An Agent Based Model of the Diel Vertical Migration Patterns of Mysis diluviana

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Abstract

Recent work indicates that the macro-invertebrate *Mysis* exhibits partial diel vertical migration (DVM), whereby one part of the population remains on the lake bottom at night while the other migrates up the water column. The drivers underlying the decision to migrate remain unknown. We developed an agent-based model that simulates thousands of individual mysids decision-making processes at an hourly time step throughout a year. The model takes into account a daily and seasonally changing environment, including light, temperature, resources, predation risk, and body condition. We found that the simulated *Mysis* population is highly sensitive to changes in the energy cost of preforming migration. In addition to testing hypotheses about migration drivers, the model, once parameters have been calibrated with real data, will help facilitate more efficient field sampling and prediction of resource availability for mysivorous fishes by evaluating the potential for seasonality in Mysis migration patterns.

Keywords: Mysis, Modeling, Ecology

1. Introduction

Mysis diluviana (*Mysis*) is a macroinvertebrate crustacean that lives in deep glacial lakes. They exhibit a behavior known as diel vertical migration (or DVM) and in doing so transfer nutrients from the benthic to the pelagic environments of a lake. Previous research efforts into *Mysis* have been focused on particular aspects of their migrations (Watkins et al. [1]). Here we take a step back and access the sensitivity of migration to changes in different environmental parameters using Monte-Carlo-style simulation of many individuals at an hourly time step over a year.

1.1. Why Modeling?

More traditional methods of measuring the effects of environmental changes are costly and time consuming, requiring many hours of sampling and with the inherent noise of real world sampling. By modeling we are able to investigate effects at a much lower cost and gain picture of the trends of effects.

1.2. Modeling is not perfect

It should be noted that the results and their specific units and/or amounts may not be exact, but what is important are the trends. We hope that the results from this modeling based exploration into DVM will help drive future real-world sampling efforts in a more efficient and impactful direction.

2. Methods

2.1. Programming Language

The programming language used for the model is R (R Core Team [2]). R was chosen due to its high adoption rate in the ecology community. This will allow for easier dissemination of the workings of the model and expansion by future researchers.

2.2. Agent-Based

An agent based approach was chosen for the model as it allows for the interrogation of effects on the population and also the detection of multiple stable strategies while at the same time accounting for the inherent stochasticity of variables such as weather.

2.3. Expandability

The environmental variables fed into the agent-based main model are generated using their own sub-models. This design was chosen because it allows the perturbation of environmental factors but also for the ease in which real data can be substituted for the generated data. As data are gathered from the environment they can be gradually integrated into the model to allow for more accurate measurements of effects and potentially in the future, predictions of *Mysis* locations.

2.4. Variables

The following are the variables used throughout the model.

Variable	Value	Description and Units	
s	1 for winter/spring, -1 for summer/fall	Seasonality	
M	40	Max Depth	Meters
K_t	.003	Curve Steepness	
K_p	.03		
m_t	1667	Midpoint of curve	Hours
m_p	120		Energy
h	1,2,...,8750	Hour of year	Hours
min	0.15	Min value of food availability ratio	
max	0.95	Max value of food availability ratio	
s	$(min - max)/(2)$		
a	$(min + max)/(2)$		
t	$\frac{1}{365 \cdot 24}$	Sinusoidal scaler	
H	5040	Hour of peak availability	Hours
c	$27.8 \cdot 24$	Moon cycle length	Hours
h_c	h modulous c	The point in the moon cycle	Hours
k	0.3	Extinction coefficient of lake (Jensen et al. [3])	UNITS
I_x	1×10^{-3}	Mysis Light threshold (Boscarino et al. [4])	Lux
I_o	(input)	Light level at lake surface	Lux
n	250	# of mysids	
r_h		Average hourly reward	Energy
m_c		Daily migration cost	Energy

