A Light or Depth Situation: Modelling the Vertical Migration of *Daphnia*

Bennett McAfee

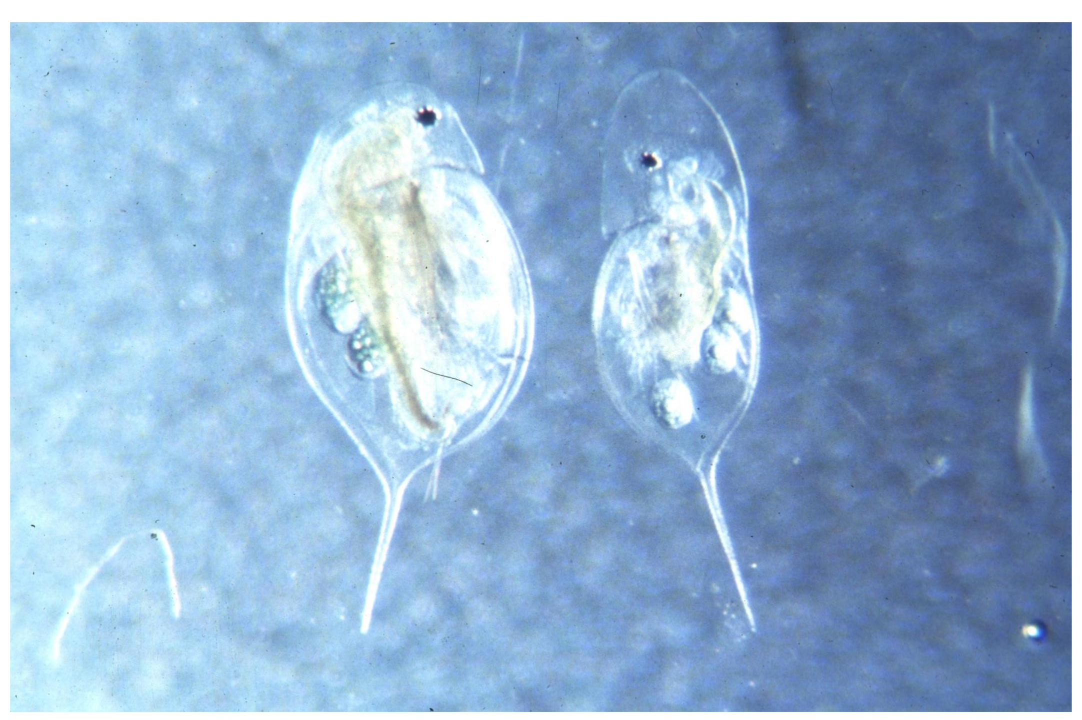
ABSTRACT

Diel vertical migration is a well-studied predator avoidance strategy carried out by zooplankton, including the water flea *Daphnia*. In *Daphnia*, migration behavior is known to change in response to environmental factors such as light intensity, predator abundance, and food availability. While changes in migration behavior have been observed in numerous field studies, attempts to predict vertical distribution of zooplankton mathematically have been too cumbersome to use and yield results too abstract to be practical. We have begun development of a package for the programming language R that uses the physical properties of a lake to predict a probable vertical distribution of *Daphnia*. The package does this via dynamic programming, wherein the position of *Daphnia* is predicted through simulating a series of choices that lead a *Daphnia* to optimal fitness. Initial results of the program have shown promise in predicting the depth for optimal *Daphnia* fitness which we have found to often correlate with the depth of greatest abundance in field data.

BACKGROUND

What are diel vertical migration and *Daphnia*?

Diel vertical migration of zooplankton is the daily cycle of movement towards and away from the surface of a lake that results from the need to avoid predation and forage for food. The process of diel vertical migration is one of the main forces creating the spatial and temporal structure of aquatic food webs, often acting as the biological pump that moves carbon around an aquatic environment (Brierley 2014). In *Daphnia*, a genus of crustacean zooplankton, this behavior is triggered in response to both light intensity and chemical signaling by predators. As a result, diel vertical migration changes in intensity in response to fish populations and conditions in the lake that affect light penetration.



