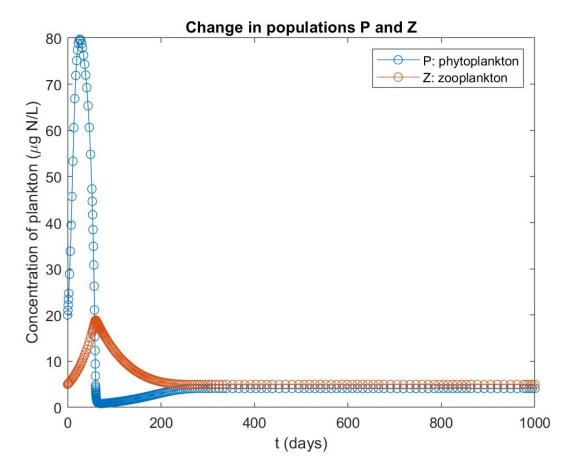
Plankton Population Dynamics

PopulationFixedPoints.m

PopulationFixedPoints.m, planktonderivs.m, and PopulationFixedPoints.m have been created to model the populations of zooplankton and phytoplankton. After setting the initial populations of phytoplankton (P_i) and zooplankton (Z_i) to 20 and 5 respectively, ode45 was used to solve the differential equations with a stable fixed point occurring at P_i =4.116 and Z_i =4.950.

By setting the starting plankton population densities to random variables between 0 and 100, the system settles at the same fixed points. A stable fixed point has been obtained by taking the average of the non-trivial stable points.

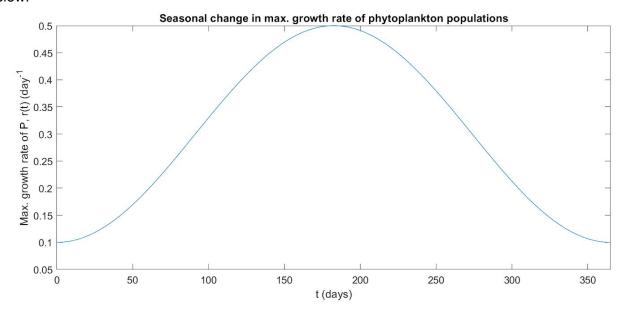
Stable fixed point: (P, Z) = (4.1168, 4.9503), where P represents the phytoplankton population and Z the zooplankton population. This will be rounded to (4.12, 4.95) in its use onwards. ode45 results in the following graph, plotting the population trajectories:

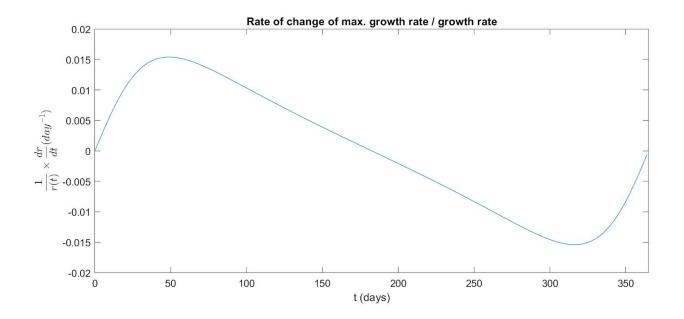


SeasonalForcingModel.m

The function planktonderivs_seasonal.m has been written to calculate the maximum growth rate of P (the phytoplankton population) as a function of time, r(t), where it varies seasonally. The maximum growth rate has been written as $r(t) = A_0 \sin(2\pi \frac{t}{365} - \frac{\pi}{2}) + 0.3$.

SeasonalForcingModel.m has been written to plot this function as well as the rate of change of r(t) in proportion to the value of r(t). Plotting the accelerating growth of P relative to the speed of its growth demonstrates how this forcing function will cause rapid changes in the dynamics of P seasonally, followed by more gentle changes. The two plots can be seen below:





Take note that this second graph has characteristics similar to a reverse sawtooth function and does not display a simple sinusoidal function.

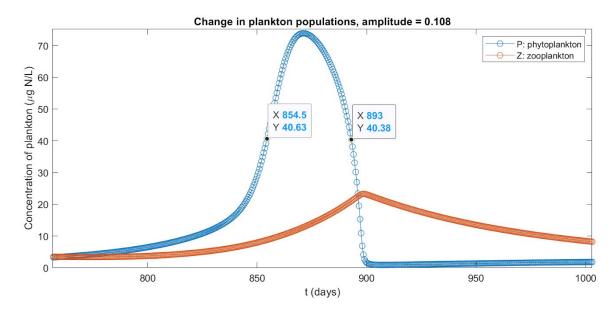
SeasonalBlooms.m

A bloom is a strong increase in phytoplankton population density that persists for at least a few weeks.¹ The elevated population level is many times larger than the stable, pre-outbreak level. Typically, the outbreak (and its eventual collapse) is rapid in comparison to the timescale of its persistence (growing substantially in around one week).

