A Stage-structured Individual-based Model to Study Ecological and Evolutionary Dynamics of *Drosophila melanogaster* Populations Adapted for Larval Crowding

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Introduction

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Chapter 2

Prelimineries

2.1   Moran Model

We consider one of the most significant work on Markov chain modelling in population genetics. The following model was proposed by P. A. P. Moran in 1958.

2.1.1   Model Dynamics

We consider a haploid population with two genotypes A and a. This model envisages to follow population through its birth-death events. Precisely, the new generation is formed from the old generation in a certain manner.

From the existing population, one individual is chosen randomly to give birth and the offspring would be of the same genotype. At the same time, one randomly chosen individual from the old population dies. Therefore, the population size remains constant. We denote it by N. Also, we denote by X_n, the number of A genes in the nth generation. By nth generation, we understand that population has undergone n birth-death events. We want to study the Markov chain $(X_n)_{n \geq 0}$, which has state space 0, 1, ..., N.

2.2   Markov Chains

2.2.1   Basic Definitions and Properties

Markov chains often describe the movements of a system between various states. In this paper, we will discuss *discrete-time* Markov chains, meaning that at each step our system can either

stay in the state it is in or change to another state. We denote the random variable X_n as a sort of marker of what state our system is in at step n. X_n can take the value of any $i \in I$, where each i is a *state* in the *state-space*, I. States are usually just denoted as numbers and our state-space as a countable set.

We will call $\lambda = (\lambda_{i_1}, \lambda_{i_2}, \ldots) = (\lambda_i \mid i \in I) the probability distribution on X_n$ if:

$\lambda_i = P(X_n = i)$ and $\sum_{i \in I} \lambda_i = 1$. Also, a matrix $P = \{p_{ij}\}$, where $i, j \in I$, is called *stochastic* if $\sum_{j \in I} \lambda_{ij} = 1$, $\forall i \in I$, i.e. every row of the matrix is a distribution. Now we can define a Markov chain explicitly.

$(X_0, X_1, \ldots) = (X_n)_{n \geq 0}$ is a *Markov chain with initial distribution λ and transition matrix P,* shortened to *Markov(λ, P)*, if

- λ is the probability distribution on X_0;

- given that $X_n = i$, $(p_{ij} \mid i, j \in I)$ is the probability distribution on X_{n+1} and is independent of $X_k, 0 \leq k < n$, i.e. $P(X_{N+1} = j \mid X_n = i) = p_{ij}$.

$(X_n)_{0 \leq n \leq N}$ is Markov(λ, P) if and only if

$$P(X_0 = i_0, X_1 = i_1 \ldots, X_N = i_N) = \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}. \tag{2.1}$$

First, suppose $(X_n)_{0 \leq n \leq N}$ is Markov(λ, P), thus

$$P(X_0 = i_0, X_1 = i_1, \ldots, X_N = i_N)$$

$$= P(X_0 = i_0)P(X_1 = i_1 \mid X_0 = i_0) \cdots P(X_N = i_N \mid X_0 = i_0, \ldots, X_{N-1} = i_{N-1})$$

$$= P(X_0 = i_0)P(X_1 = i_1 \mid X_0 = i_0) \cdots P(X_N = i_N \mid X_{N-1} = i_{N-1})$$

$$= \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}$$

Now assume that (1.3) holds for N, thus

$$P(X_0 = i_0, X_1 = i_1 \ldots, X_N = i_N) = \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}$$

$$\sum_{i_N \in I} P(X_0 = i_0, X_1 = i_1 \ldots, X_N = i_N) = \sum_{i_N \in I} \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-1} i_N}$$

$$P(X_0 = i_0, X_1 = i_1 \ldots, X_{N-1} = i_{N-1}) = \lambda_{i_0} p_{i_0 i_1} p_{i_1 i_2} \cdots p_{i_{N-2} i_{N-1}}$$

And now by induction, (1.3) holds for all $0 \leq n \leq N$. From the formula for conditional probability, namely that $P(A \mid B) = P(A \cap B)/P(B)$, we can show that

$$P(X_{N+1} = i_{N+1} \mid X_0 = i_0, \ldots, X_N = i_N) = \frac{P(X_0 = i_0, \ldots, X_N = i_N, X_{N+1} = i_{N+1})}{P(X_0 = i_0, \ldots, X_N = i_N)}$$

$$= \frac{\lambda_{i_0} p_{i_0 i_1} \cdots p_{i_{N-1} i_N} p_{i_N i_{N+1}}}{\lambda_{i_0} p_{i_0 i_1} \cdots p_{i_{N-1} i_N}}$$

$$= p_{i_N i_{N+1}}$$

Thus, by definition, $(X_n)_{0 \leq n \leq N}$ is Markov(λ, P).

The next theorem emphasizes the memorylessness of Markov chains. In the formulation of this theorem, we use the idea of the *unit mass at i*. It is denoted as $\delta_i = (\delta_{ij})$ where

$$\delta_{ij} = \begin{cases} 1 & \text{if } i = j \\ 0 & \text{otherwise} \end{cases}$$

Let $(X_n)_{n \geq 0}$ be Markov(λ, P). Then, given that $X_m = i$, $(X_l)_{l \geq m}$ is Markov(δ_i, P) and is independent of X_k, $0 \leq k < m$. Let the event $A = \{X_m = i_m, \ldots, X_n = i_n\}$ and the event B be any event determined by $X_0, \ldots, X_m$. To prove the theorem, we must show that

$$P(A \cap B \mid X_m = i) = \delta_{i i_m} p_{i_m i_{m+1}} \cdots p_{i_{n-1} i_n} P(B \mid X_m = i)$$

thus the result follows from Theorem 1.2. First, let us consider any elementary event

$$B = B_k = \{X_0 = i_0, \ldots, X_m = i_m\}$$

Here we show that

$$P(A \cap B_k \text{ and } i = i_m \mid X_m = i) = \frac{\delta_{i i_m} p_{i_m i_{m+1}} \cdots p_{i_{n-1} i_n} P(B_k)}{P(X_m = i)}$$

which follows from Theorem 1.2 and the definition of conditional probability. Any event, B, determined by $X_0, \ldots, X_m$ can be written as a disjoint union of elementary events, $B = \bigcup_{k=1}^{\infty} B_k$. Thus, we can prove our above identity by summing up all of the different B_k for any given event.

An additional idea that is going to be important later is the idea of conditioning on the initial state, X_0. We will let $P(A \mid X_0 = i) = P_i(A)$. Similarly, we will let $E(A \mid X_0 = i) = E_i(A)$.

2.2.2   Stopping Times and the Strong Markov Property

We start this section with the definition of a stopping time. A random variable T is called a *stopping time* if the event $\{T = n\}$ depends only on $X_0, \ldots, X_n$ for $n = 0, 1, 2, \ldots$.

