Modeling the direct and indirect ecological effects of a trophical transmitted parasite using Agent Based Modeling

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Summary

In host-parasite systems, parasites lives on or within the host and benefit from the host's resources and/or tissues, while the host is typically harmed in some way by the parasite's presence. Parasites in general are involved in various ecological processes, they can alter food web dynamics and provoke changes in entire ecosystems. A fundamental characteristic of trophically transmitted parasites is the ability to manipulate their intermediate hosts' behaviour in order to increase their own fitness. With this characteristic in mind, parasites have a multitude of effects on their hosts, including changes not only in behaviour, but also growth and reproduction. These changes influence the direct and indirect ecological effects of their respective hosts, which can ultimately change the structure and function of entire ecosystems. In this thesis, I aim to create a better understanding of the dynamics of host-parasite interactions in trophically transmitted parasites by using an agent-based model of the life cycle of *Schistocephalus solidus*. The results showed a multitude of direct and indirect ecological effects of the parasite on the simulated ecosystem. Upon introduction of the parasite, we observed density shifts along the expected trophic cascades in the entire community. In conclusion, the model achieves to reflect the real world in different settings and produces stable results.

1. Introduction

Parasites are essential members of ecosystems, as they heavily impact other species in their community and drive change in their ecosystem as a whole, acting as *ecosystem engineers* (Hatcher et al., 2012). They highly influence food webs, affecting their structure, chain length and linkage density (Lafferty et al., 2006). Their direct effects on their respective hosts lead to changes in behaviour, competition, predation and herbivory and therefore effect species coexistence and influence other ecosystem properties (Hatcher et al., 2012). Furthermore, parasites can inflict density-mediated indirect effects through consumptive effects and trait-mediated indirect effects through nonconsumptive effects (Buck, 2019).

As ecosystem properties, such as biodiversity, affect parasite populations, there is a potential for feedback between parasitism and ecosystem states, therefore creating a bidirectional interdependence (Hatcher et al., 2012).

Host-parasite interactions are also key drivers of evolutionary dynamics, as they are omnipresent and are able to alter their host fitness dramatically. They can evolve rapidly and strongly depend on existing environmental conditions. As a result, host-parasite and host-ecosystem interactions often culminate in co-evolution, functionally linking evolutionary and ecological processes (Brunner et al., 2017).

However, the interactions between parasites and hosts and their effects are very complex and often multifactorial. Experimentally investigating their effects is a daunting task - particularly the effects of parasites with multiple hosts. One way to better understand the effects of parasites and their role on ecosystems is by mathematically modeling their interactions or by using computer simulations to understand these complex effects (DeAngelis, 2018).

One of these effects of host-parasite interactions are trophic cascades, which are a central aspect of this thesis.

1.1 Trophic Cascades

Trophic levels are one of the pillars of ecology, providing many of its basic predictions, among them predator-prey oscillations and trophic cascades (Barbier and Loreau, 2019). In an ecosystem, every species can be partitioned into a trophic level based on its diet (Barbier and Loreau, 2019). These trophic levels are linked to one another through the interaction of organisms in different trophic levels. This interaction can result in trophic cascades and are used to describe population cycles (Barbier and Loreau, 2019; Ye et al., 2013).
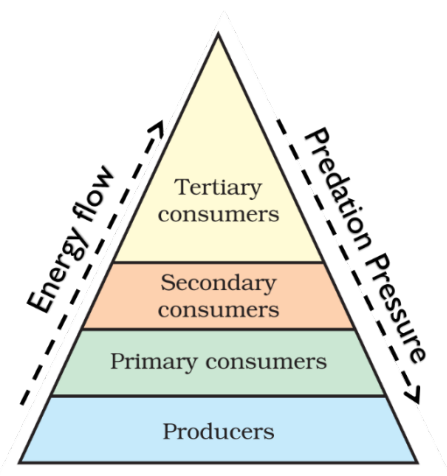
Figure 1: Trophic cascades

In general, there are two types of forces that can regulate the energy flow in ecosystems, top-down and bottom-up forces. Top-down forces are expressed by an upper-level predator, which impacts the lower trophic levels (Pace et al., 1999). Changes in density at a higher trophic level trigger opposite changes in their respective lower trophic level. This inverse correlation is able to ripple (or *cascade*) down a food chain and therefore extend to the autotrophic level, as every single entangled trophic level is able to function as a top down force and is consequently not exclusive to the highest level consumer (Buck and Ripple, 2017; Pace et al., 1999). Nontheless, apex predator loss or even changes in their behaviour usually entail major shifts in the abundance and density across all lower levels because of the altered predation pressure (Buck and Ripple, 2017; Luhring and Delong, 2020). These changes have can have far reaching effects. Consequently, the manipulation of one species can reshape the entire food web (Estes et al., 2011; Wood et al., 2020). One has to note that the effects of top-down forces are not limited to changes in density, but are also trait mediated, such as shifts in body-mass - which has been considered as a key mediator of trophic cascades (Buck and Ripple, 2017; Luhring and Delong, 2020).

Bottom-up cascades on the other hand occur, when changes in resources and nutrient supply at lower levels lead to similar changes in equilibrium abundances in higher trophic levels as well (Heath et al., 2014). Pace et al. (1999) state, that top-down and bottom-up forces operate simultaneously and are often hard to separate in practice. Bottom-up forces are ubiquitous and necessary to account for the responses of ecosystems to any disruptions, but they are not sufficient. Therefore both forces need to be considered, in order to properly understand trophic cascades (Estes et al., 2011).

It becomes evident, that trophic cascades result in enormous relevance for the ecosystem and entail the possibility of extinction of entire species or changes in power structures (Estes et al., 2011; Lafferty et al., 2008). Aquatic systems, in which the metabolic rates of primary producers exceed those of their consumers, are particularly connected to strong trophic cascades (Barbier and Loreau, 2019).

1.2 Agent Based Modeling

As previously mentioned, host-parasite interactions are a complex system which can be impacted by various factors. It is known that these factors impact populations dynamics (Hudson, 2002), but there is not yet quantifiable data on which of these factors is most prevalent and to what extent. Since real experiments often fail to combine Testability and Generality (DeAngelis, 2018) this thesis harvests the power of agent-based modeling (elsewhere named individual-based modeling) in pursuance of producing reproducible data to quantify said factors.

Agent-based modeling (ABM) is a computational approach to modeling complex systems that are composed of many individual agents which interact with each other and with their environment. ABM proposes the key idea that individual agents are modeled as autonomous entities that can interact with each other and make decisions based on their own rules and behaviours. These interactions and decisions are then used to generate emergent behaviour at the macro level, such as collective decision-making, market dynamics, population dynamics, or community dynamics. In this way, ABM provides a bottom-up approach to modeling, where the behaviour of the whole system emerges from the interactions of individual agents, rather than being prescribed by a set of governing equations (Datseris et al., 2022).

One of the main advantages of ABM is its ability to handle heterogeneity and nonlinear interactions, which are often present in complex systems. This makes ABM a useful tool for modeling real-world systems that are often too complex to be captured by traditional models. In the field of ecology, ABM has been used to model population dynamics, such as predator-prey relationships and the spread of invasive species(Grimm & Railsback, 2005). However, there are some challenges associated with ABM. One of the main challenge is the need for a large number of parameters, which can be difficult to estimate and may result in uncertainty in

the results. In addition, ABM is computationally intensive, which can make it difficult to run large models or analyze the results in real-time. Finally, it can be difficult to validate ABM models, as there is often limited data available for complex systems (Filho et al., 2005).

In the next sections, I will describe both the life cycle of *Schistocephalus solidus* and my modeling frame work.

1.3 The Agents

1.3.1 The lifecycle of *Schistocephalus solidus*

The tapeworm *Schistocephalus solidus* is a trophically transmitted parasite with a three-host life cycle and defines the core structure for this model. The definitive host can be any warm-blooded vertebrae – mostly piscivorous birds. Here *S. solidus* undergoes reproduction and its eggs are released into an aquatic ecosystem via the vertebrae's feces (Barber and Scharsack, 2010). *S. solidus* is a simultaneous hermaphrodite and therefore able to self-fertilize or in the case of multiple infections cross-fertilize (Wedekind et al., 1998). The eggs hatch into free-swimming coracidia which are trophically transmitted to a wide range of cyclopoid copepods, the first intermediate hosts. In the copepods haemocoel, the parasite matures and develops into procercoids, therefore becoming infective to the second intermediate host – three spined sticklebacks (Wedekind et al., 1998). The time spent in the copepod determines the growth in the stickleback and the size reached in the stickleback directly correlates to the fertility in the final host and even the fitness of the next generation (Hammerschmidt et al., 2009). The infection of a stickleback is also trophically transmitted, as sticklebacks feed on parasitized copepods, hence becoming infected themselves. In the sticklebacks digestions system, the procercoids shed their outer layer and penetrate the wall in order to reach the intestine, where the parasite then develops into a plerocercoid. This plerocercoid can then grow to a large size inside the sticklebacks body cavity (Barber and Scharsack, 2010). Upon predation by the definitive host the lifecycle is completed.
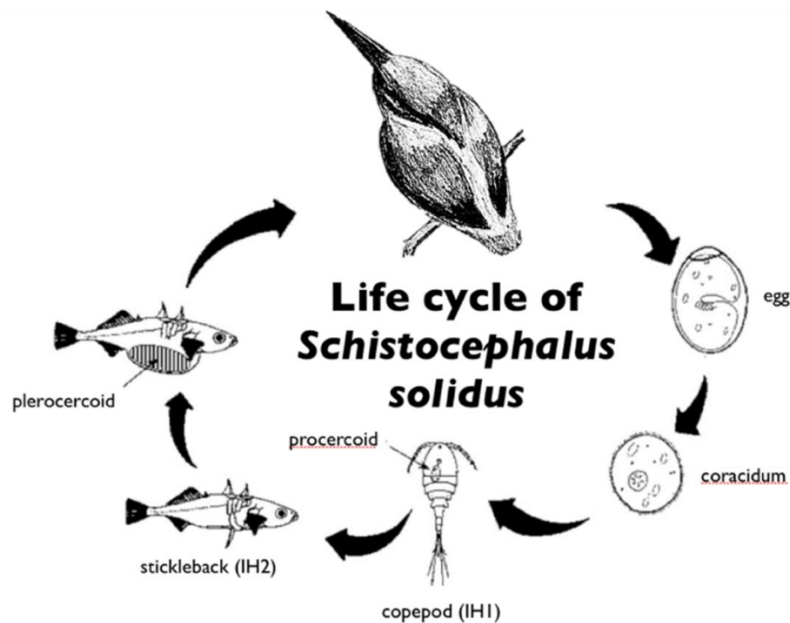
Figure 2: Life cycle of *Schistocephalus solidus* (Simmonds, 2015)

