

12.823 Pset 01

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Implementing Riley's (1946) simple plankton model:

$$\frac{\delta P}{\delta t} = P(P_h - R - G)$$

in which P is phytoplankton biomass, P_h is the photosynthetic rate, R is phytoplankton respiration, and G is grazing by zooplankton. To do this, I will use the form

$$\ln P_{(t+\Delta t)} = \ln P_t + \Delta t * \left[\frac{pI_o}{kz_1} (1 - e^{-kz_1}) (1 - N)(1 - V) - R_0 e^{rT} - gZ \right]$$

where P_t and $P_{(t+\Delta t)}$ are the values for estimated population of phytoplankton at time t and $(t + \Delta t)$ days, respectively, both measured in $C\ m^{-2}$; p is the photosynthetic constant, in units of $day^{-1}(g\ cal\ cm^{-2}\ min^{-1})^{-1}$; I_o is the incident solar radiation in $g\ cal\ cm^{-2}$; k is the extinction coefficient, equal to 1.7 (Secchi disc reading, in meters) $^{-1}$; z_1 is the depth (in meters) of the euphotic zone, defined as the depth where light intensity is 0.0015 $g\ cal$; $(1 - N)$ is the correction factor for the reduction in photosynthetic rate due to nutrient depletion; $(1 - V)$ is the correction factor for reduction in photosynthetic rate due to vertical turbulence; R_0 is the phytoplankton respiration rate at $0^\circ C$, in units of day^{-1} ; r is the rate of change of respiration rate with temperature, in units of $(^\circ C)^{-1}$; T is mean surface temperature in $^\circ C$; g is the zooplankton grazing rate, in units of $day^{-1}(g\ C\ m^{-2})^{-1}$; and Z is the quantity of zooplankton, measured in $g\ C\ m^{-2}$.

I will use the values reported in the Appendix of Riley (1946) for $Z(t)$, $T(t)$, $k(t)$, $z_1(t)$, $(1 - N)$, $(1 - V)$, and I will assume the same initial condition [$P_{(t=0)} = 3.4g\ C\ m^{-1}$] and parameter values:

- $p = 2.5$
- $R_0 = 0.00175$
- $r = 0.069$
- $g = 0.0075$

Lastly, I will treat a year as 12 30-day months, with $\Delta t = 15$ days.

See Figure 1 (next page) for results.

Sensitivity Analysis of Riley model

The above model was re-run with each of 5 parameters (p , $(1 - N)$, R_0 , r , and g) increased and decreased by 20%. Results are shown in Figure 2.

Clearly, an increase in either a) the photosynthetic constant (p) or b) the correction factor for the reduction in photosynthetic rate due to nutrient depletion $(1 - N)$ has the greatest impact on the model; a 20% increase in either of these parameters results in 2-3 orders of magnitude increase in the estimated values for phytoplankton abundance (P), with the population eventually blowing up. On the other hand, a 20% decrease in either value results in a population crash. This makes sense, as these parameters help establish the bottom-up controls on the phytoplankton population.

Following these parameters, the model is most sensitive to changes in grazing rate g ; a 20% decrease in grazing rate facilitates an order of magnitude increase in phytoplankton numbers, while a 20% increase leads