Daphnia pulex, photo courtesy of Bart De Stasio

OBJECTIVE

With today's computing power, reasonable estimates as to how *Daphnia* are vertically distributed within a given lake can be calculated based on conditions monitored by wildlife agencies for existing purposes such as fisheries management. We have developed a package for the programming language R that can generate an estimated vertical distribution of *Daphnia pulex* in a lake based on known temperature gradients, light level and penetration, food availability, and predator abundance. This knowledge can be useful for predicting the vertical position of *Daphnia* populations in a lake of interest for management purposes but also for making predictions about how *Daphnia* populations will respond to changing environments with conditions that do not yet exist but likely will in the future.

METHODS

Calculating Lake Conditions

- Light Intensity and Predation Risk

  Predation risk for *Daphnia* in a given depth is based on the reactive distance of fish at that depth, which is a function of both prey size and light (Vinyard and O'Brien 1976). As *Daphnia* grow larger, the risk of being preyed upon increases because larger *Daphnia* can be seen from farther away.

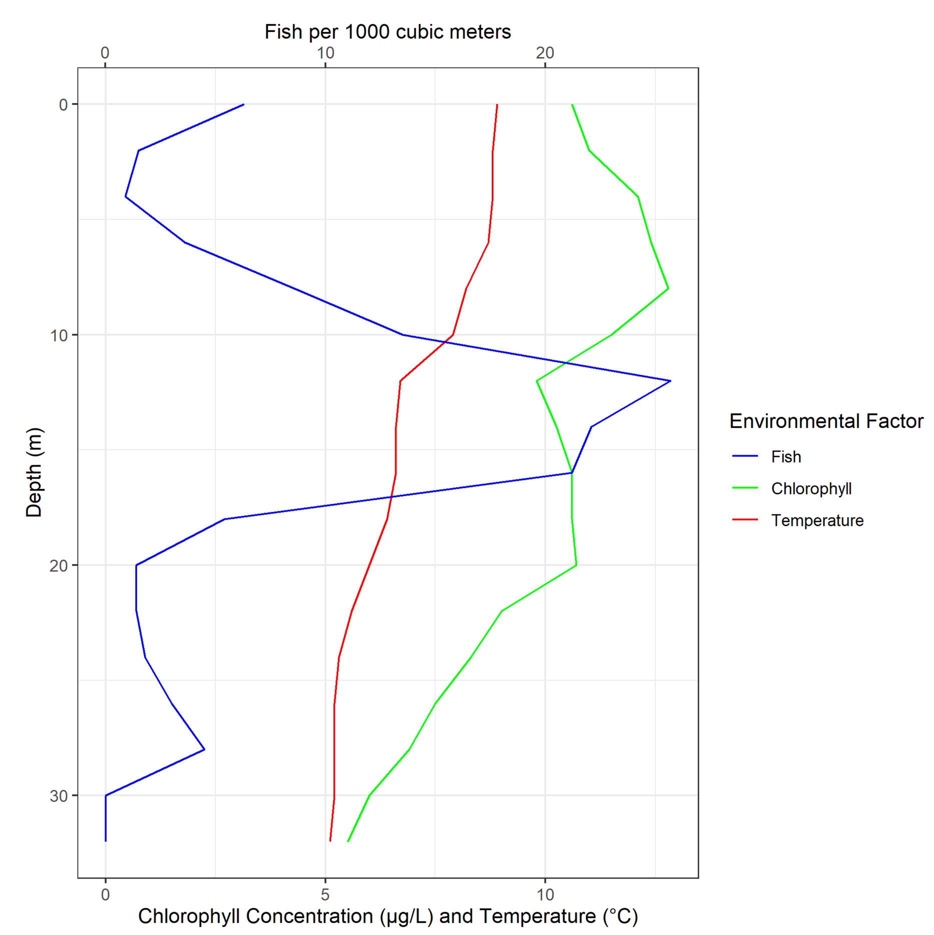
- Food Abundance

  Daphnia filter feed on phytoplankton, which are measured by proxy of the amount of chlorophyll available at a certain depth. The amount that a *Daphnia* can eat is dependent upon its size. So, between knowing the amount of food in a patch, and the size of the *Daphnia*, we can calculate how much a *Daphnia* will eat.

- Temperature

  Metabolism in *Daphnia* is temperature dependent. Lakes are generally divided into two sections, a warm epilimnion near the surface and a colder hypolimnion near the lakebed. *Daphnia* must balance metabolic costs with food availability to optimize fitness.