An order of magnitude increase in population density - from its quiescent levels - is adequate for a population change to be considered as significant. This event would qualify as a 'bloom', under the definition written here, if it persisted on a timescale for several weeks.

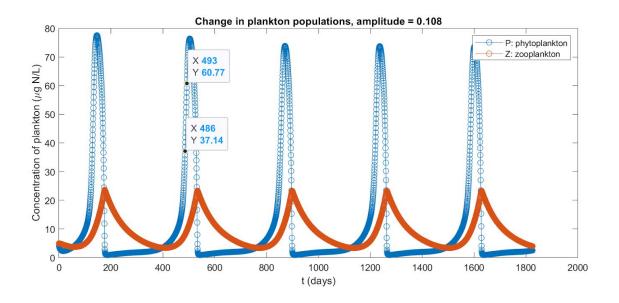
The inclusion of seasonal forcing on the plankton population model is implemented in SeasonalBlooms.m where the amplitude of the forcing can be interactively increased while observing the variation of the two plankton populations over many years, as well as a phase plane plot of the two populations.

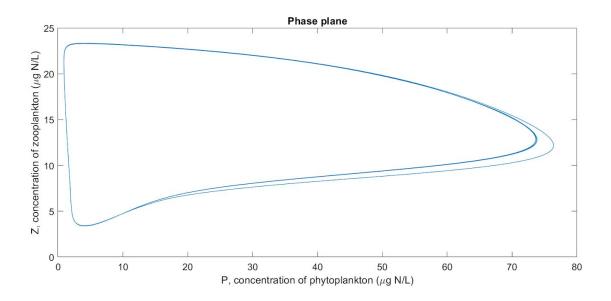
A bloom can be observed for a forcing amplitude of A = 0.108 day-1, with the phytoplankton population density nearly reaching 80µg N/L, almost 20 times larger than P's stable population density levels. The system maintains densities greater than 40µg N/L (an order of magnitude larger than P's stable value in an unforced system) for 39 days (5.5 weeks). The dynamics and timescale of a bloom under this system can be seen in the MATLAB figure here:



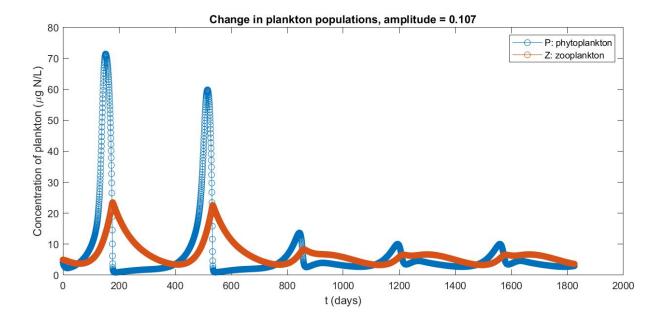
¹ Winder, Monika, and James E. Cloern. "The annual cycles of phytoplankton biomass." Philosophical Transactions of the Royal Society B: Biological Sciences 365.1555 (2010): 3215-3226.

The full dynamics of this seasonally blooming system can be seen below, where a phase plane plot is included to demonstrate how rapid changes in P occur with relatively slight changes in the value of Z (and vice versa, during bloom collapse). The presence of a limit cycle is a result of the event being a seasonal feature, rather than a result of a noisy/chaotic system.