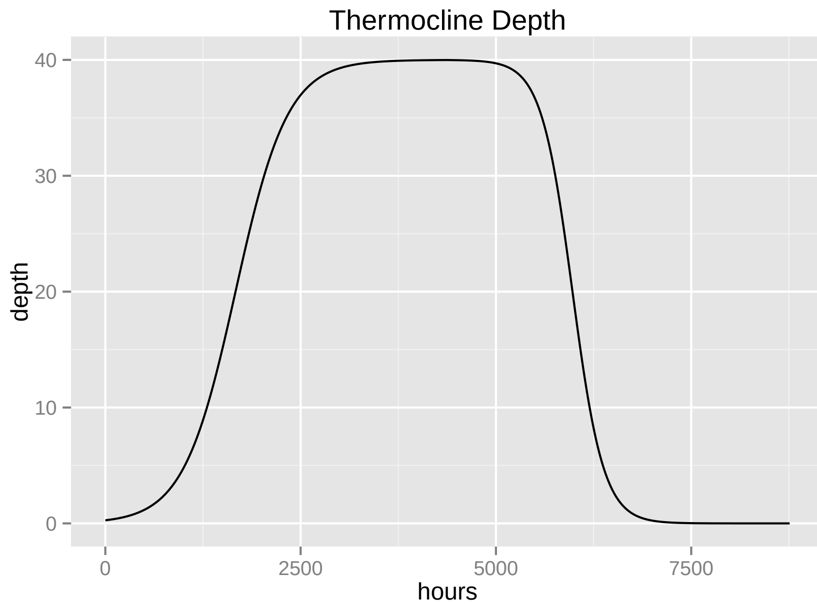
2.5. Sub-Models

Four sub-models were developed to generate environmental variables for the main model. R scripts for the generation of all data are available in the appendix and at rpubs.com/nstrayer.

2.5.1. Thermocline Model:

The first is a model of the depth in the water column at which ten degrees celsius is attained. This temperature was chosen as a Mysis threshold based upon the work of Jensen et al. [3]. To model this location over the year two sigmoidal curves were joined together to form the pattern observed in most large bodies of water.

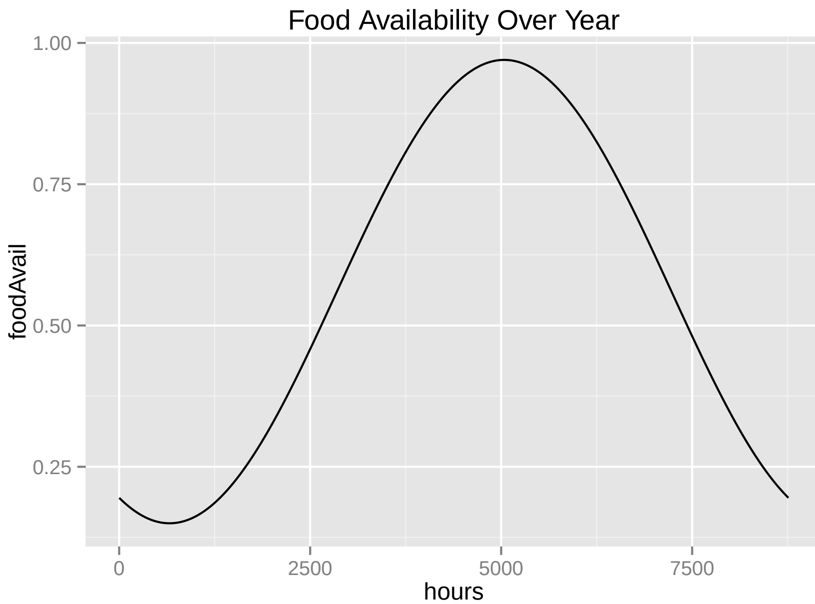
$$Th(h) = \frac{s \cdot M}{1 + e^{-k_t(h - m_t)}}$$



2.5.2. Food Availability

The food availability ratio is bounded between 0 and 1 and is a normalized measure of food quality/quantity in the pelagic (surface) environment to the benthic (bottom) environment. E.g. A food availability score of 0.8 implies 80% of the food is available in the pelagic waters.