1.3.2 First Host: Cyclopoid copepods

Macrocyclops albidus is a copepod from the Cyclopoidae family and will provide the structure of the copepod simulated in this thesis. Cyclopoids are predatory copepods that prey on smaller zooplankton and belong to the most abundant predators in freshwater habitats (Roura et al. 2018, (Marten and Reid, 2007). Their typical fast movements, which alternate with passive sinking behaviour, are often described as jumps or hops. These jumps make them great hunters but also rapid escapers. While fleeing themselves, copepods can reach a maximum speed of 5 mm/sec (Marten and Reid, 2007). Cyclopoids themselves hunt actively by detecting their prey through mechanoreceptors which spot movements within a distance of about 1mm. In comparison to other species, they show an aggressive behaviour when it comes to prey, which can sometimes be almost twice as big as the cyclopoid itself (Marten and Reid, 2007; Rey et al., 2004). Cyclopoids reproduce sexually, as the females produce a paired egg sac from which a new batch of eggs is fertilized and then released every 3-6 days (Marten and Reid 2007). During development from egg to adult, copepods pass through six naupliar stages and five copepoid stages, while shedding their skin at every stage. This development can take from a few days to several weeks, depending on environmental conditions (Marten and Reid, 2007). As an adult, a copepod livespan can entail between one and two months under optimal conditions (Marten and Reid 2007). Since copepods directly affect the resource availability and the energy transfer in aquatic food webs (van Someren Gréve et al., 2019), understanding the effects of *S. solidus* on the zooplankton community through their effects of copepods will give us a better understanding of the role of *S. solidus* in particular and of parasites in general.

1.3.3 Effects of *S.Solidus* on *M. albidus*

We have established that Parasites are able to influence intermediate hosts in a way that optimizes their growth and transmission to the next host. In the case of *S. solidus*, these influences are mainly threefold.

Firstly, copepods that are infected with *S. solidus* are expected to show an increased level of general activity level (Franz and Kurtz, 2002). But as stated earlier, the time spent inside the copepod correlates to further reproduction success in the stickleback. Therefore, *S. solidus* decreases its hosts' activity during the first days of infection in order to avoid premature predation (Hammerschmidt et al., 2009). The increased level of general activity is only displayed after a couple of days post infection.

When the cestode becomes infective to its second intermediate host, it manipulates the copepod to develop risky behavior to increase the chance of predation (Hammerschmidt et al., 2009). Paired with a general increased level of activity, the likelihood of transmission increases (Franz and Kurtz, 2002)

Furthermore, the feeding rates of infected copepods are elevated due to the higher energy consumption and to enhance parasite growth (Berkhout and Barber, 2019) .

Lastly, infected female copepods show a slight inhibition in reproduction, as their egg sacs contain fewer eggs (Wedekind, 2017).

1.3.4 Phytoplankton and grazering zooplankton

Phytoplankton are primary producers and build the foundation of any aquatic food web, since like land plants, they convert solar energy into organic compounds using chlorophyll that serve as a nutritional basis for most zooplankton (Lindsey et al., 2010; Jakhar, 2013). Phytoplankton growth depends on the availability of numerous abiotic factors, such as light intensity, carbon dioxide availability and the presence of various nutrients (Lindsey et al., 2010).

Zooplankton on the other hand is a collective term for omnivoric organisms with the capacity for phagotrophy, consisting of species belonging to the Rotifera, Copepoda, Protozoa and Cladocera (Sterner, 2009). They build the intermediate trophic level between phytoplankton and fish, and act as an important component of carbon and nutrient cycles, accounting for a large proportion of the energy transfer in aquatic ecosystems (Everett et al., 2017).

For the creation of this model, the only important (behavioural and dietary) attributes of zooplankton are herbivory and evasion of potential predators, thus no single species will be discussed in detail.

Next to other biotic and abiotic factors, zooplankton play an important role in phytoplankton density control via grazing (Lampert et al., 1986), which is why henceforth zooplankton will be refered to as *grazers* here and in the following code snippets.

2. The model

2.1 Structure of the Agents and their environment

As the name *agent based modeling* suggests, at the heart of the model are its agents. Their environment is set as a three dimensional continuous space, a representation of agent dynamics on a continuous medium where agent position, orientation and speed, are true floats, with dimensions 100 x 100 x 50.

As shown in figure 1, agents are provided with multiple (mutable) fields, which essentially simulate important characteristics from their real-world counterparts. Most notably, every agent is allocated with an *id* to ensure uniqueness, a *position* in the space as described above and of course a *type* – one of the earlier introduced important actors. Furthermore, every agent is provided with a set of basic settings, such as *energy* (initial energy), *Δenergy* (energy gain upon predation) and reproduction probability. Lastly, two very important fields are the *infected* and *infectionsdays* parameters, which alter the behaviour of the agent at the very center of this research: The copepod.

The model is initialized with a certain amount of agents as depicted in figure 3. This code also shows some of the values which are allocated to the different agent types, such as *velocity*, *reproduction probabilitys, vision radius* and *energy values*.

```
mutable struct CopepodGrazerParasitePhytoplanktonStickleback <: AbstractAgent
    id::Int
    pos::NTuple{3, Float64}
    type::Symbol
    energy::Float64
    Δenergy::Float64
    reproduction_prob::Float64
    infected::Int
    infectiondays::Int
    […]
End
```

Figure 3: The initialization of the Agents with its different fields

```
function initialize_model(;                          # vision radius
    # initial amount of Agents                           copepod_vision = 10,
    n_copepod = 100,                                     grazer_vision = 10,
    n_phytoplankton = 400,                               stickleback_vision = 10,
    n_grazer = 300,                                  # reproduction probability
    n_parasite = 2000,                                   copepod_reproduce = 0.15,
    n_stickleback = 20,                                  grazer_reproduce = 0.2,
                                                         phytoplankton_reproduce = 0.14,
                                                         stickleback_reproduce = 1.0,
    # energy gain on predation
    starting_energy_copepod = 5,
    starting_energy_grazer = 5,                      # movement rates
                                                         copepod_vel = 1.1,
                                                         copepod_infected_vel = 1.2,
                                                         grazer_vel = 1.0,
                                                         stickleback_vel = 1.3,
```

Figure 4: Initial values and settings

2.2 Agent and Model Dynamics

2.2.1 Stepping and Dynamics

The model iterates over a certain amount of steps (n = 60). In every step, each agent themselves is stepped once. Stepping an agent includes that their energy level is lowered for each iteration and if it drops below zero, the agent is removed from the model. Furthermore, each step there is a chance of reproduction (realized via a random number generator), the agent is moved along its planned route and is also scanning its vicinity for food or prey. We will take a look at the movement in detail in the next chapter.

In pursuance of meaningful results, the agent and model behaviour is set to be as realistic as possible. As shown in Figure 5, the model displays the predator prey dynamics to its full extend. From the top down: Sticklebacks actively prey on copepods and grazers, copepods themselves hunt grazers and eat phytoplankton, while grazers only consume phytoplankton. Parasites are excluded from the active movement, that the other agents display. Instead, they swim around given random positions. Also, the last definitive host of the *Schistocephalus solidus* lifecycle, e.g. a piscivorous bird, is ommited in order to keep the model computable.

Upon infection, the behaviour of copepods changes. Firstly, an infection inhibits their ability to reproduce. Furthermore, infected copepods receive an increased feeding rate, increased chance of predation by displaying risk inducing behaviour and faster movement.
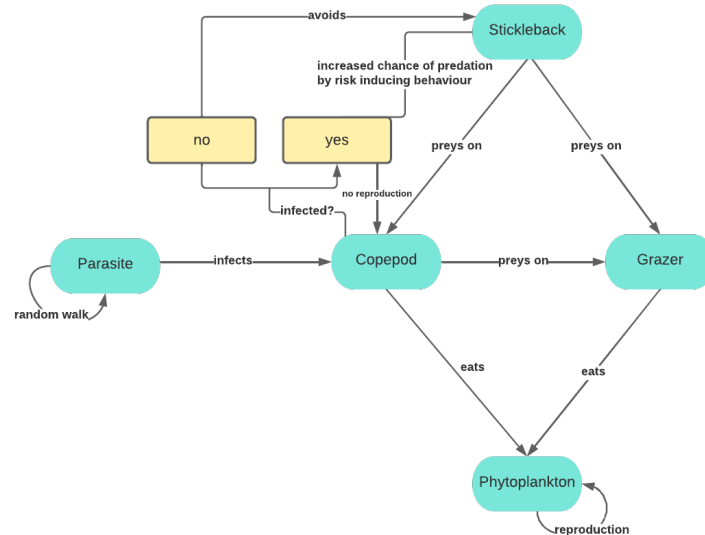
Figure 5: Agent and Model Dynamics

2.2.2 Realization of movement

The following code snippets display the realization of copepod behaviour while also providing an example of how the movement of the agents is computed. For the sake of readability these examples are written pseudocode - for the exact Julia syntax please visit my Github (App. 6). Starting with the movement of agents, the following computations are only made if the agent is stationary, meaning that the agent has not planned a route in a previous step. Also, every recognition of another agent is limited by the vision radius of the scanning agent. The values differ based on agent type, as seen in chapter 2.1. With this out of the way, there are a couple of different events.

