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# Numerical Stability of the Escalator Boxcar Train under reducing System of Ordinary Differential Equations

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**Abstract.** The Escalator Boxcar Train (EBT) is one of the most popular numerical methods used to study the dynamics of physiologically structured population models. The original EBT-model accumulates an increasing system of ODEs to solve for each time step. In this project, we propose a merging procedure to overcome computational disadvantages of the EBT method, the merging is done as an automatic feature. In particular we apply the model including merging to a colony of *Daphnia Pulex*.

**Keywords:** Escalator Boxcar Train, physiologically structured population models, *Daphnia*, merging.

## 1 Introduction

Physiologically structured population models (PSPMs) describe the dynamics of an arbitrary number of biological populations. The basic idea of the EBT-technique is to group individuals of similar state into cohorts, in which the dynamics is prescribed by ODEs which are tracked throughout their entire life history. The individual population dynamics in physiologically structured population models are given by birth rates, death rates, and growth rates, which are dependent of the environment and their physiological state. These states can describe any data of individual physiology, for example; length, size, age, height or weight (Metz and Diekmann[8]).

In this paper, we will for convenience work with a one-dimensional state space describing an individual's length. In the PSPMs, the death rate, the growth rate and the birth rate of the individuals are assumed to have the form  $\mu(x, E_t)$ ,  $g(x, E_t)$  and  $b(x, E_t)$  respectively, where  $x$  is the length of the individual at time  $t$  and  $E_t$  is the environment. Furthermore, offspring are assumed to have the same birth size  $x_b$ . With these assumptions, one can show (see, e.g., de Roos[2]) that the density  $u(x, t)$  of individuals of state  $x$  at time  $t$  satisfies the first order, nonlinear, nonlocal hyperbolic partial differential equation with

nonlocal boundary condition

$$\frac{\partial}{\partial t}u(x, t) + \frac{\partial}{\partial x}(g(x, E_t)u(x, t)) = -\mu(x, E_t)u(x, t), \quad (1a)$$

$$g(x_b, E_t)u(x_b, t) = \int_{x_b}^{\infty} b(\xi, E_t)u(\xi, t)d\xi, \quad (1b)$$

$$u(x, 0) = u_0(x), \quad (1c)$$

where  $x_b \leq x < \infty$  and  $t \geq 0$ .

The EBT method, developed by de Roos[3], solves these kind of partial differential equations, using an increasing system of ODEs. In this article, we propose a procedure of merging internal cohorts in order to reduce the system of ordinary differential equations. We show that this merging procedure does not affect the properties of the solution and in addition, the computation time decreases from polynomial to linear time when the EBT of Daphnia is simulated.

The convergence of the Escalator Boxcar Train has been established in a series of papers, see for example; de Roos and Mets[4], Brännström *et al.*[1], and Carrillo *et al.*[7]. This report consists of four parts. The first part consists of concept, definitions and formulations of the EBT model in Section 2. In the second part, Section 3, Daphnia's model specifications is described. The third part, Section 4, presents a mathematical proof of convergence. And, in the last part, Section 5, we present results from simulations of the Daphnia model, with and without merging.

## 2 The Escalator Boxcar Train

The Escalator Boxcar Train is a numerical method for solving physiologically structured population models (PSPMs). This method is widely used in theoretical biology since the components of the numerical scheme can be given a biological interpretation. To study the dynamics of a PSPMs numerically, the structured population is subdivided into distinct groups of individuals that are similar, these groups are called cohorts.

The cohorts are separated into internal cohorts and a boundary cohort, where the latter has the unique property that the numbers of individuals may be growing because of newborn individuals. The newly born individuals are assumed to have the same physiological properties and are accumulated in the boundary cohort. The remaining cohorts are called internal cohorts. We set the index of the boundary cohort to be zero and the internal cohorts are indexed by  $i = 1, 2, \dots, N$ .

