps incorporating a vector of g-values rather than a fixed rate.

***See accompanying annotated code for model, plots, and calculations.

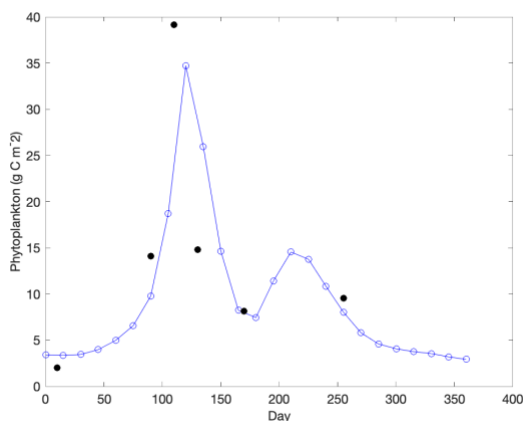


Figure 1. Base model (blue) with observed values (filled black circles).

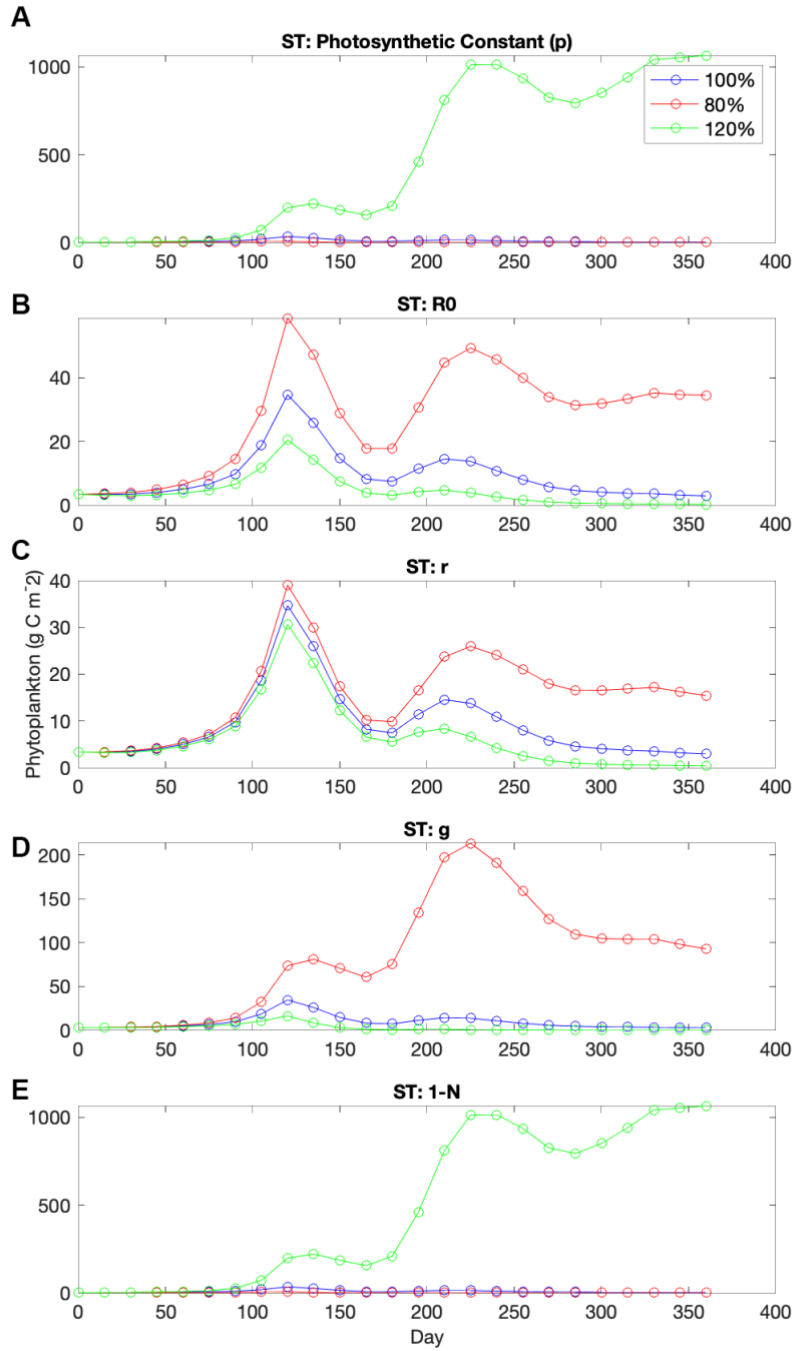


Figure 2. Results of sensitivity tests to various parameters. For each test, blue points indicate the base model, red points indicate a -20% perturbation of the indicated parameter, and green points indicate a +120% perturbation of the observed parameter. Tests were performed on p (A), R_0 (B), r (C), g (D), and $1-N$ (E).