Conditions of Trout Lake (Vilas County, WI) in May of 1992



Stochastic Dynamic Programming

- Stochastic dynamic programming is a technique for modelling decision making under uncertainty.
  - All risks and rewards are calculated and then iterated upon over simulated time, meaning that all probabilities become certainties with set gains and deficits.
  - After several timesteps, the optimal choices that lead to the best outcome can be identified. For *Daphnia*, these choices are depths.
- Predation risk, metabolic cost, and food availability are calculated for every size of *Daphnia* at every possible depth.
  - These values are used to inform an overall fitness value for every size at every depth.
  - Fitness values are recorded for use in backwards iteration and the optimal depths are decided after a user-defined number of timesteps, usually 12.

Generating Vertical Distributions

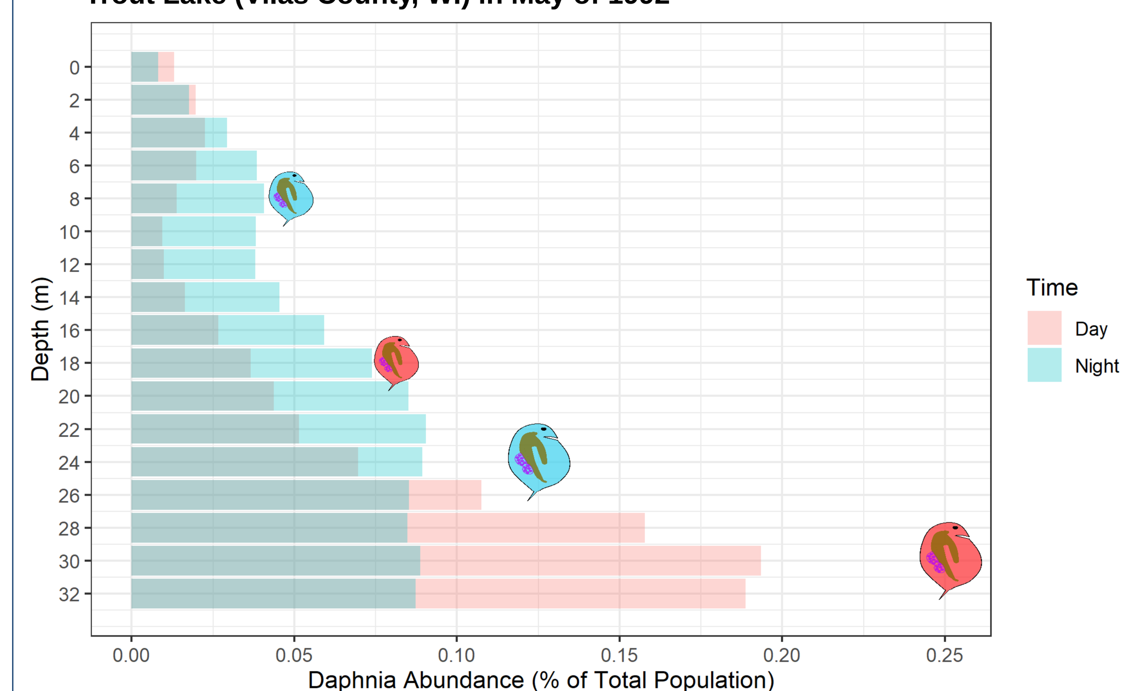
- Distributions of *Daphnia* are estimated by using the optimal depths calculated by stochastic dynamic programming as the means of generated normal distributions with standard deviations based on field data. These distributions for each size of *Daphnia* are added together and then converted into a proportion to give the user an estimated distribution.