The number of individuals in the  $i^{th}$  cohort is denoted by  $N_i(t)$ . As the sizes of the individuals in each cohort are similar, the mean individual state will be used and is denoted by  $X_i(t)$ .

We consider the numerical solution of the one-dimensional PSPM with a single birth state  $x_b$  defined by Equation (1). The EBT method approximates the measure induced by the solution rather than approximating the solution

directly. The approximation is given by linear combination of Dirac measures, and the approximated measured-value solution  $\zeta_t^N$  to the PSPMs is

$$\zeta_t^N = \sum_{i=0}^N N_i(t) \delta_{X_i(t)}. \quad (2)$$

We biologically interpret each of the terms in the approximation as a cohort composed of  $N_i$  individuals with average individual state  $X_i$  at time  $t$  (see for example Brännström et al[1]). The environment  $E_t$  is often directly or in-directly dependent of the solution  $\zeta_t^N$ .

## 2.1 The dynamics of internal cohorts

The internal cohorts can be characterized by the number of individuals and by a representative size for these individuals. We will adopt the mean length as the characteristic measure of body size, since even within a cohort the individuals are not completely identical. The dynamics of the size in the internal cohorts follows the differential equation

$$\frac{dX_i}{dt} = g(N_i, E_t), \quad (3)$$

which is simply the growth equation for an individual.

The dynamics of the number (density) of individuals in the internal cohort is defined by:

$$\frac{dN_i}{dt} = -\mu(X_i, E_t)N_i. \quad (4)$$

## 2.2 The dynamics of the boundary cohort

The boundary cohort is characterized by the number of individuals it contains and by a representative size measure. The number of individuals and length of individuals in the boundary cohort are denoted by  $N_0(t)$  and  $X_0(t)$ , respectively. If there is no reproduction at all, the boundary cohort could be identical to all other cohorts as the dynamics  $N_0(t)$  and  $X_0(t)$  is described by

$$\begin{aligned} \frac{dN_0}{dt} &= -\mu(X_0, E_t)N_0, \\ \frac{dX_0}{dt} &= g(X_0, E_t). \end{aligned}$$

If reproduction does occur, the contribution is summed for the offspring in all cohorts, where the offspring, produced in cohort  $i$ , equals  $b(X_i, E_t)N_i$ . Thus the total population fecundity will be  $\sum_{i=0}^N b(X_i^t, E_t)N_i^t$ .

This total population birth rate is represented by the newborn individuals which are all accumulated into the current boundary cohort. Hence the dynamics of the number of individuals in the boundary cohort become:

$$\frac{dN_0}{dt} = -\mu(X_0, E_t)N_0 + \sum_{i=0}^N b(X_i, E_t)N_i,$$

which depends upon the one hand for the mortality process of the individuals that have recently been born and on the other hand for the addition of offspring.

The dynamics of the size  $X_0(t)$  in the boundary cohort, follow the same equation as the dynamics of the size in the internal cohort, i.e.,

$$\frac{dX_0}{dt} = g(X_0, E_t).$$

This dynamics was introduced in [1], and have been shown to have the same convergence rate as the original dynamics in [3], see [12].

### 2.3 Process of internalizing the boundary cohort

In the course of time, both the number and size of individuals in the boundary cohort change according to the reproduction of individuals and the environment. If the size of the boundary cohort grows to large, it will produce an inapplicable large approximation error. Therefore, the boundary cohort must be internalized sufficiently often.

At each time step, we check if the current boundary cohort's density is zero (no reproduction has occurred), in this case we reset the size of individuals in the boundary cohort to  $x_b$ , otherwise, we will introduce a new boundary cohort. Whenever a new boundary cohort is introduced, the old boundary cohort is transformed into an internal cohort. For this reason, the number of internal cohorts will be increased due to internalization. This will be inconvenient for computational purposes, (see Table 5.1). To overcome the growing number of internal cohorts, we apply a merging procedure for internal cohorts containing a small number of individuals.