The first possibility: Random Movement. The agent does neither recognize prey nor predators in its vicinity and therefore has not acquired a target position. In this case, the agent simply moves on to a random position in the model. This event is accessible for all agent types and displayed in Figure 6.

```
#if no prey and no predator nearby, move to a random location
if is_stationary && isempty(predators) && isempty(prey)
        plan_route(agent, random_walkable)
end
```

Figure 6: Random movement

The second possibility: The Flight. The agent identifies predators in its surroundings. Here, the agent abandons all previous movement calculations and aims for the position as far away as possible from the culminated position of all predators in order to escape. The computed direction is scaling inversely with distance. As a result, closer predators contribute more to

the direction to move in. This event is only available for grazers and copepods. An example of the code is shown in Figure 7.

```
#if there are predators nearby, override any other movement and flee from it
if !isempty(predators)
        # Try and get an ideal direction away from predators
        direction = (0., 0., 0.)
        for predator in predators
                # Get the direction away from the predator
                away_direction = (agent.pos .- predator)
                direction = direction .+ away_direction ./ eunorm(away_direction) ^ 2
        end
        […]
        plan_route!(agent, direction)
end
```

Figure 7: Flight behaviour

The third possibility: The Hunt. The agent discovers prey in its environment, therefore becoming a predator and acting as such by aiming for the position of a random agent considered as prey. Notice how it targets the position of a single agent and not the entire collected prey at once. Sticklebacks and copepods may display this behaviour, which is shown in Figure 8.

```
hunt = [x for x in nearby_agents(agent, agent_vision) if x.type == :copepod || x.type ==
:grazer]
if !isempty(hunt)
        plan_route!(agent, rand(hunt.pos))
end
```

Figure 8: Hunting behaviour

There is one more, copepod exclusive, possibility: The agent can act as the hunter as well as the hunted – meaning it recognizes prey (grazers) as well as predators (sticklebacks) in its vicinity. In this case, an uninfected copepod would choose survival over predation, therefore ignoring the prey and flee from predator(s). This behaviour is displayed, if a copepod is uninfected or infected for less than 12 days.

```
direction = (0., 0., 0.)
if copepod.infectiondays <= 12
        #get an iterable of nearby prey and predators
        prey = [g.pos for g in nearby_agents(copepod, copepod_vision) if g.type == :grazer]
        predators = [s.pos for s in nearby_agents(copepod, copepod_vision) if s.type == :stickleback]
        #if there are predators nearby, override any other movement and flee from it
        if !isempty(predators)
                act as previously described in Figure 5 Flight behaviour
        #only if there are no predators nearby, the copepod will look for prey
        if !isempty(prey) && isempty(predators)
                act as previously described in Figure 6 Hunting behaviour
```

Figure 9: Copepod movement uninfected

2.2.3 Changes upon infection

Previously, we have described how the agents and especially copepods move and behave if uninfected. Let us now take a look at how the infection alters the copepods behaviour in its various ways. Firstly, the copepod shows risky movement behaviour near sticklebacks. By calculating its movement destination as a combination of the positions of prey and predators (see Figure 10), infected copepods increase their risk of entering the vision radius of a stickleback and therefore becoming hunted themselves – effectively removing the "predator nearby" override their uninfected counterparts experience.

```
# if the copepod is infected for more than 12 days
if copepod.infectiondays <= 12
        #acknowledge predators and change the direction based on their position
        if !isempty(predators)
                act as previously described in Figure 5 Flight behaviour
        #the infected copepod exudes risk behaviour, by preying while predators are nearby
        if !isempty(prey)
                for agent in prey
                        toward_direction = (copepod.pos .+ agent)
                        final_direction = direction .+ toward_direction ./ eunorm(toward_direction) ^ 2
                end
        end
plan_route!(copepod, final_direction)
end
```

Figure 10: Copepod movement infected

Moreover, infected copepods gain increased activity (in this context meaning doubling the movement per step), an **increased feeding rate**, and **increased velocity**. These changes result in a wider radius of grazer recognition (feeding rate) and more distance covered along their route in during a single step (velocity). The latter two are also the variables we are going to access in order to try and model the ecological impact of the parasite *Schistocephalus solidus* on our ecosystem.

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2.2.4 Notes on phytoplankton and sticklebacks

Phytoplankton and Sticklebacks take on special roles in this model. Phytoplankton were especially hard to keep in balance. Often they experienced genocide at an early step count because of the predation by both grazers and copepods and therefore removing the energy gain of grazers from the model. Other iterations they overgrew and forced the compilation of the model to stop, which is why we introduced a carrying capacity of 5000 for the phytoplankton agent. Furthermore, phytoplankton are given an *age restriction*: After reaching the age of 10 steps, they are removed from the model. This value is entirely arbitrary and serves only the purpose of keeping the model stable and usable.

Sticklebacks on the other hand behave like copepods in their hunting movement, but are set to a fixed population of 20 at the start of the model iteration, meaning that sticklebacks are neither removed from the model nor added as new agents. Sticklebacks therefore act only as a predator to keep the grazer and copepod population in check and also to reintroduce parasites into the system.

2.2.5 Paramscan and ensemblerun

The model inherently contains many random processes – the movement of agents, stepping order and probabilities for reproduction, mortality and infection just to name a few. With the usage of Julias aramscan and ensemblerun methods, the model was run for 54 iterations on random seeds and provided with different values for the earlier introduced variables, which are supposed to invoke a behavioural change upon infection of a copepod. The values ranged from 1.0 to 1.5 for the velocity and 2 to 10 for the change in feeding rate.

To keep the data manageable and this thesis to an appropriate length, we will focus mostly on the edge cases, as the impact will be most visible in these extremes.

3. Research question and Expectations

In this thesis, I want to model the direct and indirect ecological effect that *S. solidus* has on organisms in his ecosystem. It has been proven, that these associations between the infection of copepods with *S. solidus* and the density of zooplankton exist (Gallus, 2022). Mainly, I want to show that a model of this ecosystem is functional and that these density mediated trophic cascades take place and, if possible, are triggered by the the infection of the first intermediate host, a cyclopoid copepod.

More specifically, I expect to see negative association in every predator-prey relation, namely between grazers/copepods and phytoplankton, copepods and grazers, as well as sticklebacks and grazers/copepods. In the presence of *S. solidus,* I predict changes in the amplitude of

these impacts regarding the infected species - the copepods, especially regarding the interaction between copepods and grazers.

Furthermore, another student at the IEB found an infection rate of 12.3% in an experiment with 440 female copepods (Drakula, 2023). My goal is to create an ecosystem with a similar infection rate.

Figure 11: Expected top-effects as indicator for trophic cascades
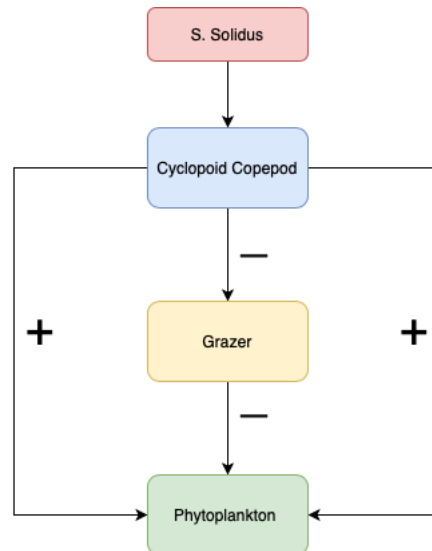
4. Results