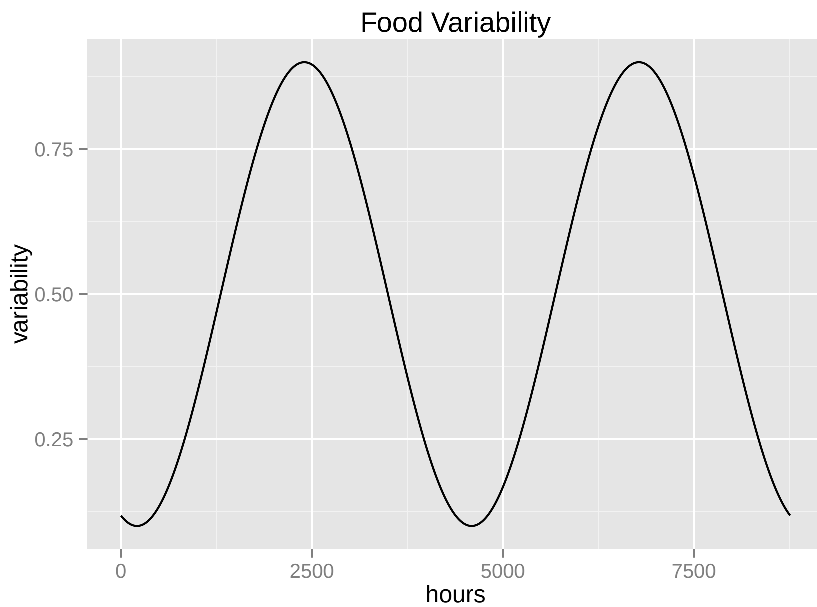
$$FA(h) = s \cdot \cos\left[(1/8750) \cdot 2\pi \cdot (h - H) + a\right]$$



2.5.3. Food Variablity

To simulate the range of possible feeding conditions throughout the year a curve depicting the variability of food availability was developed. To do this we simply doubled the frequencies of the food availability curve in the previous section to capture high variability in food availability during spring and fall (do to thawing and forming ice respectively). This value is used in the model to control the spread of the distribution upon which feeding rewards are drawn.

$$FV(h) = s \cdot \cos\left[(1/8750) \cdot 4\pi \cdot (h - H) + a\right]$$



2.5.4. Isocline Depth

Mysis are photophobic, meaning they are repealed by light. (Boscarino et al. [4]) looked at this sensitivity and found a threshold of light in lux at which *Mysis* tended to not cross. We modeled where in the water column this light level threshold was reached over the course of the entire year. To do this data of light intensity levels in Burlington were obtained from the National Renewable Energy Laboratory (NREL [5]).

2.5.5. Moon Cycle

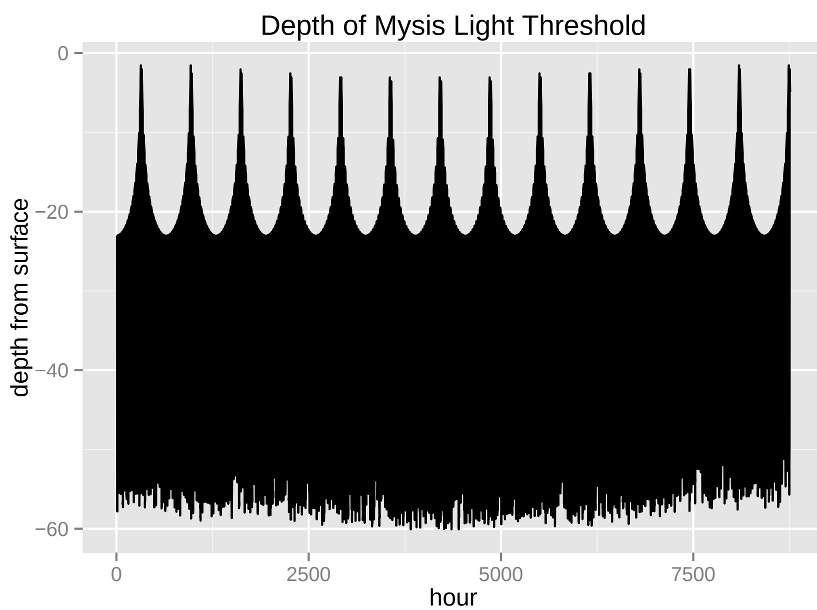
Raw data was read in from the National Renewable Energy Laboratories data explorer, however the sensitivity was not high enough to pick up the lunar cycles. To overcome this, nighttime light intensity levels (Palmer and Johnsen [6]) were filled into with a model of the lunar cycle. The greatest light intensity between the moon cycle model and real data was chosen for the final dataset.

$$MC(h_c) = 0.5\left[\cos\left(\frac{1}{c} \cdot 2\pi \cdot h_c\right)\right] + 0.5$$

2.5.6. Beer's Law

Once a complete dataset was assembled for the year, the light intensity was run through an equation derived from Beer's Law (Hutchinson [7]). This equation takes in light intensity levels and returns the depth at which the mysis light threshold is reached accounting for the dispersion of light through a particular medium. The extinction coefficient (k) used was one from Lake Superior (Jensen et al. [3]).