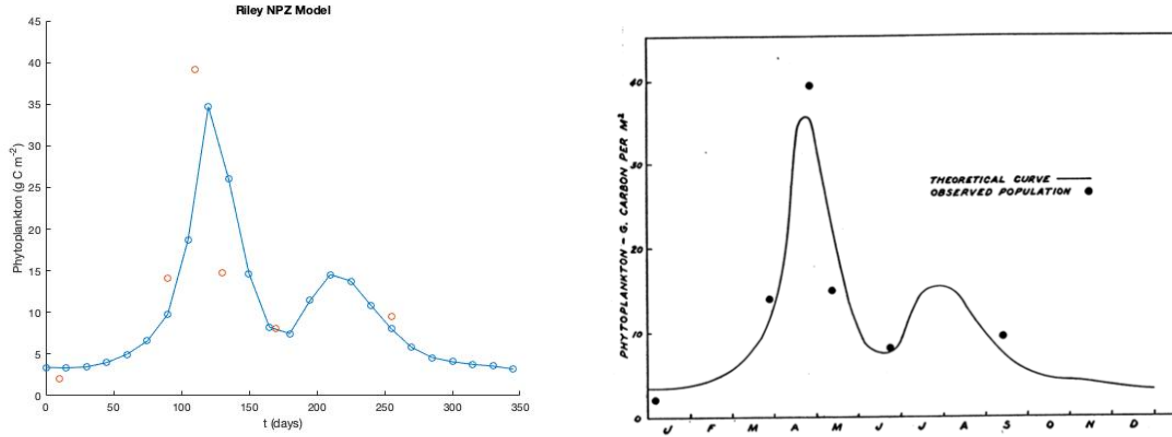


Figure 1: (Left) Recreation of Riley model. Blue line and circles denote calculated values from above equation. Red circles denote observed values for phytoplankton abundance, reported in Riley (1946). For comparison, see original Riley (1946) Figure 21 (right)

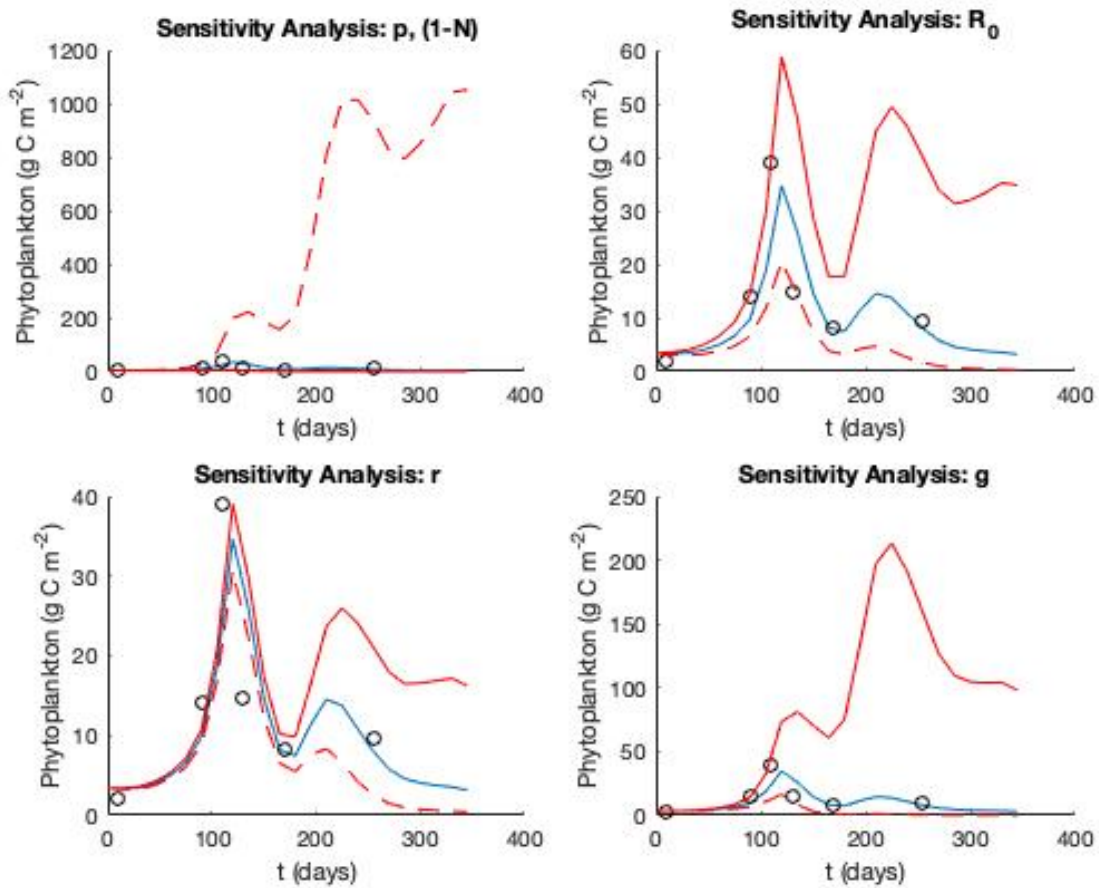


Figure 2: Sensitivity analysis for p , $(1 - N)$, R_0 , r , and g . The blue lines denote the original model, while the red lines denote the model run with the particular parameter value increased (dashed) and decreased (solid) by 20%. Original observations are shown as open circles. Note that increasing/decreasing p or $(1 - N)$ has the same effect, so only one is shown