4.1 Base Model

4.1.1 Without parasites and sticklebacks

The following figure shows a single iteration of the base model, hosting only copepods, grazers and phytoplankton. The exact values for each step can be seen in a dataframe in the Appendix (App. 1). Initial settings are the same as described in figure 4.
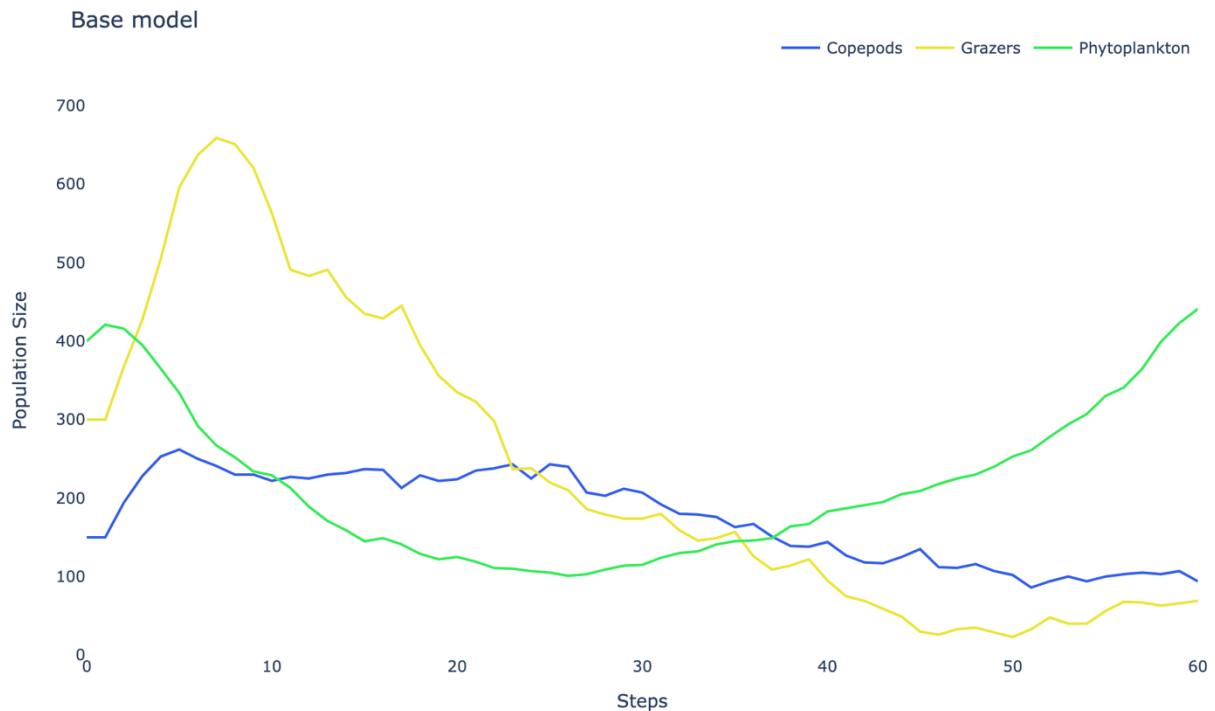
Figure 12: Single iteration base model

The phytoplankton population shrinks at the beginning because of the predation pressure exuded by the growing copepod and grazers populations. As phytoplankton agents become fewer, the grazers population starts to tumble, while the copepods mostly maintain their population due to their multifaceted diet. As the predation pressure by grazers is relieved, the phytoplankton population can recover.

4.1.2 Without parasites

The following figure shows a single iteration of the base model, hosting only copepods, grazers, phytoplankton and sticklebacks. The exact values for each step can be seen in a dataframe in the Appendix (App. 2). Initial settings are the same as described in figure 4.
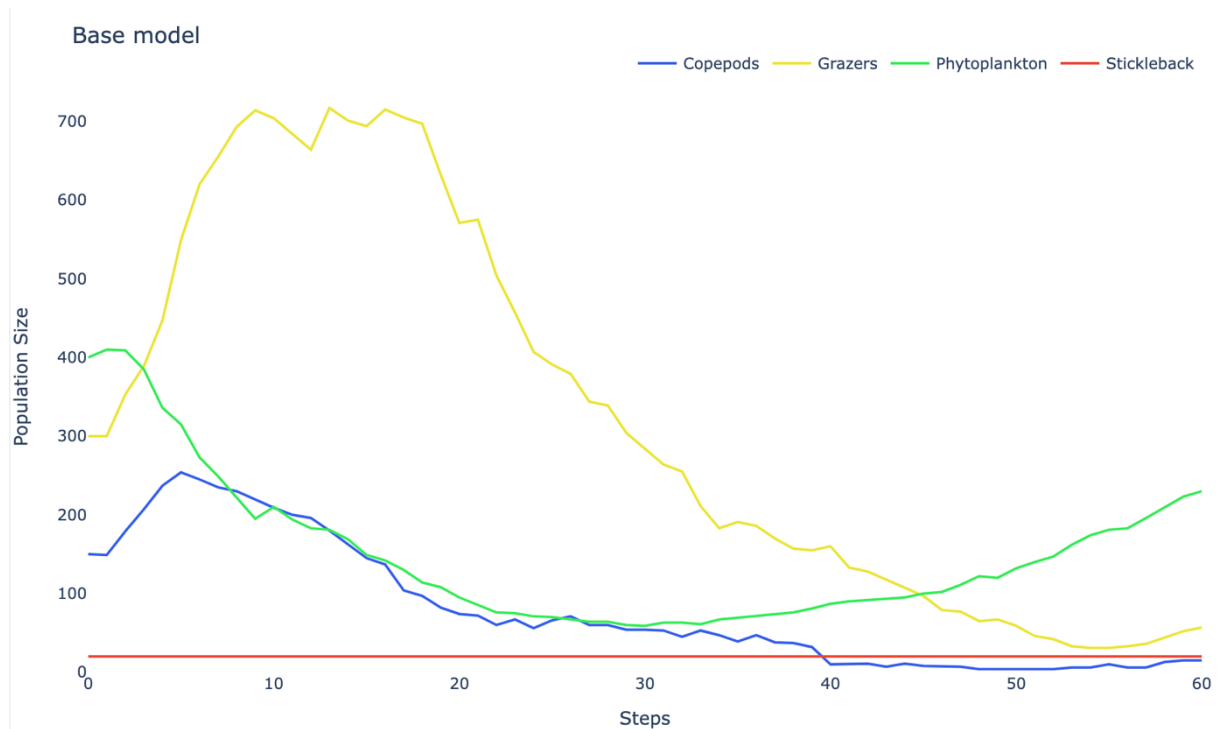
Figure 13: Single iteration base model with sticklebacks

With the introduction of sticklebacks, the copepod population experiences predation pressure for the first time and therefore starts to diminish as early as step 6. This causes the grazers population to maintain the peak of 700 agents for 11 steps until conceding to the lack of phytoplankton and also predation pressure by sticklebacks. As grazers numbers decline, the phytoplankton can recover starting from step 30. Grazer and copepod population show small regrowth after step 55, as the availability of food increases and the likelihood of encountering one of the sticklebacks is rather low at this spatial size.

4.1.3 Full Model

The following figure shows a single iteration of the full model. The exact values for each step can be seen in a dataframe in the Appendix (App. 3). Initial settings are the same as described in figure 4.
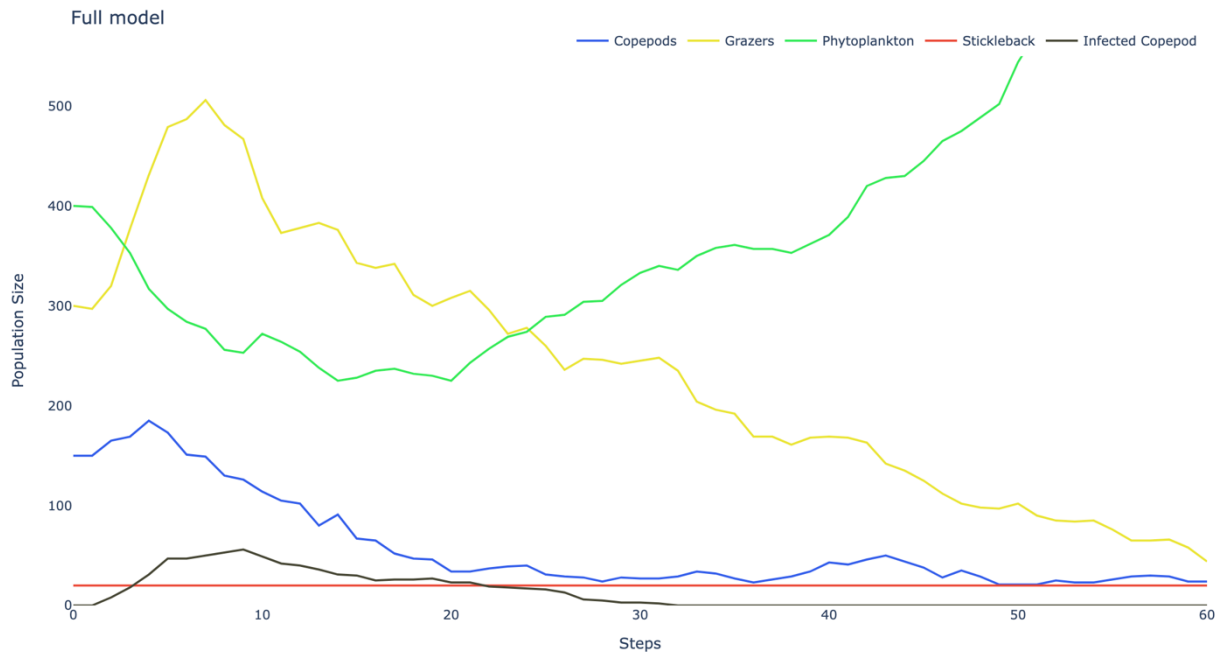
Figure 14: Single iteration of Full model. Y-axis layout modified for readability.

The addition of parasites to the model results in a different dynamic regarding population dynamics of both phytoplankton and grazers. As explained earlier, infected copepods receive not only faster movement (which, because of the scheduling nature of this ABM, results in more space traveled per step) but also receive an increased feeding rate. This leads to an increased chance of success while hunting grazers. This behavioural change explains the lower peak of 500 grazers at step 7 compared to the peak of around 700 individuals in above iterations and moreover the more drastic decline in population size of grazers. With less grazers around, the phytoplankton population can thrive and recovers from initial predation pressure by grazers and copepods around step 20. Since parasites move around randomly in the model, apparently the number of parasites after step 30 is not enough to sustain infection in this ecosystem and causes the parasite population to shrink. Lastly, the infection of copepods prevents reproduction, which leads to a smaller copepod population overall.