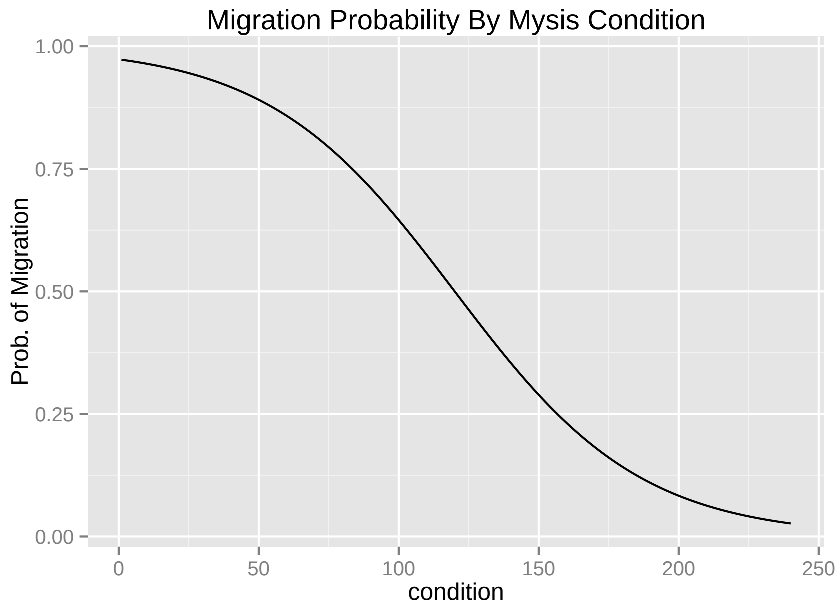
$$BL(I_o) = \frac{1}{k}\Big[ln(I_o) - ln(I_x)\Big]$$



2.5.7. Probability to Migrate

In order to simulate an individuals pressure to migrate based upon body condition we modeled the influence to migrate based upon body condition as a sigmoidal curve. With this curve a *Mysis* with a high body condition has less pressure to migrate than a mysis with a low body condition. The midpoint of the sigmoid sitting at what we decided was a 'normal' body condition.

$$PM(x) = \frac{1}{1 + e^{-k_p(x-m_p)}}$$



2.5.8. Migration Reward

If the individual has migrated on a given day then at every hour (h_i) it draws its energy reward from a normal distribution with mean scaled by food availability with a standard deviation of $FV(h_i)$. Note that this value can be negative to account for unproductive feeding efforts.

$$MR(h) = N\Big(r_h \cdot [1 + FA(h)], FV(h)\Big)$$

2.5.9. Stay Reward

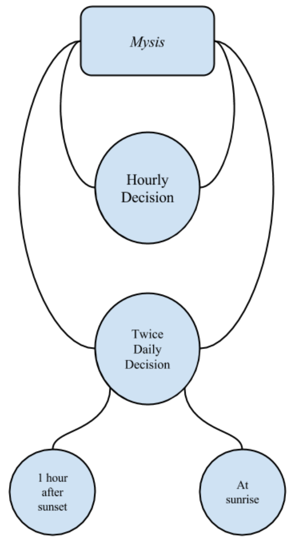
If the individual has not migrated, their reward is the largest value between twenty percent of the migration reward or 0.2 energy units.