### 2.4 Process of merging internal cohorts

If the number of individuals in an internal cohort falls below a certain threshold, and that the size of the internal cohort closest to this one, is close enough, then we merge the two cohorts together. We do this in such a way that the expected number of offspring stays the same, compared to if we had not merged the cohorts. The reason why the two merging cohorts must have similar size is explained in the proof of convergence given in Section 4.

## 3 The Daphnia's model specifications

To illustrate that the solution when merging cohorts converges, we will exemplify this with an EBT-model applied to the water flea, *Daphnia pulex*, which is the structured population in the model. The *Daphnia pulex* feeds on the algae *Chlamydomonas reinhardtii*, which specify the amount of food, the environment in the model. Biologists have been studying the behaviour of *Daphnia* extensively (see for example Hebert[13], Ebert[6]), and hence, the biological information is vast, we will therefore introduce a simple size-structured model for

Symbol	Value	Unit	Interpretation
$\nu$	0.007	$mgC/mm^2$	maximum ingestion rate per surface area
$f_h$	0.164	$mgC/L$	half saturation food density
$x_b$	0.6	$mm$	length at birth
$x_j$	1.4	$mm$	length at maturity
$l_{max}$	3.5	$mm$	maximum length
$r_g$	0.11	$d^{-1}$	growth rate
$r_{max}$	1.0	$mm^2$	maximum reproduction rate
$\mu$	0.05	$d^{-1}$	mortality rate
$\rho$	0.5	$d^{-1}$	resource regrowth rate
$k$	0.25	$mgC/L$	maximum resource density

**Table 3.1.** Interpretation of constants used for the Daphnia's life history model was presented by De Roos in (de Roos and Persson *et al.*[5]). The values are developed from practical experiments. Milligram of carbon (mgC), millimeter (mm), liter(L), and day (d) are used in units.

the life history of individual Daphnia. We will use the EBT-model, with the constants in the simulation, as given in Table 3.1. The length of the Daphnia depends on the environment, i.e., the amount of food available. More specifically, larger individuals have higher food consumption, basal metabolism and reproduction rate (Diekmann *et al.*[10]). If they can't get enough food, their growth rate will decelerate and they may even decrease in size. In particular, this implies that the mature Daphnia individuals can shrink under particular conditions (de Roos and Persson[5]) to a juvenile state, in which they do not produce any offspring.

We denote the length of an individual Daphnia by  $X$ . The reproduction of adult Daphnia is directly proportional to food ingestion. The reproduction is described by the function

$$b(X, F) = \begin{cases} r_{max} X^2 \frac{F}{f_h + F} & \text{if } X > x_j, \\ 0 & \text{if } X \leq x_j, \end{cases} \quad (5)$$

where  $b(X, F)$  denotes the birth rate of adult Daphnia per unit of time,  $f_h$  is the half-saturation food density  $F$  (the environment) and  $r_{max}$  is the maximum reproduction rate per unit of surface area.

For the growth rate of Daphnia, the von Bertalanffy growth equation (see von Bertalanffy[9]) will be applied. This growth rate is represented by:

$$\frac{dX}{dt} = r_g \left( l_{max} \frac{F}{f_h + F} - X \right), \quad (6)$$

where  $r_g$  is growth rate constant and  $l_{max}$  can be interpreted as the maximum length of Daphnia reaches under actual food condition. Note that the value of the growth rate can be negative when the value of  $F$  is small. This reflects that individuals can shrink under low food apply, as mentioned above.

We assume that all Daphnia individuals have the same risk for mortality rate,  $\mu(X, F)$ , that will be defined by a constant.

$$\mu(X, F) = \mu. \quad (7)$$

## 4 Error bounds when merging two cohorts

In this section, we present a proof of convergence to the general solution when merging two cohorts, sufficiently close together, i.e., we prove that the reduced system of ODEs will not give rise to large changes in the general solution.