4.2 Paramscan and Ensemblerun results

As outlined earlier, we ran the model multiple times using paramscan and ensemblerun from Julias Agents.jl package. Here we will compare only the *lower End* and *higher End* results, to model the impact of the parasite on the host and the entire ecosystem, as these aptly represent the amplitude of these effects. The full dataset containing all 54 runs can be found on my Github (App. 6). Since each dataset is composed of six iterations of the model, we performed a mean and standard deviation analysis of each dataset, with the standard deviation being displayed as ribbons around the mean.
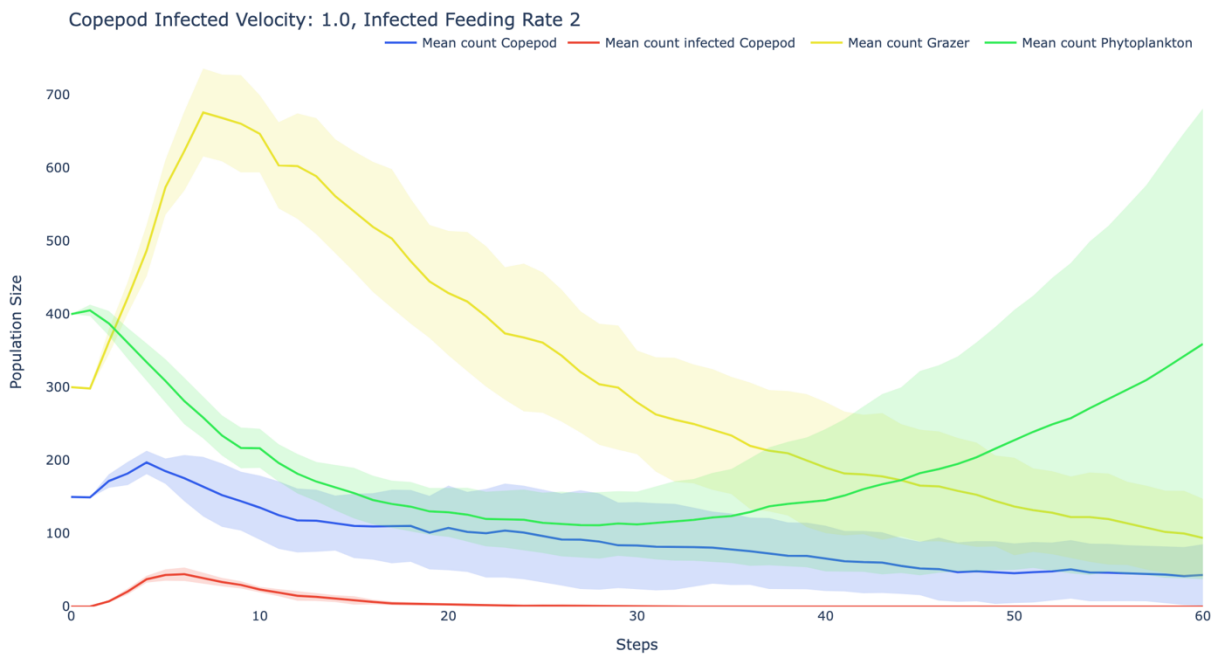
Figure 15: Lower End Analysis. Dataset contains 6 runs with different seeds.

As seen in Figure 15, the lower velocity and feeding rate while infected leads to less success on grazer predation and therefore accumulates in a more rapid decline of infected copepods, as the increased activity while infected causes them to lose more energy. This decline results in less parasites being reintroduced, as less sticklebacks get infected, and therefore ultimately, infected copepods are no longer present in the model. After this absence of infected copepods, the model behaves as explained in 4.1.2.

The following figure 16 displays the results, if we increase the velocity and feeding rate of infected copepods to the values of 1.5 and 10 respectively.
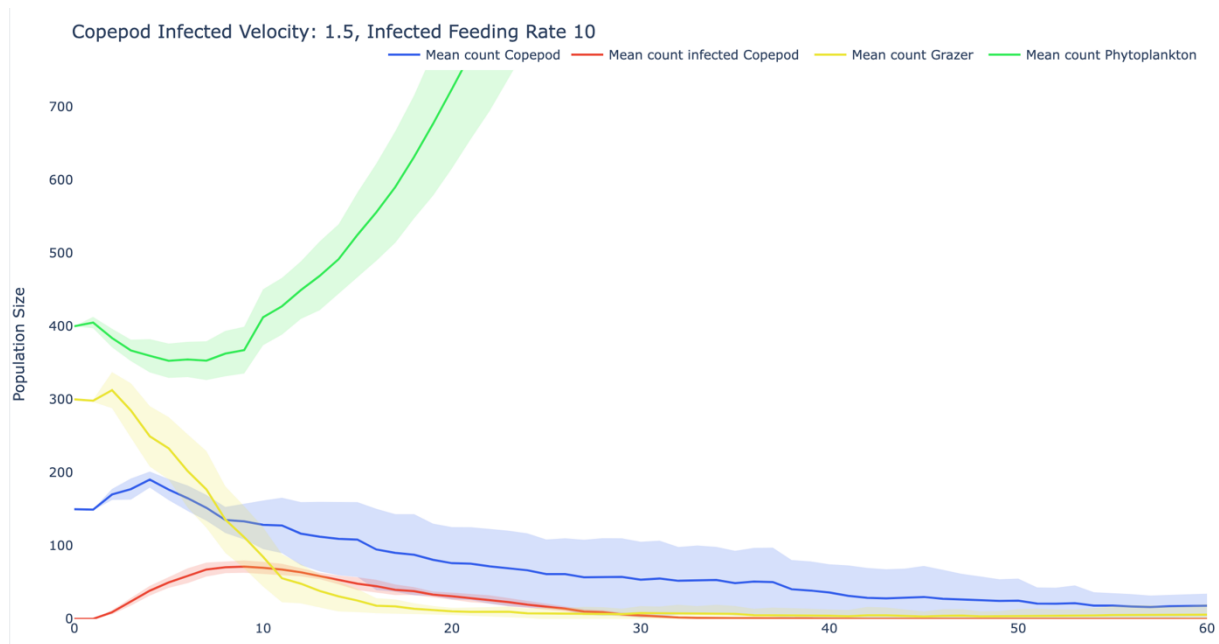
Figure 16: Higher End Analysis. Dataset contains 6 runs with different seeds. Mean count phytoplankton reaches limit 5000 at step 54. Note: Carrying capacity of model is set to 5000 phytoplankton for computability reasons. Trace not shown fully for readability.

Taking a closer look at the data above, it becomes evident that the *improved*, and consequently more deadly, copepods immediately force the grazers into genocide. As the velocity of infected copepods surpasses the velocity of sticklebacks [which is set to 1.3], the copepods are able to evade their predators until the parasite changes the behaviour to display more risky behaviour near sticklebacks. In contrast to the lower end analysis, the infected copepods gain enough energy from predation to stay alive until step 31, eventually leading to a more stabile parasite distribution and a longer presence of infected copepod. In the absence of grazers, phytoplankton immediately start to overgrow and therefore reach the carrying capacity of the model rather quickly. Uninfected copepods gain enough energy from phytoplankton in order to maintain a somewhat stable population of around 30 individuals, but are not able to regrow to their initial population level in the absence of grazers.

5. Discussion

The aim of this project is to model the direct and indirect ecological effects of the parasite on the ecosystem. As outlined earlier, it has been shown that biotic interactions such as predation, parasitism and competition exert forces on ecosystems and species densities (Duffy et al., 2005; Hatcher et al., 2012). It has also been established, that parasites have a multitude of direct effects on their hosts as they induce behavioural changes or change the host's density (Abrams, 1995; Berkhout and Barber, 2019; Franz & Kurtz, 2002, Hammerschmidt et al., 2009). These behavioural changes then invoke indirect effects such as trophic cascades, effecting lower trophic levels and even ecosystem functioning (Anaya-Rojas et al., 2019; Buck and Ripple, 2017).

As mentioned in the results, every setting of the model shows the expected dynamics: An abundance of copepods has a negative effect on grazer population and a positive effect on phytoplankton numbers as a *baseline* cascade. This classic trophic cascade, the increase in population of primary producers by reducing the density of grazers, is consistent with findings of Abrams (1995).

With the introduction of the parasite, this effect only gets amplified, as copepods increase their chance of predatory success and therefore their top-down force on grazers. This amplification is the indirect ecological effect of the parasite *Schistocephalus solidus* which we were trying to simulate. The repercussions ranged from a rather quick grazer genocide (figure 16) to a slow decline of the grazer population (figure 14). This change of magnitude regarding cascading effects reflect findings of Gallus (2022).

Furthermore, the copepod population themselves experienced some direct changes upon infection, namely the inhibition of their reproductory capacities. This resulted in a smaller population size, as also shown in figure 14.

As stated earlier, Drakula (2023) found an infection rate in real experiments of 12,3%.The lower end analysis shows around 23% percent, while the higher end analysis portrays 37% infection rate, based on the mean copepod infected to uninfected copepod ratio – therefore overshooting the 12,3% by quite a bit. Calculating the definitive infection rate for this model posed to be a difficult for various reasons. First and foremost: There are constantly copepods and parasites added and removed to the model in every step.

Additionally, as in almost every other calculation in this model, there are lot of varying factors based on random events happening, such as infection chance, reproduction possibility and movement choices. Taking this into account, the infection rate of this model is possibly close to the targeted 12,3%. But this is of course subject to speculation as I have no evidence of this as of yet and further studies would have to be made to verify this.