$$SR(h) = \max\Big[0.2 \cdot MR(h), 0.2\Big]$$

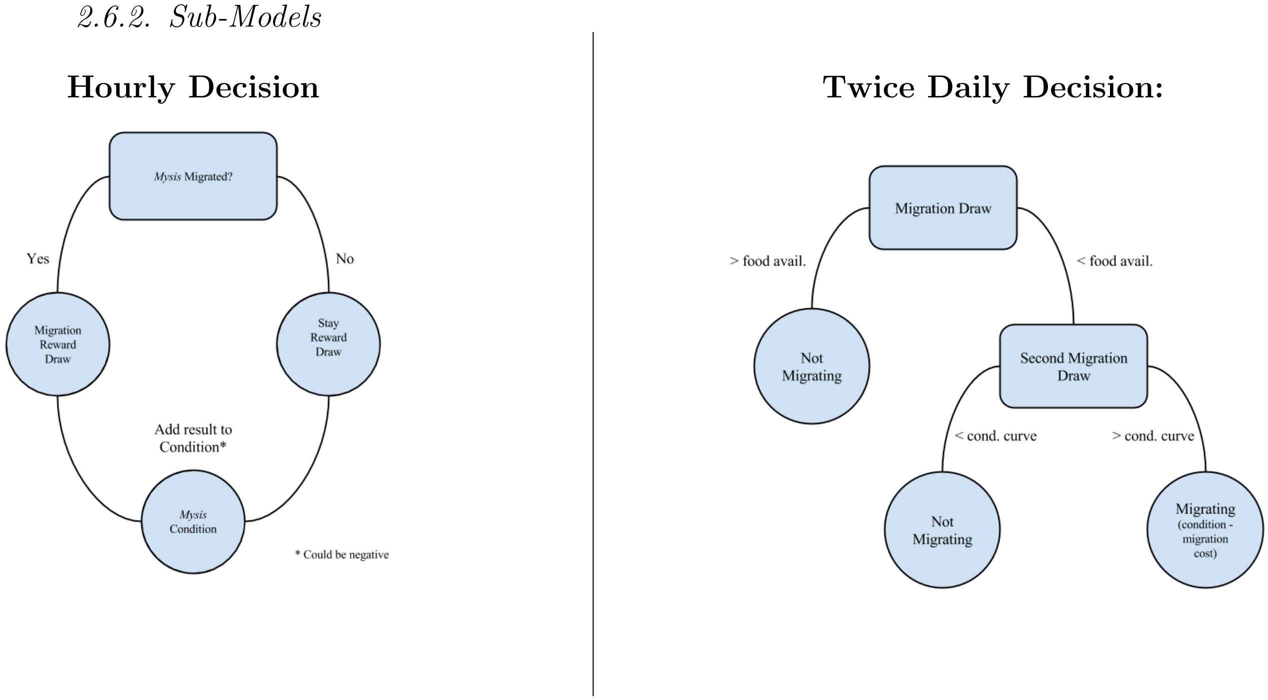
2.6. Agent-Based Model

Our agent based model runs an individual through a year on an hourly time step. At every hour the mysis attempts to feed based upon its current condition (migrated or not). Twice a day, once one hour after sunset and then again one hour before sunrise the *Mysis* decides to migrate based upon its condition and environmental food availability.