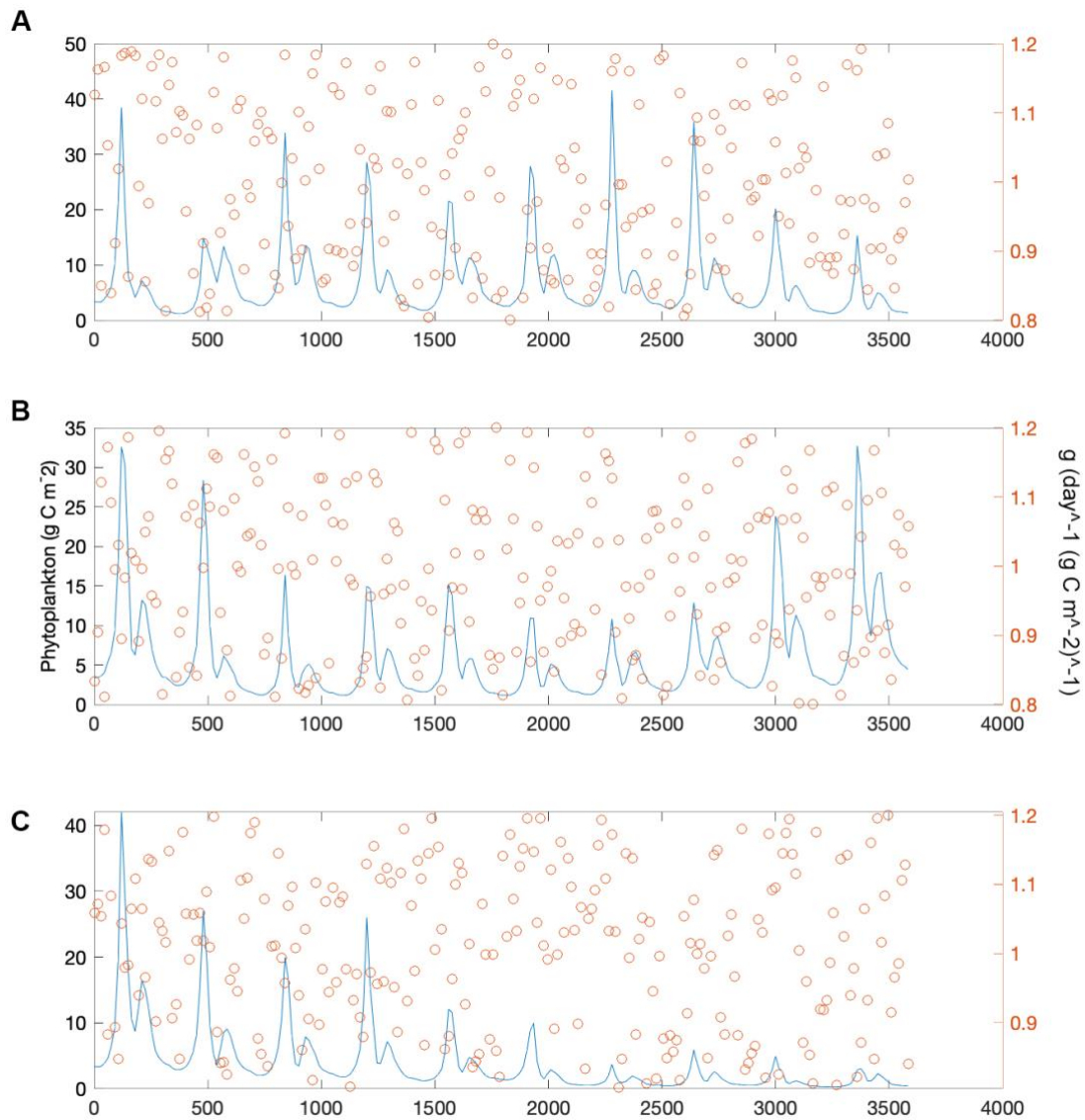


Figure 3. Ten-year time series of phytoplankton population with randomly varying g parameter. Model was run three times (A-C) with different randomly generated sets of g values. These random values are plotted as red scatter points, while phytoplankton population is plotted as a blue line. Note the varying y-scales in these plots.