Regarding the rather small sample size of only 6 ensembleruns for each value pair of *infected copepod velocity* and *infected feeding rate*, the lower end analysis returns some rather big standard deviation values: At the maximum, σ = 321,734 for phytoplankton and even σ = 100,931 for grazers. This result could be explained by the fact that the grazer population sometimes cannot withstand the predation pressure by copepods and collapses entirely - a phenomenon which occurred many times during earlier trials of the model. This collaps obviously leads to different results for the grazer population and due to trophic cascades to a more variable phytoplankton population. The many random factors (reproduction, encounter, initial placement on the map, stepping order) can accumulate in a disadvantageous manner regarding the grazer population and lead to such an incident. Any attempt to regulate this problem could eventually lead to the opposite event: grazer overgrowth. I would predict, that as the model (in this particular state) is repeated for many more runs, this standard deviation would start to decline and the analysis would become more accurate.

Moving on to the *higher end analysis*, which is depicted in figure 16, one immediately notices the smaller standard deviation in every trace, therefore concluding that this model behaviour is more easily replicable and is not as susceptible to randomized decisions. My assumption is that in this setting, the copepods have been given such immense predation pressure, that even the many random factors cannot influence the outcome of the model in a meaningful way.

In conclusion, I created a stable model which adequately reflects the behaviour of a real world ecosystem in multiple settings. The copepod as a top-predator reduces the biomass of grazing zooplankton and subsequently phytoplankton density increases. Upon infection, the magnitude of these cascading effects noticeably changes. Not only does *S. solidus* directly influence the density and traits in its host, it can further manipulate the entire structure and density of other members in the ecosystem.

6. Outlook

The model could be extended in many ways. Firstly, the model should be run for a longer period of time in pursuance of more meaningful results and provide a more stable analysis.

As mentioned in chapter 2.2.4, the implementation of sticklebacks and phytoplankton is mostly of a stabilizing nature. Julia offers an entire repository of phytoplankton individuals (PlanktonIndividuals.jl) which would better implement the behaviour of plankton. Sticklebacks should be implemented the same way grazers and copepods are, making the model more computationally costly, but at the same time more accurate.

To completely depict the lifecycle of *Schistocephalus solidus,* a sixth agent could be added to the model (e.g. a piscivorous bird). With this change, also the pathfinding and space would have to change to a water walkmap and air walkmap.

Furthermore, the values used in this ABM are not scientifically accurate enough. On the one hand this is a result of the complexity of a model like this. There are more than 50 variables in my code, which interact heavily with one another. Adding the many randomized events on top of that makes finding a realistic implementation while keeping stable population sizes near impossible. On the other hand this is due to simply no available literature on some of the agent parameters, for example vision radii or velocity.

There is a large quantity of variables and features that could be added to the model, such as phenotypic or genotypic variances like bodymass, which could then be compared to real world experiments.

Last but not least, Julia and especially Agents.jl is a heavily changing framework, constantly adding new functionality to the package. This thesis should therefore be viewed as a blueprint for future models which harvest these new functionalities to make agent-based models more accurate and scientifically usable.

7. Acknowledgement

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9. Appendix

App. 1: Dataframe Base Model, only copepod, grazers, phytoplankton

```
61×8 DataFrame
```

Row	step Int64	count_grazer Int64	count_parasite Int64	count_phytoplankton Int64	count_copepod Int64	count_copepodInf Int64	count_stickleback Int64	count_sticklebackInf Int64
1	0	300	0	400	150	0	0	0
2	1	300	0	421	150	0	0	0
3	2	367	0	416	194	0	0	0
4	3	427	0	395	228	0	0	0
5	4	505	0	365	253	0	0	0
6	5	596	0	334	262	0	0	0
7	6	637	0	292	250	0	0	0
8	7	659	0	267	241	0	0	0
9	8	651	0	252	230	0	0	0
10	9	621	0	234	230	0	0	0
11	10	563	0	229	222	0	0	0
12	11	491	0	213	227	0	0	0
13	12	483	0	189	225	0	0	0
14	13	491	0	171	230	0	0	0
15	14	456	0	159	232	0	0	0
16	15	435	0	145	237	0	0	0
17	16	429	0	149	236	0	0	0
18	17	445	0	141	213	0	0	0
19	18	395	0	129	229	0	0	0
20	19	356	0	122	222	0	0	0
21	20	335	0	125	224	0	0	0
22	21	323	0	119	235	0	0	0
23	22	298	0	111	238	0	0	0
24	23	237	0	110	243	0	0	0
25	24	238	0	107	225	0	0	0
26	25	220	0	105	243	0	0	0
27	26	210	0	101	240	0	0	0
28	27	186	0	103	207	0	0	0
29	28	179	0	109	203	0	0	0
30	29	174	0	114	212	0	0	0
31	30	174	0	115	207	0	0	0
32	31	180	0	124	192	0	0	0
33	32	159	0	130	180	0	0	0
34	33	146	0	132	179	0	0	0
35	34	149	0	141	176	0	0	0
36	35	157	0	145	163	0	0	0
37	36	126	0	146	167	0	0	0
38	37	109	0	149	151	0	0	0
39	38	114	0	164	139	0	0	0
40	39	122	0	167	138	0	0	0
41	40	95	0	183	144	0	0	0
42	41	75	0	187	127	0	0	0
43	42	69	0	190	118	0	0	0
44	43	59	0	195	117	0	0	0
45	44	49	0	205	125	0	0	0
46	45	30	0	209	135	0	0	0
47	46	26	0	218	112	0	0	0
48	47	33	0	225	111	0	0	0
49	48	35	0	230	116	0	0	0
50	49	29	0	240	107	0	0	0
51	50	23	0	253	102	0	0	0
52	51	33	0	261	86	0	0	0
53	52	48	0	278	94	0	0	0
54	53	40	0	294	100	0	0	0
55	54	40	0	307	94	0	0	0
56	55	56	0	330	100	0	0	0
57	56	68	0	341	103	0	0	0
58	57	67	0	365	105	0	0	0
59	58	63	0	399	103	0	0	0
60	59	66	0	423	107	0	0	0
61	60	69	0	441	94	0	0	0

App. 2: Dataframe Base Model, only copepod, grazers, phytoplankton, stickleback

Row	step Int64	count_grazer Int64	count_parasite Int64	count_phytoplankton Int64	count_copepod Int64	count_copepodInf Int64	count_stickleback Int64	count_sticklebackInf Int64
1	0	300	0	400	150	0	20	0
2	1	300	0	410	149	0	20	0
3	2	353	0	409	179	0	20	0
4	3	389	0	385	207	0	20	0
5	4	447	0	336	237	0	20	0
6	5	549	0	315	254	0	20	0
7	6	620	0	273	245	0	20	0
8	7	655	0	249	235	0	20	0
9	8	693	0	222	230	0	20	0
10	9	714	0	195	219	0	20	0
11	10	704	0	210	209	0	20	0
12	11	684	0	194	200	0	20	0
13	12	664	0	183	196	0	20	0
14	13	717	0	181	180	0	20	0
15	14	701	0	169	162	0	20	0
16	15	694	0	149	145	0	20	0
17	16	715	0	142	137	0	20	0
18	17	705	0	130	104	0	20	0
19	18	697	0	114	97	0	20	0
20	19	632	0	108	82	0	20	0
21	20	571	0	95	74	0	20	0
22	21	575	0	86	72	0	20	0
23	22	504	0	76	60	0	20	0
24	23	457	0	75	67	0	20	0
25	24	407	0	71	56	0	20	0
26	25	391	0	70	66	0	20	0
27	26	379	0	67	71	0	20	0
28	27	344	0	64	60	0	20	0
29	28	339	0	64	60	0	20	0
30	29	304	0	60	54	0	20	0
31	30	284	0	59	54	0	20	0
32	31	264	0	63	53	0	20	0
33	32	255	0	63	45	0	20	0
34	33	211	0	61	53	0	20	0
35	34	183	0	67	47	0	20	0
36	35	191	0	69	39	0	20	0
37	36	186	0	72	47	0	20	0
38	37	170	0	74	38	0	20	0
39	38	157	0	76	37	0	20	0
40	39	155	0	81	32	0	20	0
41	40	160	0	87	10	0	20	0
42	41	133	0	90	11	0	20	0
43	42	128	0	92	11	0	20	0
44	43	118	0	93	7	0	20	0
45	44	107	0	95	11	0	20	0
46	45	97	0	100	8	0	20	0
47	46	79	0	102	8	0	20	0
48	47	77	0	111	7	0	20	0
49	48	65	0	122	4	0	20	0
50	49	67	0	120	4	0	20	0
51	50	59	0	132	4	0	20	0
52	51	46	0	140	4	0	20	0
53	52	42	0	147	4	0	20	0
54	53	33	0	162	6	0	20	0
55	54	31	0	174	6	0	20	0
56	55	31	0	181	10	0	20	0
57	56	33	0	183	6	0	20	0
58	57	36	0	196	6	0	20	0
59	58	44	0	210	13	0	20	0
60	59	52	0	223	15	0	20	0
61	60	57	0	230	15	0	20	0