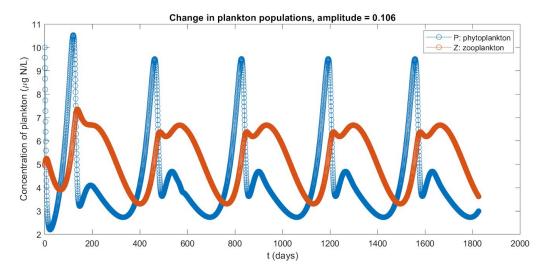


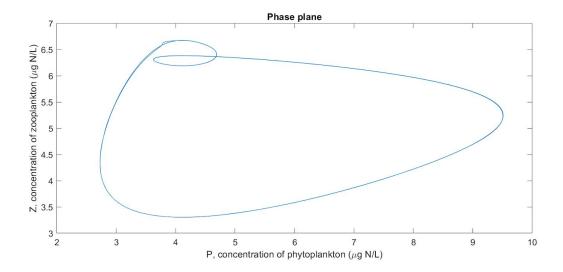


As can be seen in the figure below, the dynamics observed for a system with a forcing amplitude of $0.107~\text{day}^{-1}$ also shows a blooms for the first two years but then ends up with populations that reside at usual levels from then on, indicating that blooming P is a result of unstable starting parameters rather than being the system's natural dynamics. This value, however, is *sufficient* for triggering a bloom (given the right starting conditions) therefore the minimum forcing amplitude, A_0 , is equal to $0.107~\text{day}^{-1}$. For large P_i (e.g. $10~\mu g~\text{N/L}$), $0.107~\text{and}~0.108~\text{day}^{-1}$ are not yet large enough to be sufficient for triggering blooms.

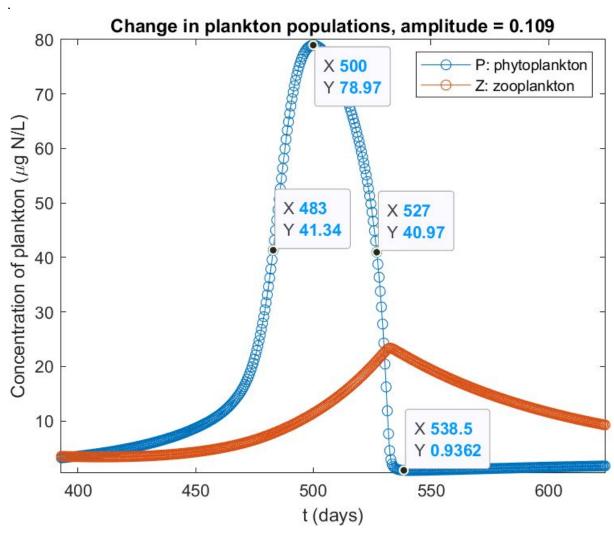


When the forcing amplitude is decreased slightly further to 0.106 day⁻¹, no blooms occur, since the value of P remains well within one order of magnitude:

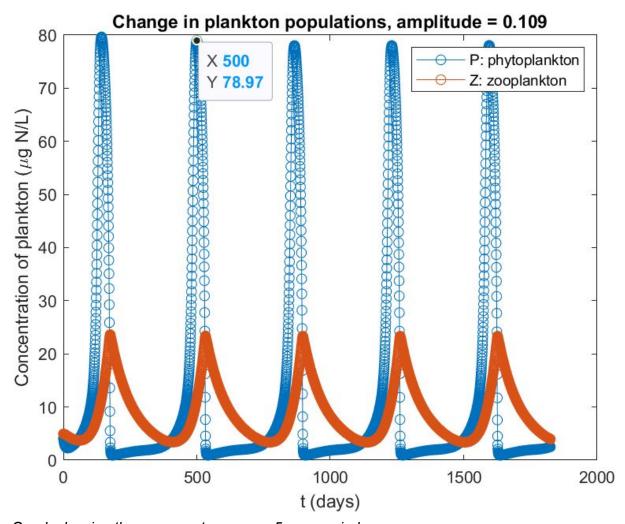




For larger A, the bloom characteristics persist. For A=1.09 day⁻¹, the P reaches higher values (79 μ g N/L), and the bloom persists for longer (over 6 weeks above 40 μ g N/L) but otherwise qualitatively repeat the dynamics of the A=1.08 day⁻¹ system.



Graph showing the shape and key values of a single "bloom", for a seasonal forcing amplitude of 0.109.



Graph showing the same system over a 5 year period.

DiurnalGrazing.m

When taking into account the fact that the system dynamics vary within 24 hours, further changes to the model can be made. By focusing on the variation in zooplankton grazing throughout the day, functions grazingrate.m, planktonderivs_diurnal.m and script DiurnalGrazing.m were written.