An example of a stopping time would be the *first passage time*

$$T_i = \inf\{n \geq 1 \mid X_n = i\}.$$

where we define $\inf \emptyset = \infty$. This is a stopping time since $\{T_i = n\} = \{X_k \neq i,$ $X_n = i \,|\, 0 < k < n\}$. Now we will define an expansion of this idea that we will use later. The *rth passage time* $T_i^{(r)}$ to state i is defined recursively using the first passage time.

$$T_i^{(0)} = 0, \qquad T_i^{(1)} = T_i$$

and, for $r = 1, 2, \ldots,$

$$T_i^{(r+1)} = \inf\{n \geq T_i^{(r)} + 1 \,|\, X_n = i\}.$$

This leads to the natural definition of the *length of the rth excursion* to i as

$$S_i^{(r)} = \begin{cases} T_i^{(r)} - T_i^{(r-1)} & \text{if } T_i^{(r-1)} < \infty \\ 0 & \text{otherwise.} \end{cases}$$

The following theorem shows how the Markov property holds at stopping times.

Let T be a stopping time of $(X_n)_{n \geq 0}$ which is Markov(λ, P). Then given $T < \infty$ and $X_T = i$, $(X_l)_{l \geq T}$ is Markov(δ_i, P) and independent of X_k, $0 \leq k < T$. First, we already have that $(X_l)_{l \geq T}$ is Markov(δ_i, P) by Theorem 1.4, so we just need to show the independence condition. Let the event $A = \{X_T = i_0, \ldots, X_{T+n} = i_n\}$ and the event B be any event determined by $X_0, \ldots, X_T$. It is important to notice that the event $B \cap \{T = m\}$ is determined by $X_0, \ldots, X_m$. We get that

$$P(A \cap B \cap \{T = m\} \cap \{X_T = i\}) = P_i(X_0 = i_0, \ldots, X_n = i_n)P(B \cap \{T = m\} \cap \{X_T = i\})$$

If we now sum over $m = 0, 1, 2, \ldots$ and divide each side by $P(T < \infty, X_T = i)$ using the definition of conditional probability, we obtain

$$P(A \cap B \,|\, T < \infty, X_T = i) = P_i(X_0 = i_0, \ldots, X_n = i_n)P(B \,|\, T < \infty, X_T = i)$$

which gives us the independence we desired.

2.2.3 Recurrence and Transience

Let $(X_n)_{n \geq 0}$ be Markov with transition matrix P. We say that a state i is *recurrent* if

$$P_i(X_n = i \text{ for infinitely many } n) = 1,$$

and we say that a state i is *transient* if

$$P_i(X_n = i \text{ for infinitely many } n) = 0.$$

The following results allow us to show that any state is necessarily either recurrent or transient.

For $r = 2, 3, \ldots$, given that $T_i^{(r-1)} < \infty$, $S_i^{(r)}$ is independent of X_k, $0 \leq k \leq T_i^{(r-1)}$ and

$$P(S_i^{(r)} = n \mid T_i^{(r-1)} < \infty) = P_i(T_i = n).$$

We can directly apply Theorem 2.3 where $T_i^{(r-1)}$ is the stopping time T, since it is assured that $X_T = i$ when $T < \infty$. So, given that $T_i^{(r-1)} < \infty$, $(X_l)_{l \geq T}$ is Markov(δ_i, P) and independent of X_k, $0 \leq k < T$, the independence wanted. Yet, we know

$$S_i^{(r)} = \inf\{l - T \geq 1 \mid X_l = i\}$$

so $S_i^{(r)}$ is the first passage time of $(X_l)_{l \geq T}$ to state i, giving us our desired equality.

The idea of the *number of visits to i, V_i*, is intuitive and can be easily defined using the indicator function

$$V_i = \sum_{n=0}^{\infty} 1_{\{X_n = i\}}$$

A nice property of V_i is that

$$E_i(V_i) = E_i\left(\sum_{n=0}^{\infty} 1_{\{X_n=i\}}\right) = \sum_{n=0}^{\infty} E_i(1_{\{X_n=i\}}) = \sum_{n=0}^{\infty} P_i(X_n = i).$$

Another intuitive and useful term is the *return probability to i*, defined as

$$f_i = P_i(T_i < \infty).$$

$P_i(V_i > r) = (f_i)^r$ for $r = 0, 1, 2, \ldots$. First, we know that our claim is necessarily true when $r = 0$. Thus, we can use induction and the fact that if $X_0 = i$ then $\{V_i > r\} = \{T_i^{(r)} < \infty\}$ to conclude that

$$P_i(V_i > r + 1) = P_i(T_i^{(r+1)} < \infty)$$

$$= P_i(T_i^{(r)} < \infty \text{ and } S_i^{(r+1)} < \infty)$$

$$= P_i(S_i^{(r+1)} < \infty \mid T_i^{(r)} < \infty)P_i(T_i^{(r)} < \infty)$$

$$= f_i \cdot (f_i)^r = (f_i)^{r+1}$$

using Lemma 3.2, so our claim is true for all r.

The following two cases hold and show that any state is either recurrent or transient:

1. if $P_i(T_i < \infty) = 1$, then i is recurrent and $\sum_{n=0}^{\infty} P_i(X_n = i) = \infty$;

2. if $P_i(T_i < \infty) < 1$, then i is transient and $\sum_{n=0}^{\infty} P_i(X_n = i) < \infty$.

If $P_i(T_i < \infty) = f_i = 1$ by Lemma 3.5, then

$$P_i(V_i = \infty) = \lim_{r \to \infty} P_i(V_i > r) = \lim_{r \to \infty} 1^r = 1$$

so i is recurrent and

$$\sum_{n=0}^{\infty} P_i(X_n = i) = E_i(V_i) = \infty.$$

In the other case, $f_i = P_i(T_i < \infty) < 1$ then using our fact about V_i

$$\sum_{n=0}^{\infty} P_i(X_n = i) = E_i(V_i) = \sum_{n=1}^{\infty} n P_i(V_i = n) = \sum_{n=1}^{\infty} \sum_{r=0}^{n-1} P_i(V_i = n)$$

$$= \sum_{r=0}^{\infty} \sum_{n=r+1}^{\infty} P_i(V_i = n) = \sum_{r=0}^{\infty} P_i(V_i > r) = \sum_{r=0}^{\infty} (f_i)^r = \frac{1}{1 - f_i} < \infty$$

so $P_i(V_i = \infty) = 0$ and i is transient.

2.2.4   Communication Classes and Recurrence

State i *can send to* state j, and we write $i \to j$ if

$$P_i(X_n = j \text{ for some } n \geq 0) > 0.$$

Also i *communicates with* j, and we write ij if both $i \to j$ and $j \to i$.

For distinct states $i, j \in I$, $i \to j \iff p_{ii_1} p_{i_1 i_2} \cdots p_{i_{n-1} j} > 0$ for some states $i_1, i_2, \ldots, i_{n-1}$. Also, is an equivalence relation on I.   ()

$$0 < P_i(X_n = j \text{ for some } n \geq 0) \leq \sum_{n=0}^{\infty} P_i(X_n = j) = \sum_{n=0}^{\infty} \sum_{i_1, \ldots, i_{n-1}} p_{ii_1} p_{i_1 i_2} \cdots p_{i_{n-1} j}$$

Thus, for some $p_{ii_1} p_{i_1 i_2} \cdots p_{i_{n-1} j} > 0$ for some states $i_1, i_2, \ldots, i_{n-1}$.