App. 3: Dataframe Full Model

```
61×8 DataFrame
 Row │ step   count_grazer  count_parasite  count_phytoplankton  count_copepod  count_copepodInf  count_stickleback  count_sticklebackInf
     │ Int64  Int64         Int64           Int64                Int64          Int64             Int64              Int64
─────┼──────────────────────────────────────────────────────────────────────────────────────────────────────────────────────────────
   1 │    0            300            2000                  400            150                 0                 20                     0
   2 │    1            297            2000                  399            150                 0                 20                     0
   3 │    2            320            1992                  378            165                 8                 20                     1
   4 │    3            377            2132                  353            169                18                 20                     4
   5 │    4            431            2584                  317            185                31                 20                     4
   6 │    5            479            2964                  297            173                47                 20                     4
   7 │    6            487            3427                  284            151                47                 20                     2
   8 │    7            506            3591                  277            149                50                 20                     6
   9 │    8            481            3994                  256            130                53                 20                     4
  10 │    9            467            4461                  253            126                56                 20                     3
  11 │   10            408            4822                  272            114                49                 20                     4
  12 │   11            373            5124                  264            105                42                 20                     7
  13 │   12            378            5940                  254            102                40                 20                     5
  14 │   13            383            6471                  238             80                36                 20                     3
  15 │   14            376            6846                  225             91                31                 20                     2
  16 │   15            343            6961                  228             67                30                 20                     3
  17 │   16            338            7130                  235             65                25                 20                     2
  18 │   17            342            7320                  237             52                26                 20                     0
  19 │   18            311            7193                  232             47                26                 20                     2
  20 │   19            300            7321                  230             46                27                 20                     2
  21 │   20            308            7306                  225             34                23                 20                     0
  22 │   21            315            7112                  243             34                23                 20                     2
  23 │   22            296            7037                  257             37                19                 20                     4
  24 │   23            272            7305                  269             39                18                 20                     2
  25 │   24            278            7402                  274             40                17                 20                     1
  26 │   25            260            7290                  289             31                16                 20                     0
  27 │   26            236            6974                  291             29                13                 20                     1
  28 │   27            247            6753                  304             28                 6                 20                     1
  29 │   28            246            6486                  305             24                 5                 20                     0
  30 │   29            242            6082                  321             28                 3                 20                     1
  31 │   30            245            5775                  333             27                 3                 20                     0
  32 │   31            248            5368                  340             27                 2                 20                     0
  33 │   32            235            5034                  336             29                 0                 20                     0
  34 │   33            204            4664                  350             34                 0                 20                     0
  35 │   34            196            4323                  358             32                 0                 20                     0
  36 │   35            192            3970                  361             27                 0                 20                     0
  37 │   36            169            3620                  357             23                 0                 20                     0
  38 │   37            169            3323                  357             26                 0                 20                     0
  39 │   38            161            3043                  353             29                 0                 20                     0
  40 │   39            168            2724                  362             34                 0                 20                     0
  41 │   40            169            2423                  371             43                 0                 20                     0
  42 │   41            168            2114                  389             41                 0                 20                     0
  43 │   42            163            1845                  420             46                 0                 20                     0
  44 │   43            142            1596                  428             50                 0                 20                     0
  45 │   44            135            1392                  430             44                 0                 20                     0
  46 │   45            125            1238                  445             38                 0                 20                     0
  47 │   46            112            1075                  465             28                 0                 20                     0
  48 │   47            102             941                  475             35                 0                 20                     0
  49 │   48             98             808                  489             29                 0                 20                     0
  50 │   49             97             674                  502             21                 0                 20                     0
  51 │   50            102             566                  544             21                 0                 20                     0
  52 │   51             90             448                  574             21                 0                 20                     0
  53 │   52             85             358                  614             25                 0                 20                     0
  54 │   53             84             253                  641             23                 0                 20                     0
  55 │   54             85             159                  657             23                 0                 20                     0
  56 │   55             76             104                  686             26                 0                 20                     0
  57 │   56             65              72                  698             29                 0                 20                     0
  58 │   57             65              52                  746             30                 0                 20                     0
  59 │   58             66              31                  801             29                 0                 20                     0
  60 │   59             58              18                  858             24                 0                 20                     0
  61 │   60             44              12                  909             24                 0                 20                     0
```

App. 4: Low End Paramscan

Row	step	count_copepod_mean	count_copepod_std	count_copepodInf_mean	count_copepodInf_std	count_grazer_mean	count_grazer_std	count_parasite_mean	count_parasite_std	count_phytoplankton_mean	count_phytoplankton_std
	Int64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64
1	0	150.0	0.0	0.0	0.0	300.0	0.0	2000.0	0.0	400.0	0.0
2	1	149.333	0.778499	0.0	0.0	298.167	1.52753	2000.0	0.0	405.0	7.73422
3	2	171.75	9.16639	7.25	1.95982	362.083	17.0851	1990.92	2.84312	387.167	16.9321
4	3	182.0	15.8688	20.6667	3.98482	422.333	21.6767	2013.08	80.5949	359.917	21.1594
5	4	197.083	15.9229	37.4167	4.67991	486.833	35.0242	2325.92	234.794	334.25	25.6129
6	5	185.167	17.2986	43.1667	7.73226	573.417	37.459	2748.5	286.775	308.5	29.5743
7	6	175.583	31.5752	44.25	9.22571	622.917	54.0092	3296.83	483.611	281.0	31.7519
8	7	164.0	40.6314	38.5833	7.22946	675.583	60.0098	3801.25	593.549	258.417	28.4364
9	8	152.417	43.2613	33.5	5.77613	668.083	59.2199	4270.83	689.747	233.917	27.4884
10	9	144.167	40.1629	29.6667	4.92366	660.25	66.4737	4686.83	821.866	216.917	27.8517
11	10	135.333	43.862	23.3333	3.65148	646.417	52.6989	5103.83	933.166	216.417	26.7393
12	11	125.083	46.1706	19.0833	4.77605	603.333	58.9689	5513.83	1015.04	196.417	25.4753
13	12	117.75	43.7142	14.75	6.70312	602.25	72.1087	5912.08	1209.0	181.667	27.0028
14	13	117.417	42.4145	13.3333	5.58135	588.333	79.3489	6204.58	1211.66	170.917	26.7529
15	14	114.167	37.6415	10.8333	4.72582	561.167	77.7102	6364.5	1213.61	162.75	31.0604
16	15	110.333	43.8786	8.5	5.80752	540.083	82.4339	6506.5	1267.02	155.167	34.5486
17	16	109.667	45.3899	6.33333	3.20038	519.167	88.986	6499.75	1329.67	145.75	33.2487
18	17	109.5	50.2277	4.41667	2.64432	503.167	94.8279	6490.17	1367.76	140.333	31.77
19	18	110.333	49.085	3.91667	2.19331	472.25	85.3699	6407.92	1361.66	136.667	33.7109
20	19	101.167	50.2572	3.0	1.7581	444.583	77.2051	6339.33	1369.43	130.167	32.0903
21	20	107.583	57.806	3.08333	1.37895	425.0	85.0437	6238.33	1393.89	128.917	33.3486
22	21	102.167	54.6673	2.33333	1.66969	417.083	95.0946	6112.25	1383.45	125.75	36.7204
23	22	100.333	60.542	1.58333	1.44338	396.667	95.9567	5907.25	1358.79	119.75	37.2537
24	23	104.0	64.1631	1.25	1.21543	373.5	90.5222	5694.25	1327.07	119.333	38.7963
25	24	101.25	63.9291	1.16667	0.834847	367.917	100.931	5468.0	1289.04	118.667	41.3331
26	25	96.4167	63.8613	1.25	0.866025	360.917	95.9019	5201.92	1230.03	114.5	41.2542
27	26	91.75	63.0124	1.25	1.95982	343.167	90.1068	4917.0	1193.9	113.0	44.2945
28	27	91.5833	67.4839	1.08333	1.97523	320.917	82.8124	4610.17	1144.59	111.417	43.7814
29	28	88.9167	65.8338	0.916667	1.31137	304.0	82.712	4255.33	1098.17	111.333	45.7172
30	29	83.8333	58.5147	0.666667	0.778499	299.417	84.9122	3881.75	1053.4	113.667	44.1533
31	30	83.5833	59.2874	0.666667	0.887625	279.25	70.7622	3496.08	1004.73	112.333	44.8479
32	31	81.8333	59.5297	0.5	0.522233	262.75	78.1992	3087.75	941.894	114.333	49.8185
33	32	81.8333	58.6109	0.25	0.452267	255.5	84.7301	2804.67	905.29	117.167	54.322
34	33	81.4167	53.8676	0.0833333	0.288675	249.75	81.2875	2532.83	871.36	118.583	55.76
35	34	80.5833	49.2885	0.0833333	0.288675	242.167	82.409	2237.5	818.026	121.917	60.8119
36	35	78.4167	48.8736	0.0833333	0.288675	234.0	80.0011	1941.33	754.892	123.833	64.2026
37	36	75.75	45.9409	0.166667	0.57735	219.75	86.4714	1648.25	691.495	129.333	73.5173
38	37	72.6667	48.513	0.416667	0.792961	213.167	82.9204	1390.0	658.813	137.083	80.5204
39	38	69.5	45.5422	0.0833333	0.288675	209.667	85.1334	1160.17	615.315	140.417	84.8212
40	39	69.25	45.5155	0.0833333	0.288675	199.583	90.7979	962.917	579.637	142.5	88.7115
41	40	65.9167	44.5328	0.0	0.0	190.0	89.5839	789.417	540.115	145.417	97.2667
42	41	62.0833	41.3246	0.0	0.0	182.0	84.6189	641.75	492.135	151.917	104.372
43	42	60.8333	42.5501	0.0833333	0.288675	180.667	81.6237	517.75	452.567	160.583	113.029
44	43	60.1667	41.5032	0.0	0.0	178.0	86.5185	421.167	410.452	167.333	123.196
45	44	55.5833	38.2301	0.0	0.0	172.833	76.7639	350.667	366.608	172.833	126.914
46	45	52.1667	36.4987	0.0	0.0	165.5	76.4288	296.583	331.218	182.5	139.657
47	46	51.3333	43.0609	0.0833333	0.288675	164.417	75.1368	251.25	299.853	188.083	141.827
48	47	47.0833	40.572	0.0	0.0	158.25	72.251	214.083	273.968	195.083	146.968
49	48	48.4167	41.0642	0.0	0.0	152.917	71.2275	183.167	249.35	204.25	157.078
50	49	46.5	42.9175	0.0	0.0	144.333	62.0547	157.417	231.035	216.083	166.332
51	50	45.5833	40.6436	0.0	0.0	136.917	66.638	130.917	204.327	228.0	177.617
52	51	47.0	41.2795	0.0	0.0	131.917	57.1369	110.583	181.324	238.917	186.096
53	52	48.0833	39.5554	0.0	0.0	128.417	56.6672	94.1667	157.456	249.083	200.11
54	53	50.8333	39.9541	0.0	0.0	122.333	55.4147	79.75	138.963	257.667	212.247
55	54	46.6667	39.3962	0.0	0.0	122.333	61.04	65.5833	120.343	271.167	227.996
56	55	46.3333	39.3847	0.0	0.0	119.667	62.2449	52.5833	100.95	284.167	236.613
57	56	45.6667	38.1417	0.0	0.0	113.75	56.8493	41.3333	86.3232	296.083	252.152
58	57	45.25	37.9045	0.0	0.0	107.917	57.3053	32.9167	73.0821	309.667	266.484
59	58	43.8333	38.9588	0.0	0.0	102.083	56.4228	25.9167	59.4711	325.833	286.475
60	59	41.75	39.5799	0.0	0.0	100.0	58.3329	19.8333	46.1122	343.083	304.463
61	60	43.1667	41.9281	0.0	0.0	93.9167	53.5494	15.6667	36.0765	359.167	321.734