We consider two cohorts  $(X_a, N_a)$  and  $(X_b, N_b)$ , where  $N$  denotes the number of individuals in a cohort and  $X$  the mean size.

In a small time step,  $\Delta t$ , the food available in the system is assumed to be constant, which implies that the growth rate and fecundity rate are both constant in the time interval  $0 \leq t \leq \Delta t$ . In this model, the death rate,  $\mu$  is constant, see Equation (7).

For notational purpose, we assume that  $X_b \geq X_a$  at time  $t = 0$ . At the start of the time step, we denote the initial data with a sub-index zero, e.g.,  $X_{a_0} = X_a(0)$ ,  $N_{a_0} = N_a(0)$  and so on. The difference,  $\Delta x_0 = X_{b_0} - X_{a_0}$ , between the sizes of these cohorts is assumed to be sufficiently small.

With the above assumptions, the dynamics of the internal cohorts become simplified. From Equation (4) we get

$$N'(t) = -\mu N(t), \quad (8)$$

and from Equation (6) we get

$$X'(t) = c_1 \left( 1 - \frac{X(t)}{K} \right), \quad (9)$$

with parameters  $K = l_{max} \frac{F}{f_h + F}$  and  $c_1 = r K$ .

When we consider the reproduction from the two cohorts, without merging, we get from Equation (5) the contribution to the boundary cohort as

$$b_w(t) = c_2 N_a(t) X_a^2(t) + c_2 N_b(t) X_b^2(t), \quad (10)$$

where  $c_2 = r_{max} \frac{F}{f_h + F}$ .

When merging the two cohorts  $(X_a, N_a)$  and  $(X_b, N_b)$  into one merged cohort  $(X_m, N_m)$ , we naturally add the number of individuals in both cohorts, i.e.,

$$N_{m_0} = (N_{a_0} + N_{b_0}) \quad (11)$$

and, in view of Equation (10), we initialize the merged cohort size to

$$X_{m_0} = \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}}, \quad (12)$$

since this formula best preserves the expected number of offspring. In the case when we merge the two cohorts, we get the dynamics of the fecundity, Equation (5), as

$$b_m(t) = c_2 N_m(t) X_m^2(t). \quad (13)$$

We will now show that the general solution of the merged cohort converges to the general solution without any merging, this is the main result of the paper.

**Theorem 1.** *Under the above assumptions we get*

$$b_m(\Delta t) = b_w(\Delta t) + O(\Delta x_0 \cdot \Delta t)$$

*Proof.* For non-merging cohort, we get an expression for the newborn individuals,  $b_w$ , by using Maclaurin expansion in  $\Delta t$

$$\begin{aligned} b_w(\Delta t) &= b_{w_0} + b'_{w_0} \Delta t + O(\Delta t^2) \\ &= c_2(N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \\ &\quad + c_2(N'_{a_0} X_{a_0}^2 + 2N_{a_0} X_{a_0} X'_{a_0} + N'_{b_0} X_{b_0}^2 + 2N_{b_0} X_{b_0} X'_{b_0}) \Delta t \\ &\quad + O(\Delta t^2) \end{aligned}$$

Where we used Equation (10) and its derivative in the last equality. To proceed, we substitute Equation (8) and Equation (9) in the above equation. Thus

$$\begin{aligned} b_w(\Delta t) &= c_2(N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \\ &\quad + c_2 \left( -\mu N_{a_0} X_{a_0}^2 + 2N_{a_0} X_{a_0} c_1 \left( 1 - \frac{X_{a_0}}{K} \right) - \mu N_{b_0} X_{b_0}^2 + 2N_{b_0} X_{b_0} c_1 \left( 1 - \frac{X_{b_0}}{K} \right) \right) \Delta t \\ &\quad + O(\Delta t^2) \\ &= c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) - \mu c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \Delta t \\ &\quad + 2c_1 c_2 (N_{a_0} X_{a_0} + N_{b_0} X_{b_0}) \Delta t - \frac{2c_1 c_2}{K} (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \Delta t \\ &\quad + O(\Delta t^2) \end{aligned}$$