2.6.1. *Main Model*



2.6.2. *Sub-Models*

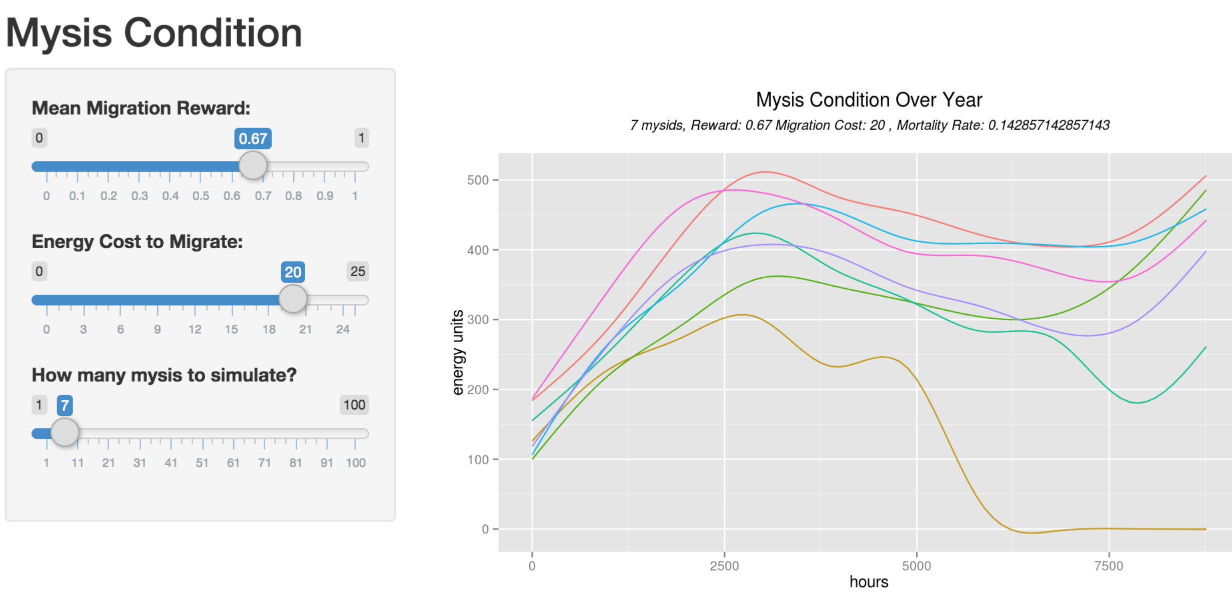


2.6.3. *Testing of Agent-Based Model*

To test the model's sensitivity to changes in variables we ran the model through an entire year, simulating n mysids while perturbing the mysids average hourly energy reward and cost of migration. At each simulation we recorded the proportion of surviving individuals with predation risk set to zero as to isolate the effects of the perturbing the variables.

2.7. Interactive Model Server

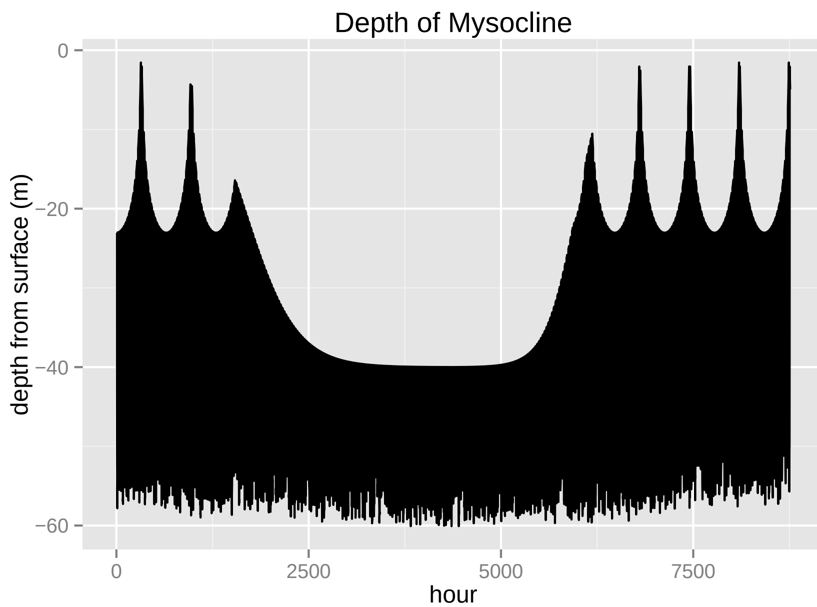
In order to help speed up analysis of variable perturbation an interactive R shiny server (Chang et al. [8]) was developed. This server allows the user through a graphical user interface to manipulate parameters of the model and in real time watch the effects of those manipulations over the course of a year on the simulated individuals. In addition to serving as a quick way of testing effects, it also allows for the model to be investigated by users not comfortable enough with code to manually change the variable values in the R script.