RESULTS

Model Results and Assessment

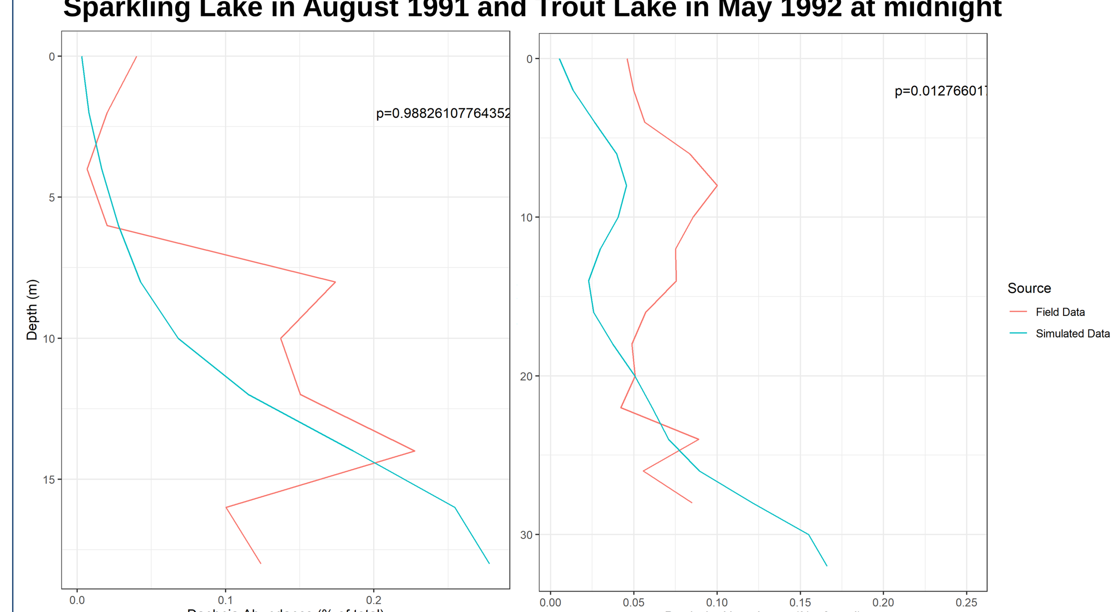
- Simulated *Daphnia* behave as expected. Smaller sizes of *Daphnia* are estimated to be higher in the water column than larger *Daphnia*, and *Daphnia* travel upwards at nighttime.
- Statistical tests find no significant different between field data and simulated data in 8 of the12 tested conditions, listed in the table below.
- The model performed better when simulating midnight as opposed to noon in 5 of the 6 tested conditions.

Simulated Vertical Distribution of *Daphnia* in Trout Lake (Vilas County, WI) in May of 1992



This figure is the direct output of the R function. Daytime simulations are in red and nighttime is in blue. The two distributions are overlayed on top of each other. The large *Daphnia* cartoons represent the optimal depth of 60 µg *Daphnia* and the smaller cartoons 10 µg.

Observed and Simulated Vertical Distribution of *Daphnia* in Sparkling Lake in August 1991 and Trout Lake in May 1992 at midnight



Distribution from field data is shown in red and simulated data is shown in blue. The *p*-value associated with a Kolmogorov-Smirnov test comparing the distributions is listed on the plot. The statistically best-performing simulation is shown on the right and the worst-performing simulation is on the left.

Results of Kolmogorov-Smirnov tests comparing vertical distributions of *Daphnia* in the field to distributions simulated by the model. The lakes are dates sampled and simulated are listed in the header. Asterisks indicate a rejection of the null hypothesis, that the simulated and real distributions are different, at the alpha = 0.1 level. This means that no asterisk indicates an accurate simulation from a statistical perspective.