App. 5: High End Paramscan

Row	step	count_copepod_mean	count_copepod_std	count_copepodInf_mean	count_copepodInf_std	count_grazer_mean	count_grazer_std	count_parasite_mean	count_parasite_std	count_phytoplankton_mean	count_phytoplankton_std
	Int64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64	Float64
1	0	150.0	0.0	0.0	0.0	300.0	0.0	2000.0	0.0	400.0	0.0
2	1	149.333	0.778499	0.0	0.0	298.167	1.52753	2000.0	0.0	405.0	7.73422
3	2	170.083	7.63316	9.08333	2.96827	312.583	24.6372	1989.83	3.76185	383.833	12.6766
4	3	177.417	14.3809	23.25	5.0475	284.833	37.1504	2042.75	95.631	366.917	14.5756
5	4	190.417	10.9167	38.5833	6.70764	249.583	41.2188	2277.58	216.276	359.583	22.7495
6	5	176.75	14.3408	49.8333	7.29674	233.083	42.705	2787.42	329.209	352.833	23.5056
7	6	165.0	17.4721	59.0	10.198	202.25	49.9438	3306.92	418.029	354.583	24.0774
8	7	151.833	17.6008	67.5	9.47245	176.917	52.3319	4007.42	408.824	353.0	26.4266
9	8	135.25	17.7053	70.5	7.87978	135.75	45.4075	4834.17	445.988	362.583	30.9823
10	9	133.25	24.6434	71.5833	8.39327	111.667	42.5063	5492.58	606.871	367.417	31.916
11	10	128.583	33.2496	69.9167	8.09555	84.8333	40.5167	6276.5	642.973	412.25	38.2269
12	11	127.75	37.7723	67.5	7.90282	55.5833	32.8065	6925.92	589.204	427.25	38.7113
13	12	116.583	43.0189	63.75	5.4793	48.1667	26.8119	7621.25	682.288	449.333	39.3223
14	13	112.417	47.5365	58.75	4.37191	38.1667	22.5561	8237.58	821.538	468.833	47.0277
15	14	109.417	49.815	53.25	6.06218	30.8333	20.5861	8865.75	938.347	491.583	47.8282
16	15	108.417	51.1103	48.1667	8.83005	25.0833	15.7276	9357.17	956.578	524.833	57.9637
17	16	94.9167	55.5231	44.75	8.61421	18.0833	10.2288	9902.75	1001.48	555.75	66.4463
18	17	90.25	52.9599	39.8333	7.24673	17.0833	9.61493	10398.3	1237.26	590.167	76.1623
19	18	87.6667	55.4672	38.0	5.3936	13.8333	7.56587	10724.3	1328.43	631.417	84.02
20	19	80.8333	49.4457	33.25	4.11483	11.8333	5.82835	10934.9	1327.59	676.417	98.133
21	20	76.1667	49.2707	31.0833	4.90748	10.3333	4.77367	11161.1	1534.3	724.0	108.599
22	21	75.5833	49.7694	28.5	5.76037	9.58333	5.48483	11416.3	1638.26	773.333	117.603
23	22	71.9167	51.0445	26.6667	5.53227	9.33333	6.75995	11516.0	1668.84	821.0	127.072
24	23	69.0	51.5928	23.0	5.47723	9.83333	7.33402	11593.4	1715.82	881.667	143.76
25	24	66.5	50.4444	19.5	5.12569	7.75	6.42615	11598.6	1761.42	940.083	157.235
26	25	61.3333	47.1599	16.75	4.10058	7.66667	8.21676	11584.2	1808.14	1001.25	167.861
27	26	61.25	48.8413	14.0833	3.87201	7.25	7.59336	11487.7	1847.94	1070.58	175.32
28	27	56.9167	51.1939	10.0	3.30289	7.58333	9.00967	11329.2	1853.35	1143.5	190.573
29	28	57.3333	52.9911	9.08333	2.87492	7.16667	8.96289	11000.2	1881.22	1221.42	198.608
30	29	57.4167	52.7524	6.16667	2.62274	6.5	7.59785	10598.8	1855.3	1296.92	204.672
31	30	53.6667	51.8325	4.5	2.23607	8.08333	9.41429	10171.0	1837.78	1382.58	216.257
32	31	55.1667	51.7438	3.0	1.80907	7.83333	9.41078	9687.17	1797.81	1476.75	231.885
33	32	52.0833	46.1804	2.0	1.2792	8.5	10.783	9313.75	1783.37	1574.75	250.1
34	33	53.0833	47.1949	1.5	1.31426	7.83333	9.70317	8793.17	1738.97	1675.17	258.853
35	34	53.25	45.1565	0.916667	0.900337	8.0	11.2896	8260.33	1705.33	1781.58	284.734
36	35	48.8333	44.1646	1.0	0.738549	6.91667	10.698	7670.0	1649.24	1902.5	307.918
37	36	51.0833	45.9554	1.16667	1.02986	5.16667	8.65325	7067.08	1577.44	2024.42	344.307
38	37	50.4167	47.0193	0.833333	0.834847	5.08333	10.4834	6482.17	1497.5	2160.33	356.627
39	38	40.5833	39.7983	0.416667	0.668558	5.08333	9.72773	5923.0	1429.27	2304.17	393.612
40	39	38.75	39.7998	0.0833333	0.288675	4.75	10.0011	5369.58	1347.43	2456.0	416.624
41	40	36.1667	38.4775	0.0833333	0.288675	4.33333	8.648	4847.5	1265.29	2612.83	450.401
42	41	31.5833	41.6118	0.166667	0.389249	3.66667	8.48885	4350.0	1184.43	2777.92	486.05
43	42	28.8333	40.8274	0.166667	0.389249	4.91667	11.4372	3878.83	1091.83	2957.5	528.268
44	43	28.0833	39.7274	0.166667	0.389249	4.91667	10.7995	3410.25	984.307	3149.75	574.97
45	44	29.0833	39.5921	0.0833333	0.288675	3.83333	9.99379	3000.0	905.917	3365.83	618.494
46	45	30.0	42.3921	0.0833333	0.288675	3.33333	6.74649	2626.17	827.149	3582.42	659.192
47	46	26.75	34.8376	0.0833333	0.288675	4.25	9.0867	2275.67	740.615	3801.17	635.187
48	47	26.75	34.8376	0.0	0.0	4.5	8.94935	1961.42	659.698	4022.33	633.037
49	48	25.9167	32.8977	0.0	0.0	3.5	6.76219	1668.5	585.285	4210.67	583.034
50	49	24.6667	29.586	0.0	0.0	3.58333	6.97343	1419.83	512.904	4406.33	505.129
51	50	25.0	30.0273	0.0	0.0	4.33333	9.13866	1191.92	440.564	4596.92	438.24
52	51	20.9167	22.146	0.0	0.0	4.41667	9.60548	990.417	372.882	4745.17	336.653
53	52	20.8333	21.9372	0.0	0.0	4.16667	9.04367	805.083	327.111	4881.83	229.62
54	53	21.5	24.3292	0.0	0.0	4.0	8.89331	647.75	282.498	4949.33	118.332
55	54	18.3333	18.1225	0.0	0.0	4.75	10.1724	504.083	235.729	5000.0	0.0
56	55	18.25	17.0727	0.0	0.0	5.33333	12.4633	385.333	199.983	5000.0	0.0
57	56	17.0	16.9973	0.0	0.0	5.33333	13.466	282.917	173.484	5000.0	0.0
58	57	16.25	15.6387	0.0	0.0	5.41667	13.2833	203.333	140.396	5000.0	0.0
59	58	17.3333	16.0189	0.0	0.0	5.0	11.9545	142.0	108.181	5000.0	0.0
60	59	17.8333	15.9478	0.0	0.0	5.25	12.5707	100.25	87.0132	5000.0	0.0
61	60	18.0833	16.4287	0.0	0.0	5.75	14.6109	69.6667	66.0142	5000.0	0.0

App. 6: Github link: https://github.com/MarvinKohnen/HostParasite

Declaration of Academic Integrity

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