3. Results

3.1. Mysocline

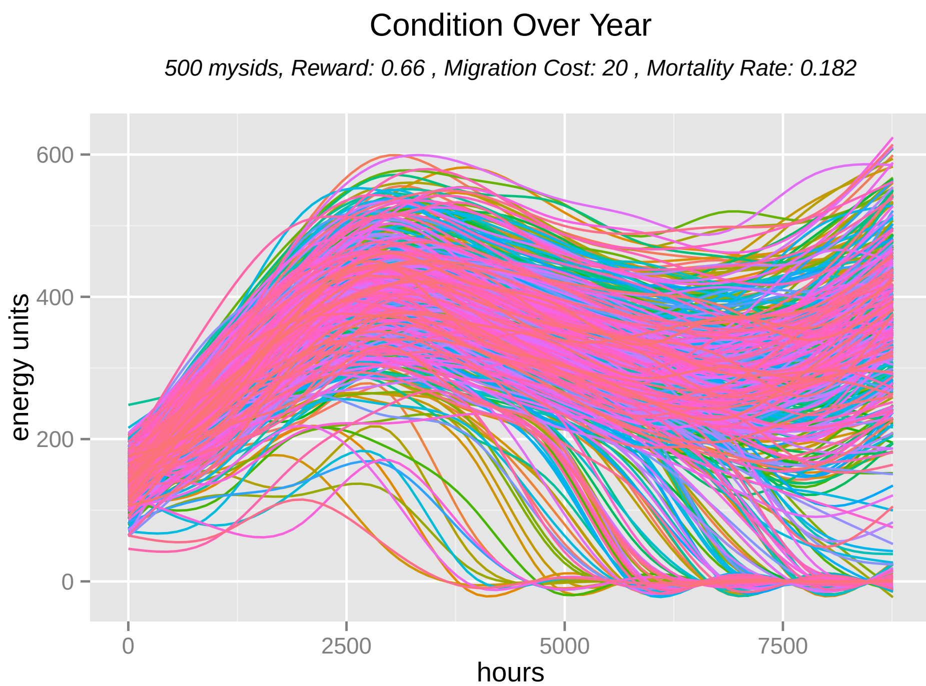
By merging the theoretical migration limit provided by where ten degrees celsius is in the water column with the location of the light threshold I_x we are able to get a macro-view of migration extent for mysids in Lake Champlain over the course of the year.



From this figure we can see that during the winter the factor limiting *Mysis* migration is the light intensity levels, whereas in the summer and early fall it is water temperature.

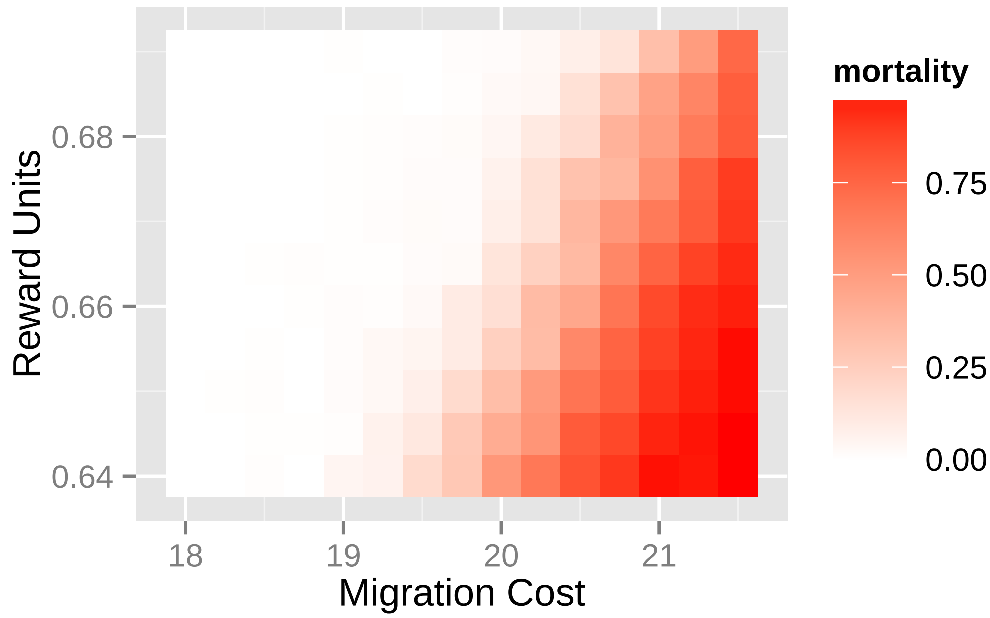
3.2. Sensitivity to Rewards and Cost

Using the shiny app we located a range of expected behavior for the parameters of average energy reward (r_h) and daily migration cost (m_c). We then set the model to run on a range of these values of 0.64 to 0.69 for r_h and 18 to 21.5 for m_c. At each combination of the variables we recorded mortality rates.



From this run over a year with 500 mysids we can see that most individuals fair very well in the first few months of the year, and then the whole population's condition starts to decline around late spring, continuing to decline until early winter and then resuming a climb in the last couple months of the year. This particular run with r_h of 0.66, and m_c of 20 has a mortality rate of 18.2%.