() Take some $i_1, i_2, \ldots, i_{n-1}$ such that

$$0 < p_{ii_1} p_{i_1 i_2} \cdots p_{i_{n-1} j} \leq P_i(X_n = j) \leq P_i(X_n = j \text{ for some } n \geq 0).$$

Now it is clear from the proven inequality that $i \to j, j \to ki \to k$. Also, it is true that ii for any state i and that $ijji$. Thus, is an equivalence relation on I.   We say that partitions I into *communication classes*. Also, a Markov chain or transition matrix P where I is a single communication class is called *irreducible*.

Let C be a communication class. Either all states in C are recurrent or all are transient.

Take any distinct pair of states $i, j \in C$ and suppose that i is transient. Then there exist $n, m \geq 0$ such that $P_i(X_n = j) > 0$ and $P_j(X_m = i) > 0$, and for all $r \geq 0$

$$P_i(X_{n+r+m} = i) \geq P_i(X_n = j)P_j(X_r = j)P_j(X_m = i).$$

This implies that

$$\sum_{r=0}^{\infty} P_j(X_r = j) \leq \frac{1}{P_i(X_n = j)P_j(X_m = i)} \sum_{r=0}^{\infty} P_i(X_{n+r+m} = i) < \infty$$

by Theorem 3.6. So any arbitrary j is transient, again by Theorem 3.6, so the whole of C is transient. The only way for this not to be true is if all states in C are recurrent. This theorem shows us that recurrence and transience is a class property, and we will refer to it in the future as such.

Suppose P is irreducible and recurrent. Then for all $i \in I$ we have $P(T_i < \infty) = 1$. By Theorem 2.3 we have

$$P(T_i < \infty) = \sum_{j \in I} P_j(T_i < \infty)P(X_0 = j)$$

so we only need to show $P_j(T_i < \infty) = 1$ for all $j \in I$. By the irreducibility of P, we can pick an m such that $P_i(X_m = j) > 0$. From Theorem 3.6, we have

$$1 = P_i(X_n = i \text{ for infinitely many } n)$$

$$= P_i(X_n = i \text{ for some } n \geq m + 1)$$

$$= \sum_{k \in I} P_i(X_n = i \text{ for some } n \geq m + 1 \,|\, X_m = k)P_i(X_m = k)$$

$$= \sum_{k \in I} P_k(T_i < \infty)P_i(X_m = k)$$

using Theorem 2.3 again. Since $\sum_{k \in I} P_i(X_m = k) = 1$ so we have that $P_j(T_i < \infty) = 1$.

Chapter 3

Interplay between Larval Trait Parameters

In the base model of larval stage, trait parameters used are initial feeding rate, efficiency, critical size and waste tolerance. These parameters can not be measured directly via experimental approaches, but their effect on other larval traits such as body size, feeding rate at the third instar, development time can be measured easily. Here, I explore how larval trait parameters interact with each other and affect body size, time to reach critical size, feeding rate at critical size and survivorship. Since feeding rate in the model stays constant after reaching critical size, it can be taken as proxy for feeding rate at the third instar stage.

3.1   Initial Feeding Rate and Efficiency

In MB culture (low density), fig 3.1 shows having higher efficiency as well as higher initial feeding rate gives higher larval body size, but lower time to reach critical size. Feeding rate at critical size is dependent on time taken to reach critical size which is dependent on body size increment at each time step. This body size increment is proportional to the current feeding rate and efficiency. Thus, efficiency and initial feeding rate both affect the feeding rate shown at the critical size. Having lower efficiency and higher initial feeding rate tends to give higher feeding rate at critical size in MB culture. Survivorship does not show any pattern at low density, since most of the larvae are competing very less and are able to survive easily.
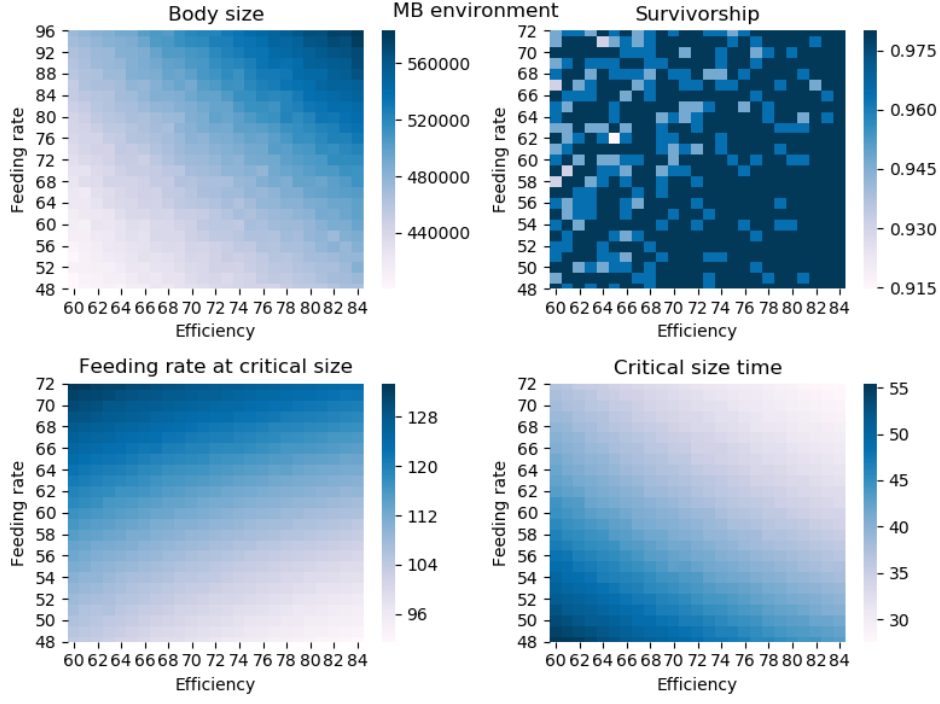
Figure 3.1: Effect of initial feeding rate and efficiency on larval traits in MB culture

In MCU and CCU cultures (high densities), fig 3.2 and fig 3.3 show that time to reach critical size show similar pattern as seen in MB culture with varying efficiency and initial feeding rate. The maxima possible is higher in high density cultures than maxima possible in low density culture, showing that it takes more time to reach given critical size at high densities than at low density with same efficiency and initial feeding rate values. Feeding rate shown at critical size also shows similar pattern as seen in MB culture but with higher maxima reached with same parameter ranges. This suggests feeding rate shown at critical size is also a density dependent trait. The complete white pixels in all heatmaps (fig 3.2 and fig 3.3) are the values where none of the larvae survived, so the trait could not be measured and are to be excluded.