to a phytoplankton population crash. This makes sense, as grazing by predators exerts a top-down control on phytoplankton.

In contrast, the model is fairly robust to changes in parameters relating to phytoplankton respiration: R_0 and r . In both cases, a 20% decrease in parameter value led to modest changes in phytoplankton biomass in the first half of the year and roughly 1 order of magnitude increase in second half. This makes sense, as sea surface temperatures in the second half of the year were much warmer ($\sim 13^\circ\text{C}$ on average, versus $\sim 4.5^\circ\text{C}$ in the first half). Therefore, a decrease in respiration rates (due to either an overall decrease in base rate or a weaker scaling with temperature) would allow a more efficient increase in phytoplankton biomass with the same photosynthetic rates, especially in warm waters (when, normally, much energy is lost to respiration).

Comparing Errors

To evaluate the model fit to observed data (Table 1), the following equation was used:

$$\text{Avg. Perc. Error} = \frac{\sum \frac{|\text{Observed} - \text{Modeled}|}{\text{Observed}}}{n} * 100$$

Table 1. Observed values, from Riley (1946)

t	P
10	2.006
90	14.076
110	39.151
130	14.807
170	8.126
255	9.52

To compare points at identical times t , model values were linearly interpolated for each sensitivity experiment. It should be noted that this same metric results in an average error of 41.6% for the recreated Riley model, above, and so the error rates calculated in Table 2 should be assessed in that context.

Table 2. Calculated error for sensitivity experiments in Figure 2

Parameter	Avg. % Error (-20%)	Avg. % Error ($+20\%$)
$p, (1 - N)$	81	2250
R_0	130	54
r	66	52
g	470	66

As described in the previous section, the model is particularly sensitive to parameters that affect the bottom-up controls on phytoplankton populations; efficiency in photosynthesis and nutrient uptake. While the photosynthetic constant p appears fairly well constrained (see Riley (1946) Figure 15), there does appear to be some variation over the course of the year. It is also entirely conceivable that this value could vary for different phytoplankton groups (especially if one were interested in both pico- and micro- phytoplankton) or, perhaps, even for the same size groups at different levels of light acclimation. Similarly, values for $(1 - N)$ varied from 0.6 to 1 over the course of the study, and these calculations were derived from a single culture study of a single diatom species. Most notably, these calculations were carried out under the assumption that phosphate was the potentially limiting nutrient, which is not necessarily the case in all regions of the global ocean.

The fact that parameter values may differ for different populations, taxonomic groups, or (in the case of

grazing by zooplankton) phytoplanktonic communities can also be applied to the remaining parameters in Table 2, and it is evident that changes to those parameters is accompanied by large variations in model accuracy. Therefore, while Riley (1946) argues that his model yields results that are in the same order of accuracy as the statistical estimate, I would caution that this accuracy was in no small part due to the careful consideration that went into selection of parameter values, and that future applications of this model should therefore be accompanied by the same level of scrutiny for each component.

Periodic Phytoplankton

To achieve a periodic phytoplankton population, grazing rate g was reduced from 0.0075 to 0.007435. However, if parameters related to photosynthetic efficiency (e.g. p , $(1 - N)$) were increased, or if the base respiration rate R_0 was decreased, higher grazing rates could be maintained. A decrease in the rate of change of respiration with temperature, r , would also facilitate higher levels of grazing, but in a nonlinear fashion.