According to Roman, Ashton and Gauzens (1998):

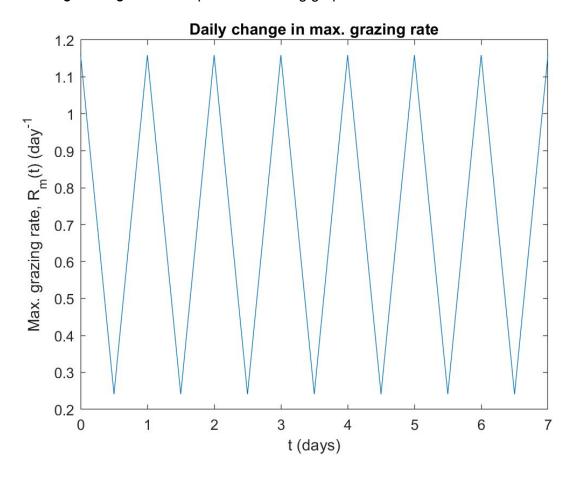
"The night/day ratio of zooplankton grazing impact on the phytoplankton community ... averaged 4.8 in the Chesapeake Bay plume and 1.6 in warm-core Gulf Stream rings".²

To see how the large day/night differences affect system dynamics, a daily-varying function based on the behaviour of Chesapeake Bay plume zooplankton was written to replace the constant $R_{\rm m}$, the maximum specific predation rate.

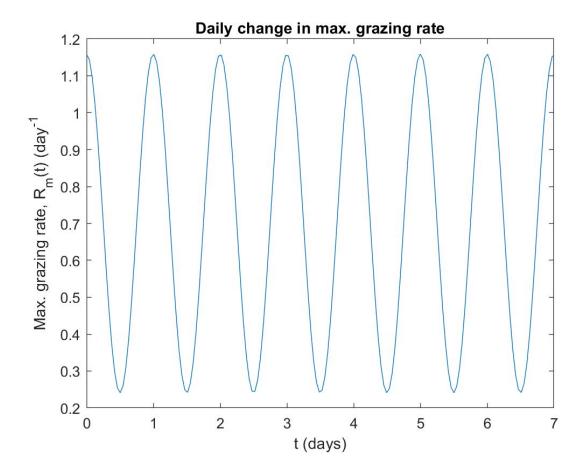
² Roman, Michael R., Kathyrn A. Ashton, and Anne L. Gauzens. "Day/night differences in the grazing impact of marine copepods." Hydrobiologia 167.1 (1988): 21-30.

While time, t, retains the units of days, and the function is called with time-steps (t_{step}) equal to half a day, it would be practical to define $R_m(t)$ as a simple multivalued function (e.g. a function that equals one value at night, another during the day). However, a sinusoidal function can achieve the same outputs for $t_{step} = 0.5$ days, while retaining the flexibility for finer time-steps, which introduce smooth variation between daytime and nighttime behaviour.

To keep the average grazing rate, $R_m(t)$, equal to the previous grazing parameter, the function has an average of 0.7, while the peak is 4.8 times larger in value than its trough. Therefore, $R_m(t) = 0.459 \times cos(2\pi t) + 0.7$. The maxima, equal to 1.159 day⁻¹, are 4.81 times larger than the minima (equal to 0.241 day⁻¹). SeasonalForcingModel.m was altered and saved as grazingrate.m to plot the following graphs:

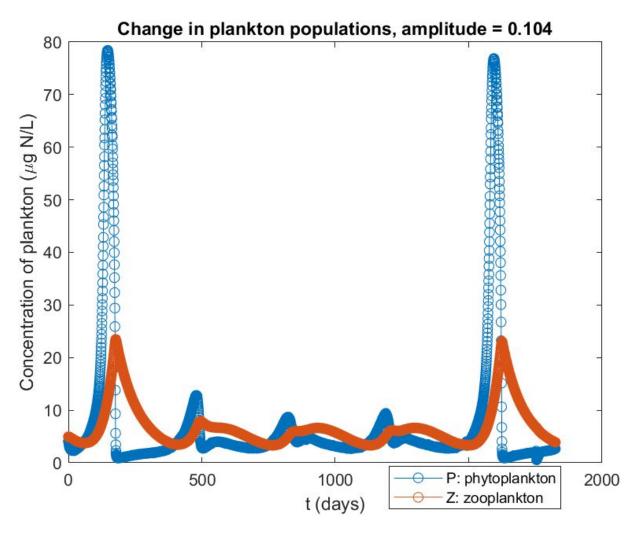


As can be seen in the figure above, when the t_{step} = 0.5 days, $R_{\text{m}}(t)$ acts as a simple two-valued function for day and night. When t_{step} = 0.042 days (~ 1 hour), the function varies smoothly (roughly synchronising with the abundance of daylight in a day/night cycle):

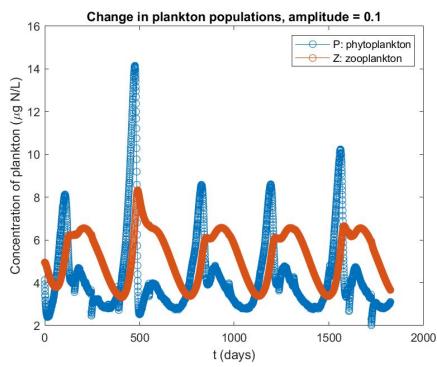


This could be expanded to model the seasonal changes in available light. Of course, zooplankton grazing rates may reach their maximum just a couple of hours after sunrise, or may change in proportion to the power of sunlight per unit area of the habitat's surface, or by (power/unit area)², or (more likely) by some other relationship that makes the function not equal to a cosine function!