At high densities, especially at MCU density, body size and survivorship are not affected by initial feeding rate, unlike at low density. Food acquired while having either higher or lesser initial feeding rate, remains almost the same. This is due to the decrease in food quality is higher for higher initial feeding rate. Thus, overall body size increment which is majorly determined by food quality at high densities, is approximately same in both cases i.e. larval growth with both higher and lower initial feeding rate. Survivorship also shows similar pattern as body size for these two parameters, since it is determined by whether critical size is reached or not.
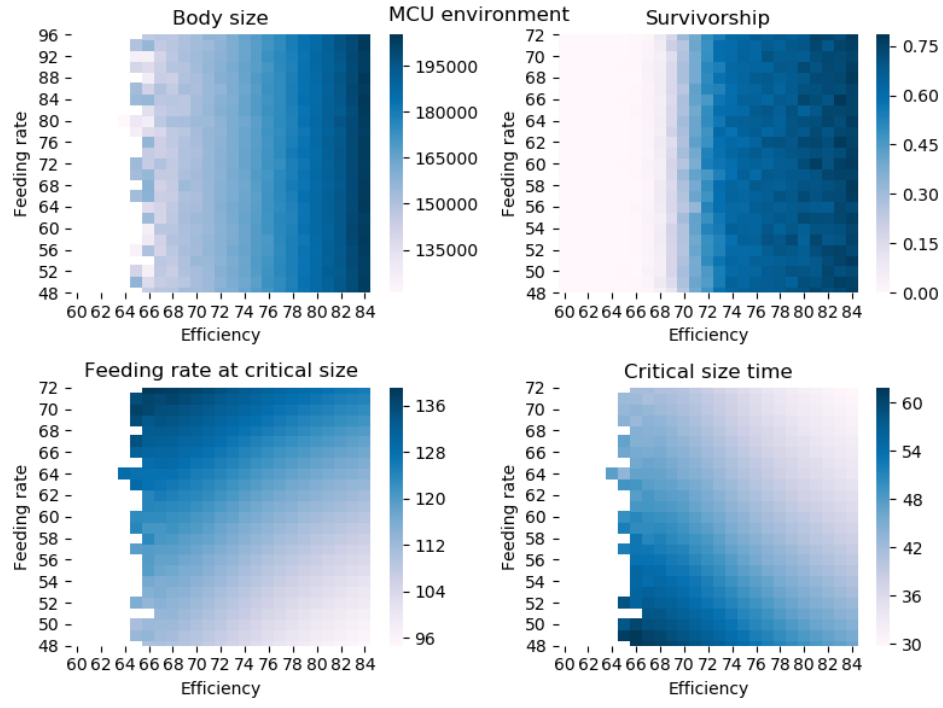
Figure 3.2: Effect of initial feeding rate and efficiency on larval traits in MCU culture
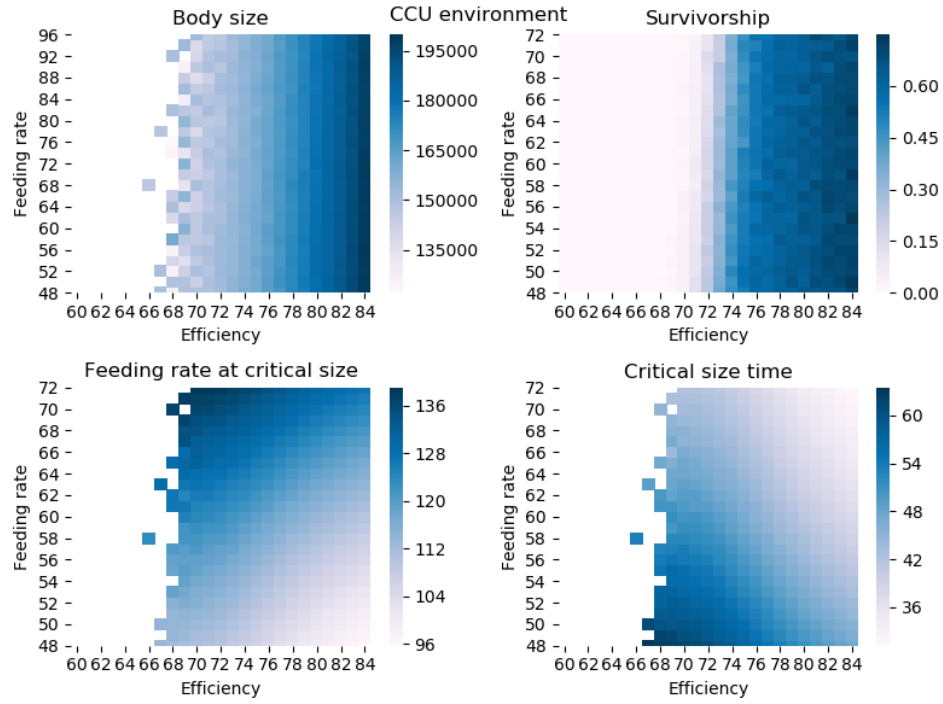

Figure 3.3: Effect of initial feeding rate and efficiency on larval traits in CCU culture
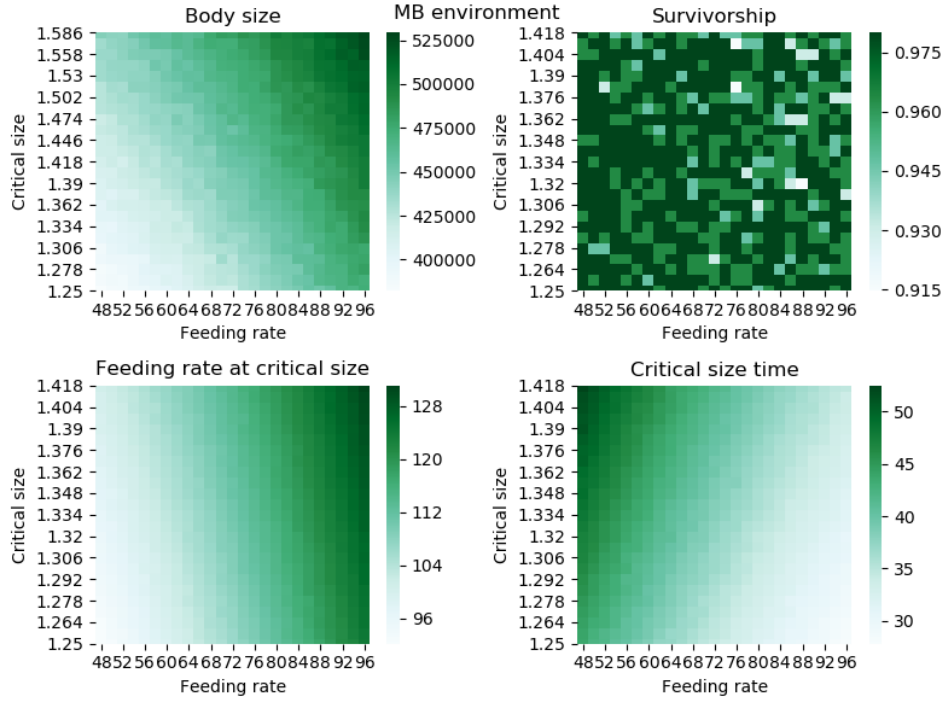
Figure 3.4: Effect of initial feeding rate and critical size on larval traits in MB culture

3.2   Initial Feeding Rate and Critical Size

In MB culture, fig 3.4 shows having higher critical size and higher initial feeding rate leads to higher larval body size. Lower critical size and higher initial feeding rate is beneficial in having lower time to reach critical size. Feeding rate at critical size is majorly determined by initial feeding rate, while having higher critical size gives slightly higher feeding rate, since time to reach critical size is more. Survivorship is not affected by either initial feeding rate or critical size at low density, since competition for food is minimal.