To simulate a 10-year series, forcing functions from Riley (1946) were repeated exactly 10 times, with the exception that zooplankton abundance Z was allowed to vary randomly by up to 20%. All other parameters were maintained at the original assumed values. The results are shown in Figure 3.

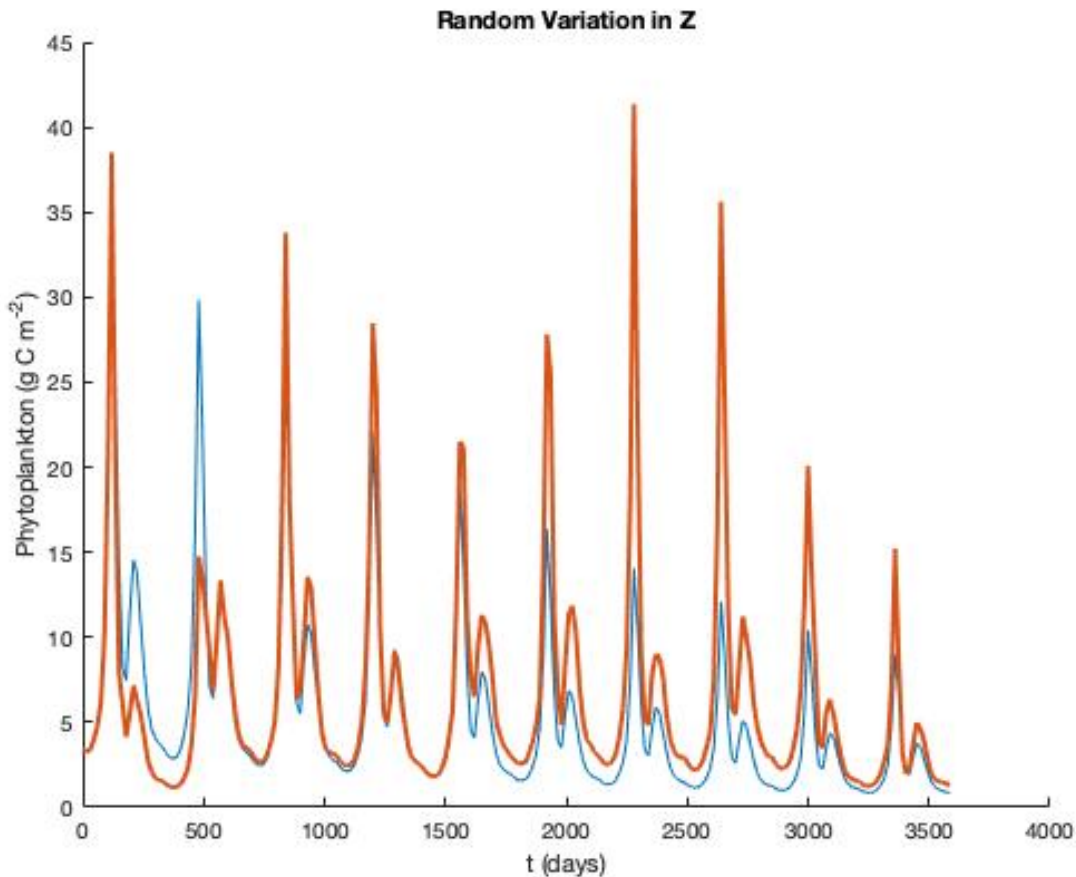


Figure 3: Simulated 10 year series, with random variation in zooplankton abundance Z and lower grazing rate g (orange). The original model, with $g = 0.0075$ and non-varying Z is shown in blue

By allowing up to 20% random variation in zooplankton abundance, spring bloom populations ranged from > 40 to ~ 15 g C m^{-2} and overall population values reached as low as ~ 1.5 g C m^{-2} (Figure 3). While the original series showed a steady decrease in peak bloom levels, some simulations containing random variation exploded to > 1000 g C m^{-2} or crashed to values < 0.5 . The main takeaway from these simulations is that a

large degree of interannual variation in phytoplankton abundance can be driven by relatively small variations in the abundance of their predators, and this may well be one of the explanatory factors for why the spring bloom varies over space and time.