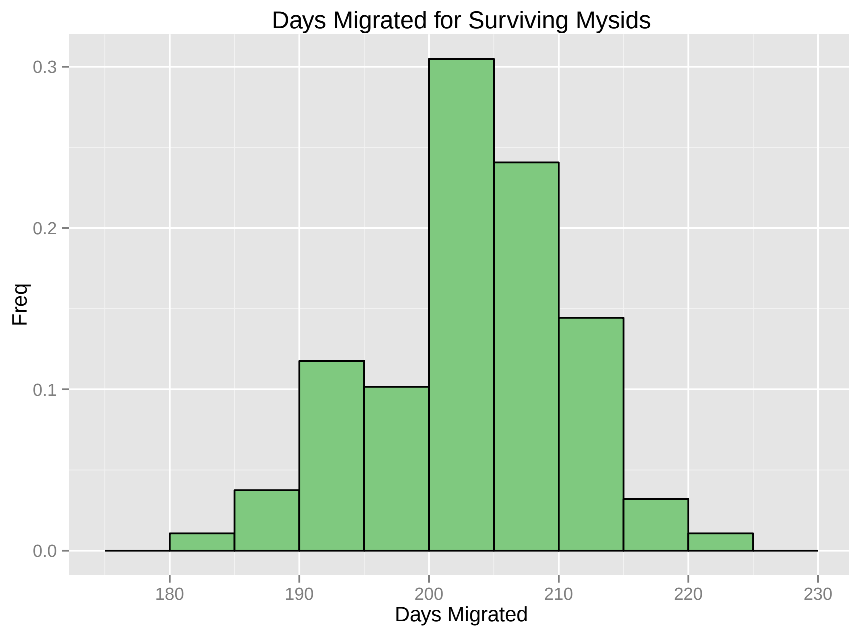
By repeating this simulation over the aforementioned ranges of r_h and m_c we can see the model's sensitivity to their changes.



From this plot we can see that if we fix the reward units and perturb the migration cost that significant mortality rates occur at every tested migration cost value, but not if we hold migration cost steady and perturb reward units. This result implies that further investigation into the energy cost of migration should be performed.

3.3. Multiple Migration Strategies

For each run the number of days that a given surviving individual chose to migrate was recorded and plotted. For a large majority of the runs the distribution of days migrated was normal, however, for some runs (such as the shown example) there appeared to be a slight bi-modal distribution. None of the results were great enough to make any definitive statements about the presence of multiple stable strategies for migration behavior.



4. Conclusions and Future Directions

4.1. Environmental Roll

The models response to variable perturbations implies high sensitivity to environmental changes.

4.1.1. Fall Condition Climb

For example, population level conditions were highly tied to the seasons with a large portion of the population getting close to starvation in the mid-summer months, if recovering brought by fall didn't occur until later in the year there is a strong potential for a high impact on the survival rate of individuals.

4.1.2. Variable Extinction Coefficient

The link between algae blooms and climate have been well established (Isenstein et al. [9]). For the current model the clarity of the water is set at a constant k. Algae blooms obviously have a large impact on the dispersion of light through the water column. A higher k value would raise the *Mysis'* migration extent during the beginning and end of the year and increase the cost of migration, thus having large impacts on population levels.

One way to investigate this would be to put a variable extinction coefficient into the model to simulate algae blooms and study the effects on the *Mysis* population.

4.1.3. Multiple Migration Strategies

In the results we saw hints at a bimodal distribution of migration strategies by looking at the number of days migrated for surviving individuals. The model in its current form does not have the ability to fully explore these patterns. Future efforts could give individuals "personalities" such as risk adverse or conservative and explore the end conditions of populations with those given traits too detect viability of differing strategies.

4.2. Role in the Lab

As previously mentioned the cost of sampling at a high enough frequency to gain a clear picture of migration patterns is prohibitively expensive and time consuming. That being said, modeling, especially with so many assumptions is not an exact science. This model will replace field sampling *Mysis* but it can have its own valuable roll in the lab. As the model is tested and calibrated with real data its ability to help influence new samplings and explain observed behaviors will expand. Simulation and real world sampling can help each other become more accurate and efficient and hopefully drive a new workflow in *Mysis* DVM research.

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