In MCU culture fig 3.5, body size is not affected by either critical size or initial feeding rate and post-critical growth is very less. Time to reach critical size and feeding rate at critical size show similar pattern as shown in MB culture with higher maxima for same values. Survivorship is only affected by critical size and initial feeding rate has no effect on survivoship at MCU density. Lower critical size shows trend for higher survivoship, since larvae are able to pupate in lesser time before food quality decreases drastically.
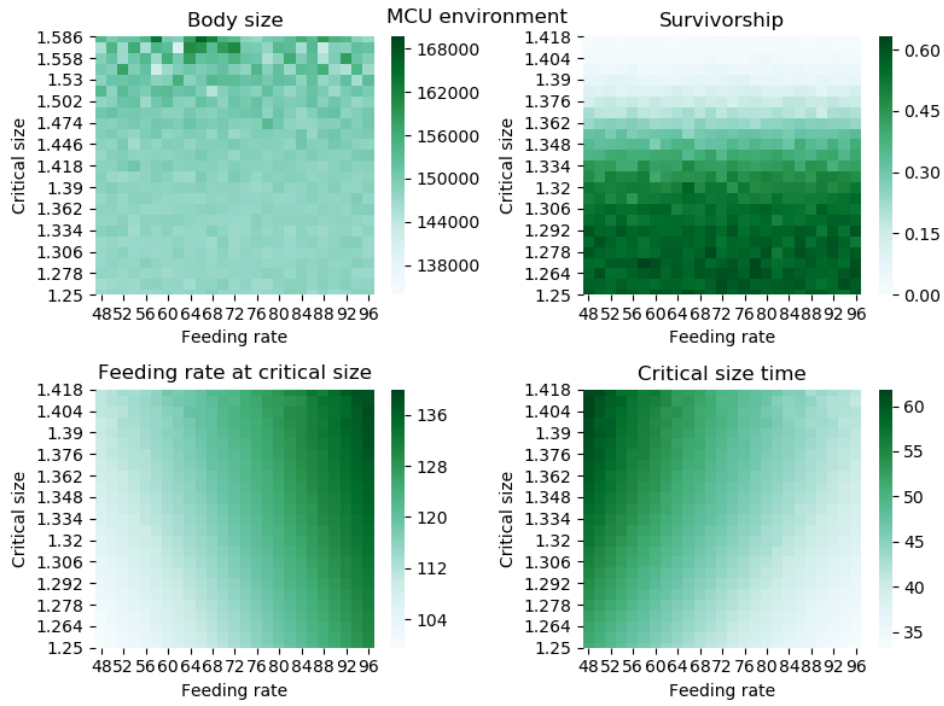
Figure 3.5: Effect of initial feeding rate and critical size on larval traits in MCU culture
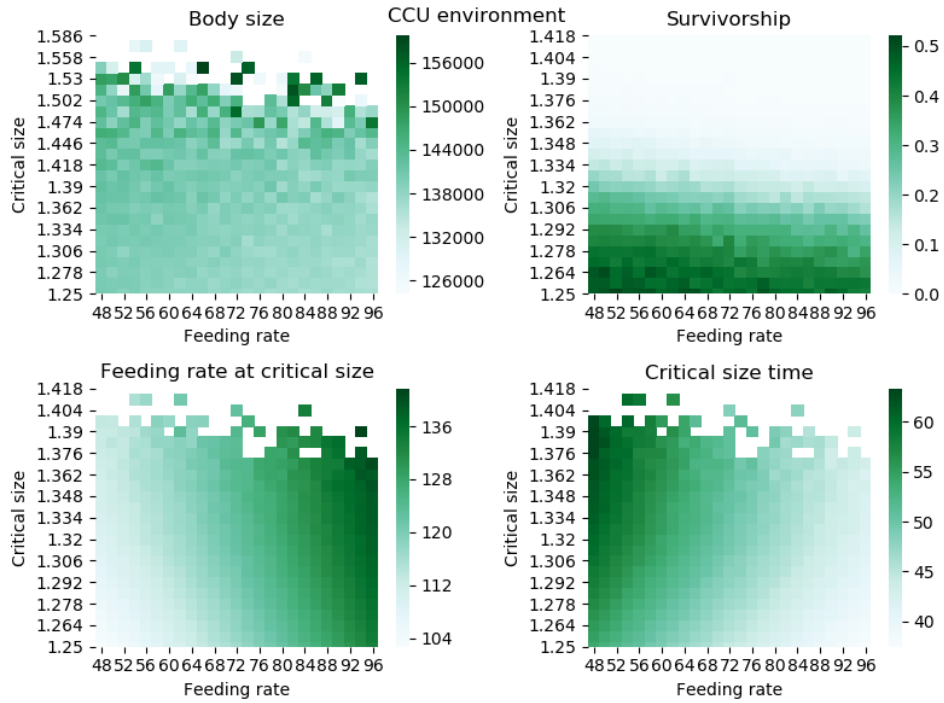

Figure 3.6: Effect of initial feeding rate and critical size on larval traits in CCU culture

In CCU culture, fig 3.6, patterns of body size, time to reach critical size and feeding rate at critical size similar to the ones in MCU culture. Survivorship shows small effect of initial feeding rate as well along with critical size. Having lesser average initial feeding rate in the population leads to slower urea build up and decrease in food quality of the feeding band, thus larvae with higher critical size are able to survive.