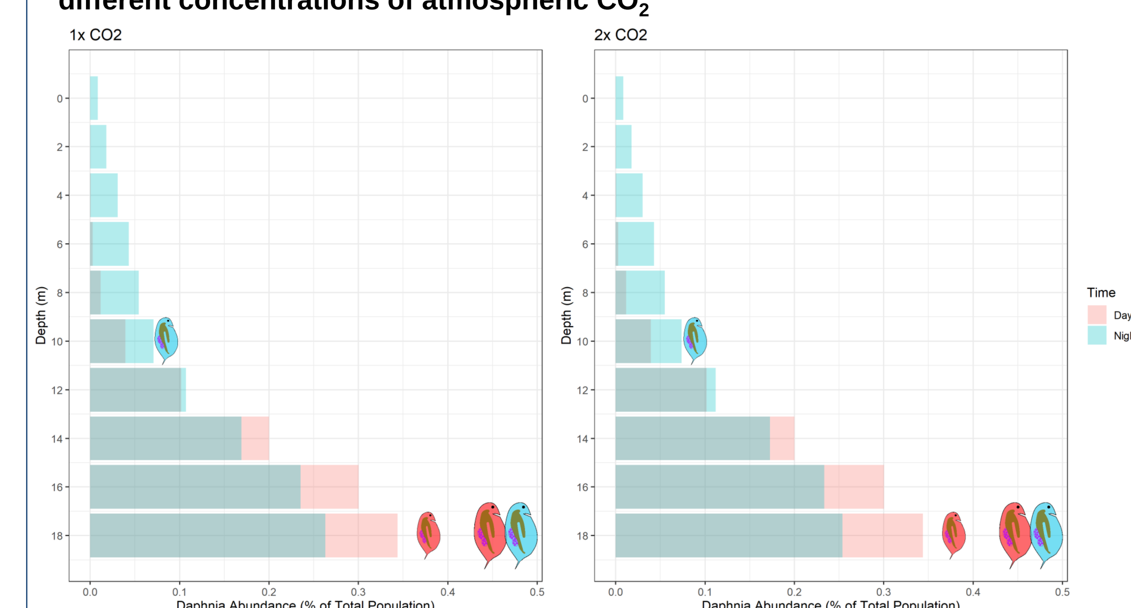
Lake	Date	Time	*p*-value
Trout Lake	May 1992	Noon	0.2498
		Midnight	0.7137
	June 1992	Noon	0.0924*
		Midnight	0.3486
	July 1992	Noon	0.0147*
		Midnight	0.0128*
	September 1992	Noon	0.0298*
		Midnight	0.5563
Crystal Lake	6th August, 1991	Noon	0.4005
		Midnight	0.7870
Sparkling Lake	7th August, 1991	Noon	0.7591
		Midnight	0.9883

RESULTS

Climate Change Simulations

- Using the conditions of Sparkling Lake (Vilas County, WI), run through the Oregon State University Atmospheric General Circulation Model (Schlesinger and Zhao 1989) to predict lake conditions with double the amount of atmospheric CO_2 (approx. the year 2100), we simulated a new vertical distribution of *Daphnia*.
  - Note that only temperature structure of the lake was changed for this model. Predator abundance and food availability was unchanged.
- The change in temperature structure under 2x atmospheric CO2 conditions resulted in very little change in the vertical distribution of *Daphnia*. Some intermediate sizes moved deeper, but this change had little noticeable effect overall.

Simulated vertical distribution of Daphnia in Sparkling Lake in 1991 in different concentrations of atmospheric CO_2



1x CO_2 is shown on the left and 2x CO_2 is shown on the right. Daytime simulations are in red and nighttime is in blue, overlayed on top of each other. The large *Daphnia* cartoons represent the optimal depth of 60 µg *Daphnia* and the smaller cartoons 10 µg.

CONCLUSIONS

- The model we developed to estimate vertical distribution of *Daphnia* is successful in many aspects. It accurately mimics *Daphnia* behavior and matched field data in most of the conditions we tested.
- The model works better for estimating nighttime distributions, which is likely related to the fact the model seems to perform better in conditions of reduced predation risk.
- With this model we can see that the environmental condition of greatest consequence to diel vertical migration behavior is the abundance of predators. The reason we saw very little change in distribution as a result of climate change is likely because we did not account for changes in fish distributions that are likely to occur with changing temperature structure.
- Enhancements to the model can still be made to achieve more accurate vertical distributions compared to field data. These possible enhancements include the addition of non-visual predators, like predatory zooplankton, to the model and integration of an uneven distribution of *Daphnia* sizes within the population.
- Development of the R package version of this model is ongoing and is planned to be publicly released upon its completion.

For additional information please contact:

Bennett McAfee
Lawrence University
BennettJMcAfee@gmail.com

References

- Brierley, A. S. (2014). Diel vertical migration. *Current Biology*, 24, R1074-R1076.
- Vinyard, G. L., & O'brien, W. J. (1976). Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *Journal of the Fisheries Board of Canada*, 33, 2845-2849.
- Schlesinger, M. E., & Zhao, Z. C. (1989). Seasonal climatic changes induced by doubled CO_2 as simulated by the OSU atmospheric GCM/mixed-layer ocean model. *Journal of Climate*, 2, 459-495.