In the case when we merge cohorts, we get an expression for the newborn individuals, using similar calculations as above

$$\begin{aligned} b_m(\Delta t) &= b_{m_0} + b'_{m_0} \Delta t + O(\Delta t^2) \\ &= c_2 N_{m_0} X_{m_0}^2 + c_2 (N'_{m_0} X_{m_0}^2 + 2N_{m_0} X_{m_0} X'_{m_0}) \Delta t \\ &\quad + O(\Delta t^2) \end{aligned}$$

We substitute equations (8), (9), (11), and (13) in the above equation.

$$\begin{aligned} b_m(\Delta t) &= c_2 (N_{a_0} + N_{b_0}) \frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}} \\ &\quad + c_2 \left( -\mu N_{m_0} \frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}} + 2(N_{a_0} + N_{b_0}) X_{m_0} c_1 \left( 1 - \frac{X_{m_0}}{K} \right) \right) \Delta t \\ &\quad + O(\Delta t^2) \\ &= c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \\ &\quad + c_2 \left( -\mu (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) + 2c_1 (N_{a_0} + N_{b_0}) X_{m_0} - 2c_1 (N_{a_0} + N_{b_0}) \frac{X_{m_0}^2}{K} \right) \Delta t \\ &\quad + O(\Delta t^2) \end{aligned}$$



$$\begin{aligned}
b_m(\Delta t) &= c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) - \mu c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \Delta t \\
&\quad + 2c_1 c_2 (N_{a_0} + N_{b_0}) \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} \Delta t \\
&\quad - \frac{2c_1 c_2}{K} (N_{a_0} + N_{b_0}) \frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}} \Delta t + O(\Delta t^2) \\
&= c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) - \mu c_2 (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \Delta t \\
&\quad + 2c_1 c_2 N_{a_0} \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} \Delta t + 2c_1 c_2 N_{b_0} \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} \Delta t \\
&\quad - \frac{2c_1 c_2}{K} (N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2) \Delta t + O(\Delta t^2).
\end{aligned}$$

Subtracting the equation for  $b_m$  from the equation for  $b_w$  gives

$$\begin{aligned}
b_w - b_m &= 2c_1 c_2 (N_{a_0} X_{a_0} + N_{b_0} X_{b_0}) \Delta t \\
&\quad - 2c_1 c_2 N_{a_0} \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} \Delta t - 2c_1 c_2 N_{b_0} \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} \Delta t \\
&\quad + O(\Delta t^2).
\end{aligned}$$

Finally, using the continuity of the square root function, we get that both

$$X_{a_0} = \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} + O(\Delta x_0)$$

and

$$X_{b_0} = \sqrt{\frac{N_{a_0} X_{a_0}^2 + N_{b_0} X_{b_0}^2}{N_{a_0} + N_{b_0}}} + O(\Delta x_0)$$

Thus, the number of newborn individuals for merging cohorts converges to the number of newborn individuals for non-merging cohort when the difference between the size of individuals for these two cohorts and that the time step goes to zero. Which completes the proof.

## 5 Simulation of the EBT and Daphnia model

The EBT of the Daphnia's life model was simulated using MATLAB. To solve the system of ODEs in each time step, we use the function ode45 because of its accuracy and speed.