3.3   Critical Size and Efficiency

In MB culture, fig 3.7, shows increase in body size with increase in critical size and efficiency. Feeding rate at critical size and time to reach critical size both increase with increasing critical size and decreasing efficiency. Higher efficiency leades to decrease in critical size thus feeding rate shown at critical size reaches lesser maxima. Survivorship shiws no effect of these parameters at low density.
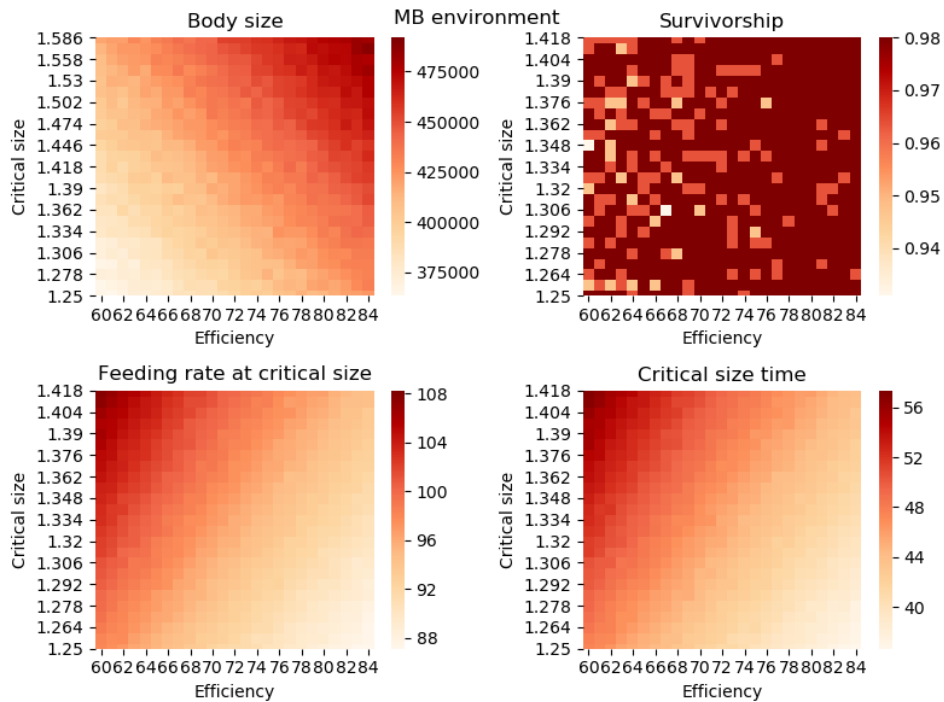

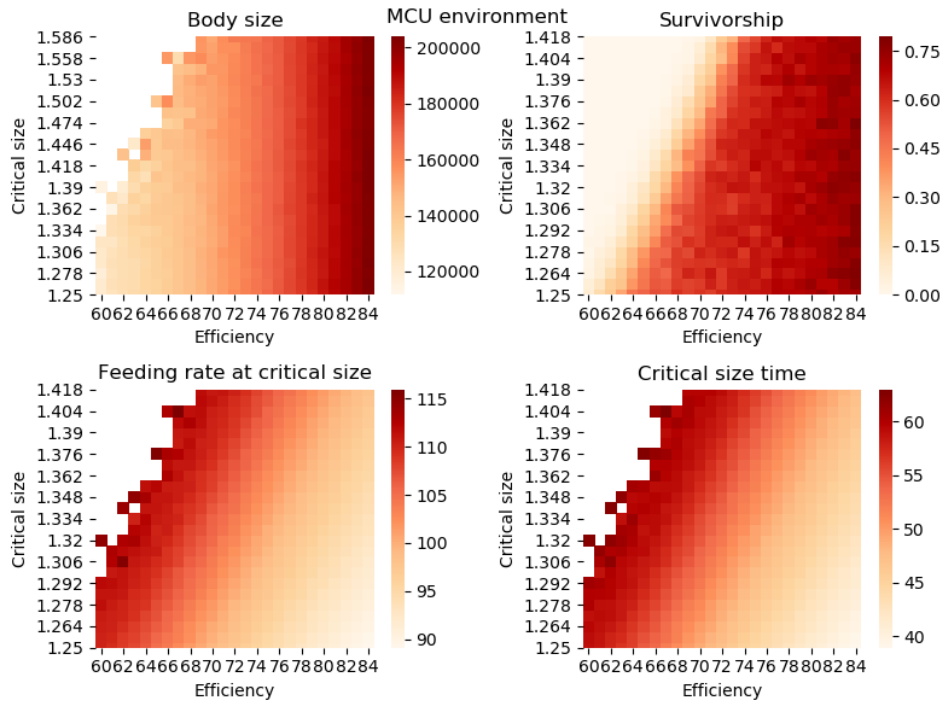Figure 3.7: Effect of critical size and efficiency on larval traits in MB culture

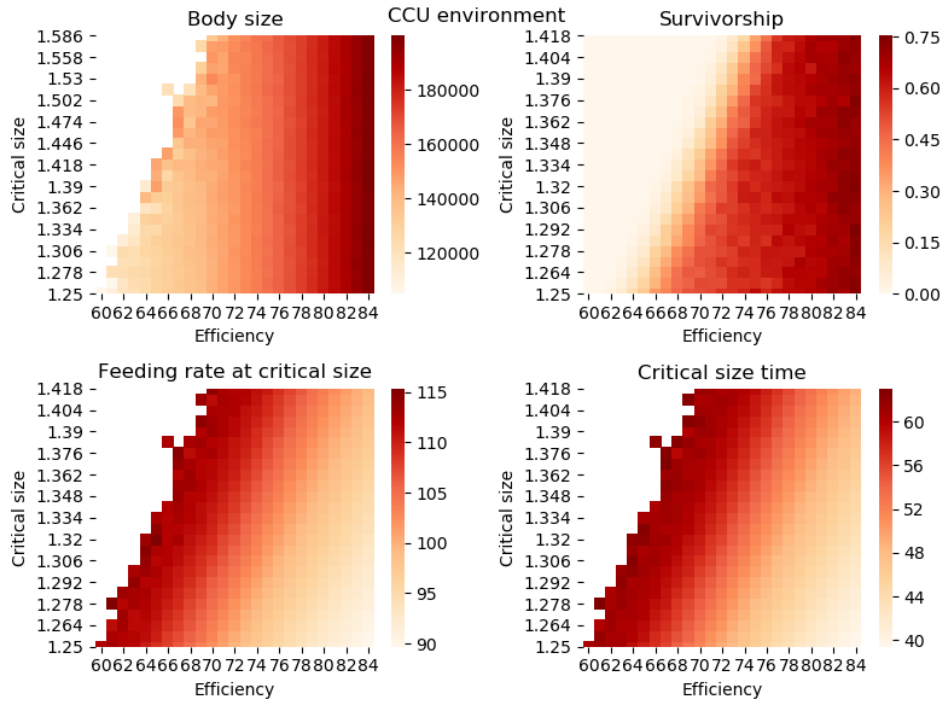Figure 3.8: Effect of critical size and efficiency on larval traits in MCU culture

Figure 3.9: Effect of critical size and efficiency on larval traits in CCU culture

In MCU and CCU culture, fig 3.8 and fig 3.9, all the larval traits show similar pattern as in MB density with critical size and efficiency. The maxima for feeding rate at critical size and time to reach critical size is higher compared to the ones at MB density. Body size and survivoship maxima are lesser at high density.

3.4   Discussion

References

Chapter 4

Modelling Evolution of Life-history Traits

4.1 Modelling Adult Stage

After modelling larval stage and calibrating, I developed the model for the adult stage of *Drosophila* life cycle. This includes randomly choosing surviving adults from all replicate larval stage vials, matings, and inheritance of larval trait parameters from parents to offspring. Female is mated once with random male chosen from the adult population with replacement for simplicity. From all the offspring produced, eggs are chosen at random with numbers respective to the crowding environment maintained for the next generation.