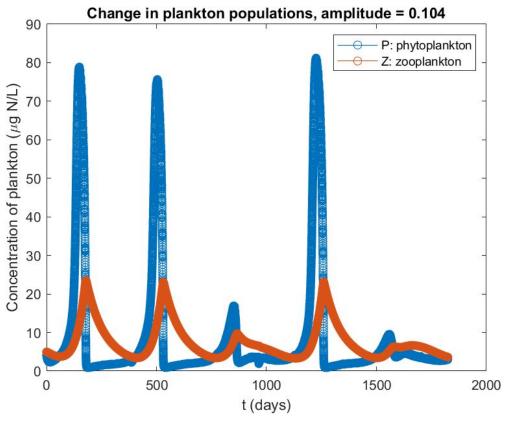
For t_{step} = 0.5 days, P_i =4.12, Z_i =4.95 (stable points for non-seasonally-varying system), the minimum bloom-triggering amplitude of season forcing A_0 is decreased to 0.104, where a bloom is seen in the first year of the model *and* in the fifth. A higher frequency of blooms are seen for larger amplitudes, of course. For different starting values of P and Z, blooms can easily be triggered in the first year, so focusing on the systems that are able to trigger blooms beyond the first couple of years (albeit occasionally) are of the most interest, since the bloom isn't simply a result of favourable starting conditions.

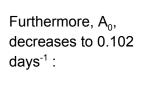


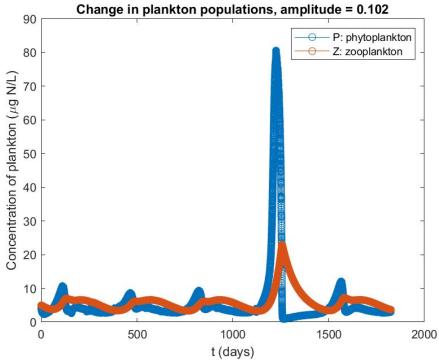
Sidenote: A = 0.1 days⁻¹ shows higher peaks in a diurnally-forced system than A = 0.106 days⁻¹ in the seasonally forced model, showing how the added free parameters may enable occasional breakouts to occur:



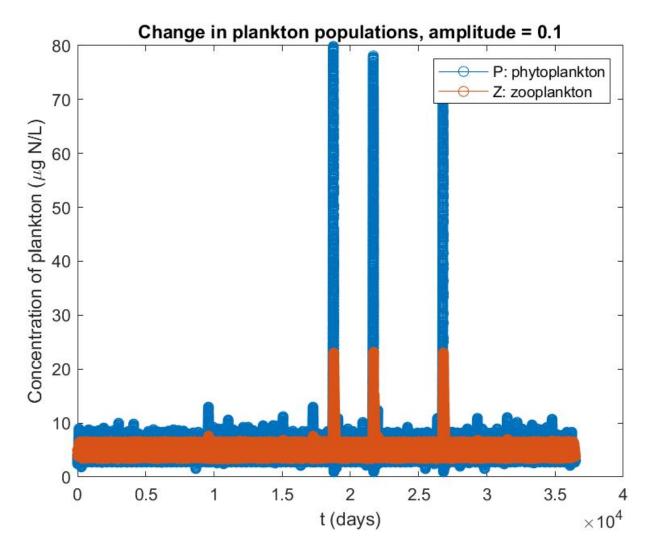
When t_{step} is decreased to be hourly, but with all other parameters remaining the same, the occurrence of blooms increases:







However, running the model for longer (10 years) reveals that blooms occur for A = 0.10 days⁻¹.



However, since long timescales are computationally expensive to calculate, and one-off blooms are feasible for lower forcing amplitudes when given longer timeframes, the definition of 'bloom sufficiency' will be restricted to the forcing amplitudes that are able to trigger blooms within a 5-year period. So, in conclusion, adding diurnal forcing decreases A_0 , and by approximately 6%: $(\frac{0.108}{0.102}-1)\times 100=5.88\%$.