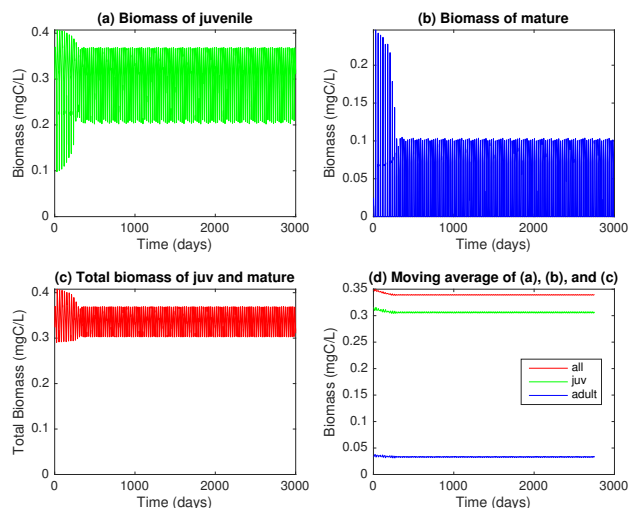
In this section, we present the behavior of a solution to the model with merging in Fig.5.1. In Table 5.1 we present simulation times, both for merging respectively non-merging of cohorts. In the simulation, at the beginning of each time step, we introduce a new boundary cohort, and internalize the old boundary

cohort. We used a least square method to fit the best monomial for the simulation time depending on the number of time steps. We found that when we simulated without merging, the power was close to 1.7, whereas, when the simulations was done with merging of cohorts, the power was close to one, i.e., the relationship between the simulation time and the number of time steps was linear.

In addition, as a consequence of Theorem 1, we see that the biomass of juveniles and adults for merging cohorts converges to the corresponding values for the non-merging simulations as  $\Delta t$  approaches to zero.

Time Span(days)	Merging	Elapsed Time(seconds)	Internal Cohorts	$j(mgC/L)$	$m(mgC/L)$	$v(mgC/L)$
2	Yes	14	45	0.3088	0.0330	0.3418
1	Yes	26	57	0.3072	0.0326	0.3398
1/2	Yes	47	72	0.3137	0.0382	0.3518
1/4	Yes	95	120	0.3132	0.0391	0.3523
2	No	21	749	0.3088	0.0330	0.3418
1	No	53	1367	0.3062	0.0335	0.3398
1/2	No	128	1681	0.3137	0.0382	0.3519
1/4	No	467	3165	0.3132	0.0392	0.3523

**Table 5.1.** Data for merging and non-merging of cohorts. The column, Elapsed Time, shows the running time for simulations, and the column, Internal Cohorts, the total number of internal cohorts for merging respectively non-merging cohorts. We also represent the value of the biomass of juvenile,  $j$ , mature,  $m$ , and the value of the total biomass of juvenile and mature,  $v$ .



**Fig. 5.1.** A graphical representation of a simulation with merging of cohorts. While (a) and (b) show juvenile and mature biomass, (c) represents total biomass of juvenile and adult. In addition, the moving average of figures (a), (b), and (c) is presented in (d) to compare for all these biomass, the moving average was taken over 250 days

## Conclusion and Future work

Physiologically structured population models are used to study biological systems. The Escalator Boxcar Train method is one of the commonly used numerical methods to find solutions to PSPMs but there are computational disadvantages of the EBT method. In this project, we have shown how to overcome the problem of the increment of ODEs over time. The main objective for this project is to present a way of how to merge cohorts in order to stabilize the number of ODEs to solve in each time step. We also constructed an EBT-solver that reduces the number of ODEs by an automatic feature of merging cohorts, in which we showed that we get a linear relationship between the number of time steps and the execution time.

The Escalator Boxcar Train method was first published in 1988 by A. de Roos[3], and a first proof of convergence appeared in 2013 by Å. Brännström, L. Carlsson, and D. Simpson[1]. The important reason for merging cohorts is that the maximum number of cohorts can be held under a certain level to make the simulation run faster. In this project, we compare the number of newborn individuals between merging and non-merging of cohorts, where we also prove that the number of newborn individuals for merging cohorts converges to the number of newborn individuals for non-merging cohorts.

Furthermore, this project uses MATLAB to simulate the Daphnia model and present graphs for the biomass of mature and juvenile.

In the future work, we want to establish EBT-solver which includes the automatic feature of merging and splitting cohorts, not only for the Daphnia model,

but for more general models as well, where we also aim to prove convergence for the merging and splitting of cohorts.

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