4.1.1 Fecundity

After each mating, the number of eggs produced for a female are derived from the fecundity equation based on the model of (ref) Tung S. (year). Fecundity is taken as a function of body size of the female and adult nutrition parameter (the amount of yeast provided). Fecundity of an ith female is given as:

$$Egg_i = Nut \cdot x_2 \cdot \log{(x_3 \cdot s_i)}$$

Here, s_i = body size of the ith female

Egg_i = Number of eggs laid by the female in a mating

Nut = Adult nutrition i.e. the amount of yeast provided

x_2, x_3 = scaling parameters

4.1.2 Inheritance

Larval trait parameters (initial feeding rate, effieciency, waste tolerance and critical size) are inherited from parents to offspring produced by each female using mid-parent value. The mid-parent value i.e. average of mother and father for each larval parameter of offspring as mean is calculated for offspring. This mid-parent value is taken as mean of a normal distribution with fixed standard deviation. The standard deviation in this normal distribution determines the heritibility of the mid-parent value and it is considered to be different for each trait parameter. Trait parameters of the offspring are assigned as:

$$T_i \in N(mpv_T, \delta_T)$$

Here,

T_i = Trait parameter assigned to i^{th} offspring from a mating

mpv_T = Mid-parent value of of the trait T for a given mating

δ_T = Stochasticity in mid-parent value of the trait T

$N(mpv, \delta)$ = Normal distribution with mpv as mean and δ as standard deviation

4.2 Effect of Laral Crowding on the Evolution of Life-history Traits

Using initial values for all parameters given in table (no.), the entire model is simulated for 100 generations with 10 replicates for MB, MCU and CCU cultures. All larval trait parameters are taken from independent distribution and there is no correlation between them. To see how larval trait parameters evolve over time, timeseries for these traits of surviving adult individuals are plotted with 95% CI.

Initial feeding rate in high density cultures increase over generations at similar rate but inital feeding rate is higher always in CCU culture always than in MCU culture. In MB culture, being control population, initial feeding rate does not evolve (fig 4.1).

Efficiency show similar trend in high density cultures i.e. it increases over generations at similar rate but is higher always in CCU culture always than in MCU culture. In MB culture, being control population, efficiency does not evolve (fig 4.2).

Critical size in high density cultures decreases at the same rate but critical size in CCU culture is always lower than in MCU culture. In MB culture, critical size does not change over generations (fig 4.3).

Waste tolerance does not evolve in all of the culture populations since there is no significant decrease/increase in waste tolerance value (fig 4.4).
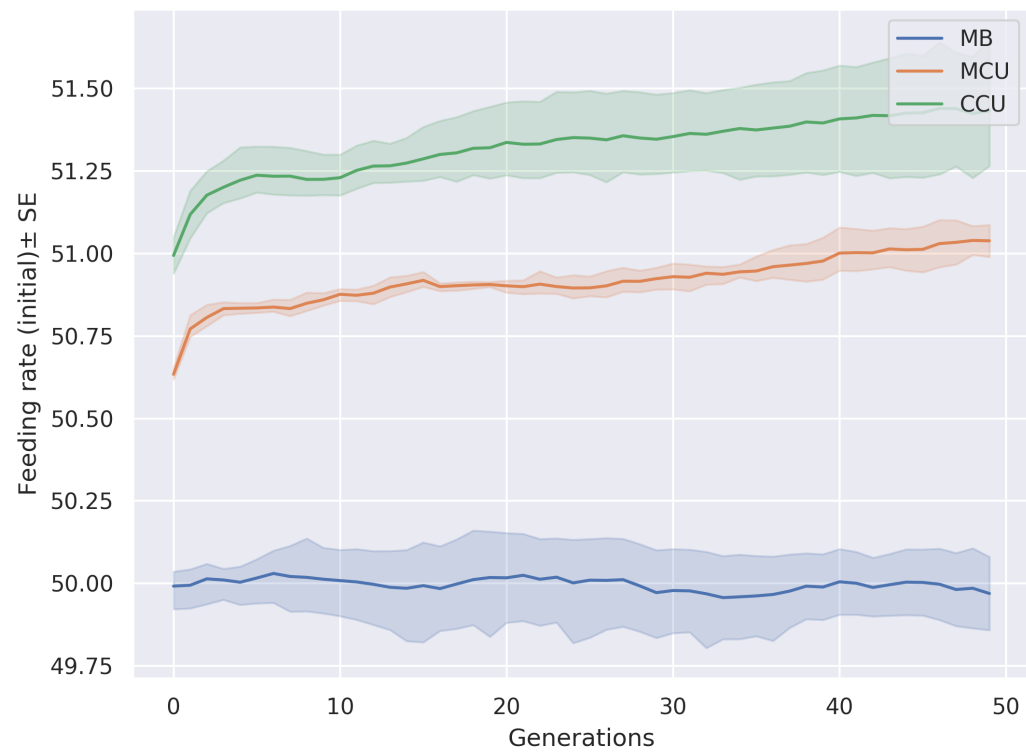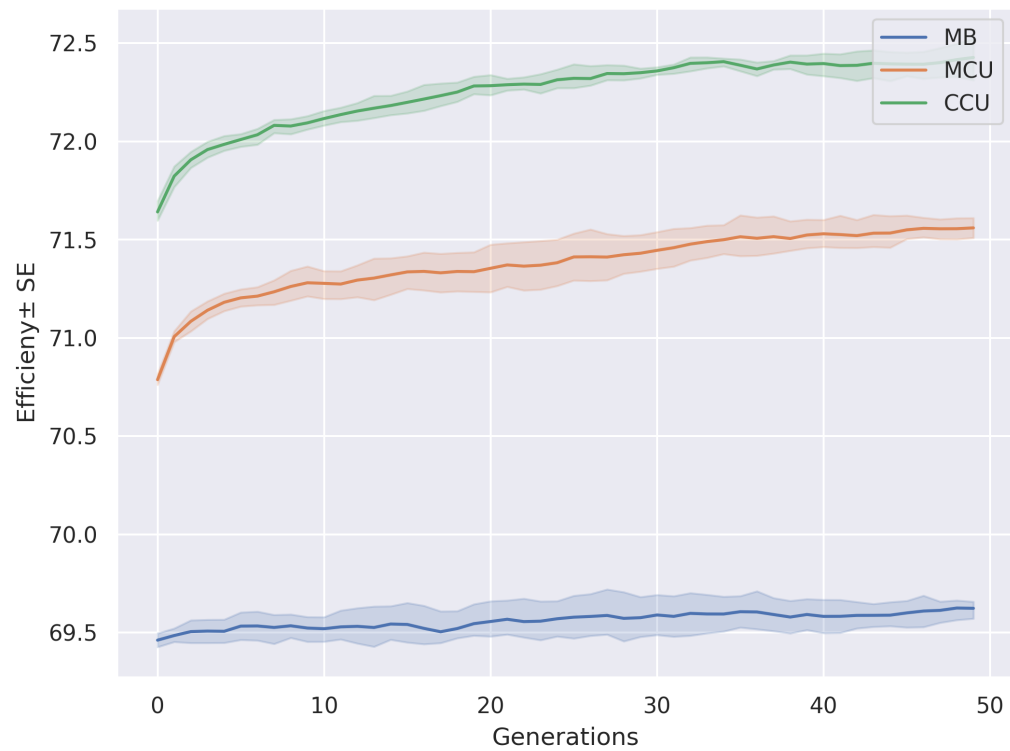
Figure 4.1: Timeseries for initial feeding rate

Figure 4.2: Timeseries for initial efficiency

4.3 Effects of Variation on the Evolution of Larval Trait Parameters

The source of variation in the model comes from the initial variation in the larval trait parameters, given as certain standard deviation in the respective initial distribution as well as from the heritibility of the mid-parent value during the inheritance of the larval trait parameters. The simulations show how these sources of variations play an important role in determining the evolutionary routes taken to acheive greater competitive ability by having maximum survivorship.

4.3.1 Variation in the Initial Distribution of Larval Trait Parameters

When timeseries are plotted for the larval trait parameters, the variation in the initial distribution of these trait parameters determine the maxima that can be achieved to increase the fitness. From fig(a), fig(b) and fig(c), it is seen that differences in variation of these trait values, maxima reached are different with similar initial mean trait values. If the initial variation in efficiency is very high compared initial variation in feeding rate, then feeding rate does not reach higher feeding rate after few generations unlike of the timeseries simulations performed with lower initial variation in the efficiency. Depending on the initial variation in each trait separately, traits can evolve differently, since these trait parameters interact with each other to give complex phenotypes suxh as body size, time to rach critical size and survivorship.
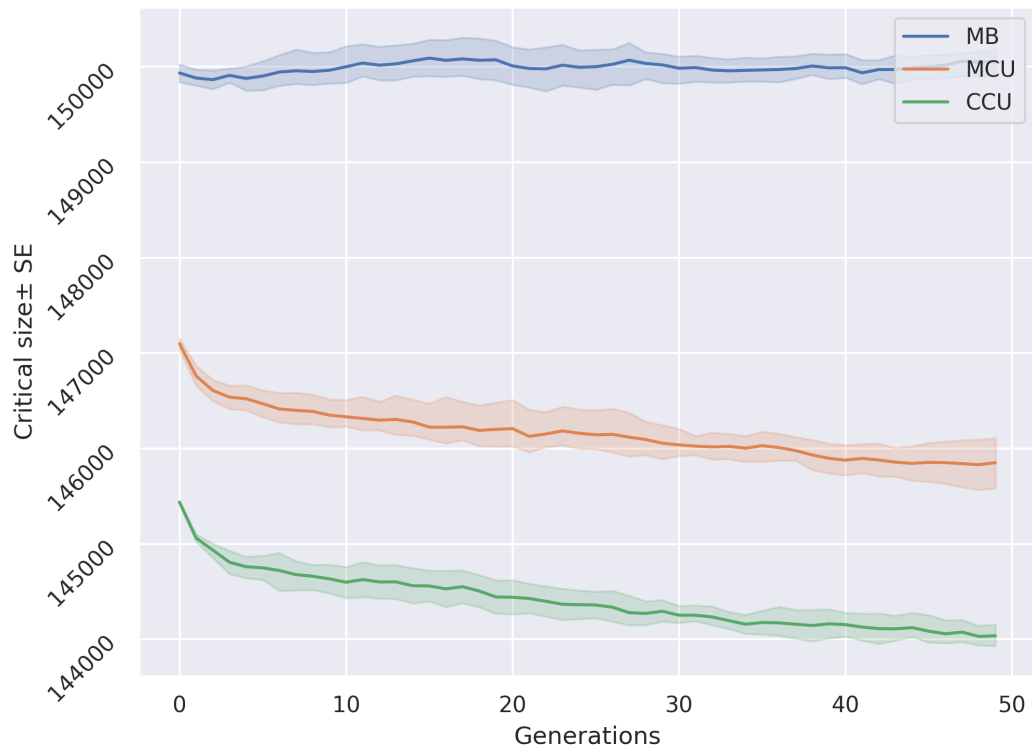
4.3.2 Heritibility in Mid-parent Value
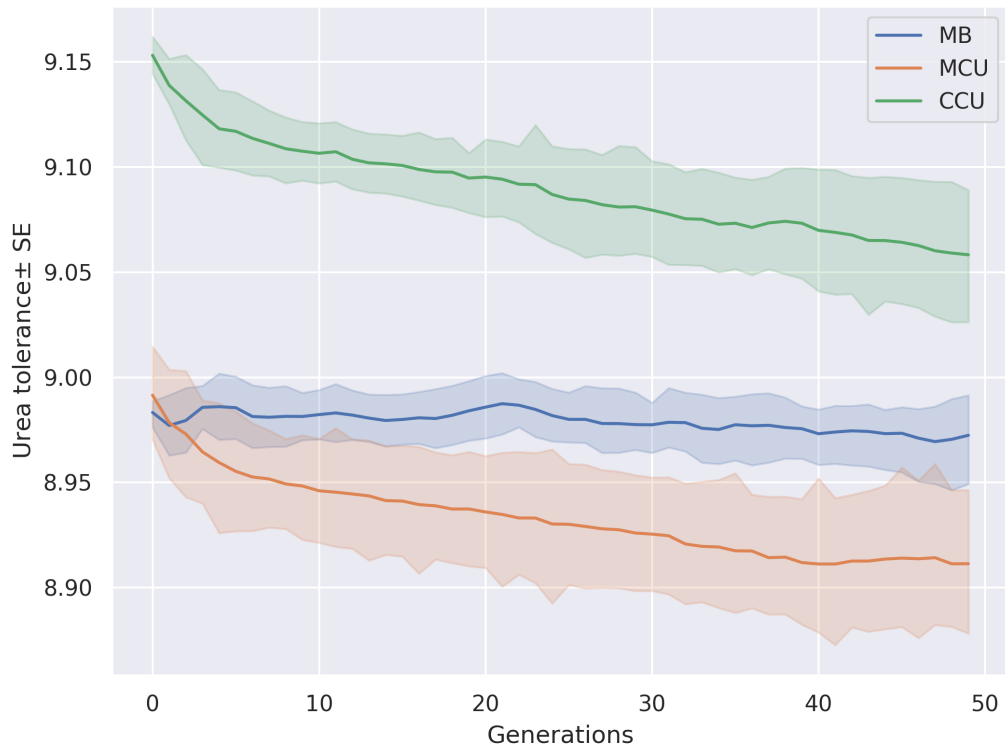
Figure 4.3: Timeseries for initial critical size

Figure 4.4: Timeseries for initial waste tolerance

References