Modeling the life history of sessile rotifers: larval substratum selection through reproduction Supplemental Document

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Our model is a system of non-autonomous, difference equations based upon Main Document, Figure 1. The first model, which we call the *basic model* will allow larvae to move in the plankton, encounter any of a certain number of different substrates, and choose to settle or not settle on that substratum. The second model, which we call the *reproductive model*, allows for the dynamics of the basic model, as well as the possibility of larvae reproducing after settling on a substrate or metamorphosing in the plankton. Both models are defined on the time interval $[0, T]$. In this model, a time step is the length of time between substrate encounters.

As described in the Main Document, little data has been collected on the life history functions used in our model. Thus, the goal of this paper is not to fit our model to real-world data, but rather to give a proof of concept that modeling the environmental and life history functions using different simple mechanisms can affect the outcome in ways that mimic observed behaviors. This model allows us to qualitatively test hypotheses regarding sessile rotifer life histories. Were real-world data to be collected, this model could easily be fit to reflect that data.

Non-autonomous systems are notoriously difficult to analyze theoretically, so our approach will be computational. Additionally, since natural processes tend to be stochastic, we allow for random variations in our initial life history function values between trials [1]. To obtain a distribution of possible outcomes, we run a series Monte Carlo simulations. [1] In order to compare outcomes across many trials, we define two notions of *fitness*.

Definition 1.

1. *The* fitness *is the average percentage of larvae that survive and settle by time T, where the average is taken over all trials. In other words, fitness is the average percentage of larvae (taken over all trials) that do not die in the plankton due to starvation or predation.*

2. *The* reproductive fitness *is the average number of offspring per larvae in the beginning cohort, where the average is first taken within a given trial and then taken across all trials run. Note that for a species to survive, the reproductive fitness must be greater than 1.*

We note that any time a fitness or reproductive fitness value is reported, it reflects the average of many trials, the specific number of which will be noted.

[1] We used Python 3 to implement our model. Our code is available by correspondence with the first author.

1 The Model

Our model is based on Main Document, Figure 1. The following notation is used in our equations:

Table 1: States of the model

Model states	Definition
$P(t)$	Number of larvae in the plankton at time t
$E_j(t)$	Number of larvae encountering substratum j at time t
$S_j(t)$	Number of larvae settling on substratum j at time t
$R_j(t)$	Number of larvae surviving to reproduction on substratum j at time t
$D(t)$	Number of dead larvae at time t
$J_j(t)$	Number of juveniles born from larvae settled on substrate j at time t
$M(t)$	Number of larvae metamorphosing in the plankton at time t
$J_M(t)$	Number of juveniles born from larvae that metamorphosed in plankton at time t

Table 2: Environmental and life history functions in the model

Functions	Definition
$d_P(t)$	Death rate in plankton at time t
$e_j(t)$, $\hat{e}_j(t)$, $\tilde{e}_j(t)$	Encountering rate of substratum j at time t
$a_j(t)$, $\hat{a}_j(t)$, $\tilde{a}_j(t)$	Acceptance rate of substratum j at time t
$s_j(t)$	Survival rate on substratum j at time t
$m(t)$	Metamorphosis (in plankton) rate at time t
$r(S_j(t))$	Density dependent reproductive rate of substratum j at time t
$r_M(t)$	Reproductive rate in the plankton at time t
n	Total number of substrates
ℓ	Length of life
S	Critical density level of settled larvae

1.1 Basic Model

The Basic Model (BM) terminates after larvae settle and survive to be reproducing adults. Fitness is defined by the percentage of larvae that settle and survive to reproduction, as in

Definition 1. The system of $3n+2$ equations are as follows:

$$\begin{aligned}
P(t+1) &= (1-(d_P(t)+\sum_{j=1}^{n} e_j(t)))P(t) + \sum_{j=1}^{n}(1-a_j(t))E_j(t),\\
E_1(t+1) &= e_1(t)P(t),\\
&\vdots\\
E_n(t+1) &= e_n(t)P(t),\\
S_1(t+1) &= a_1(t)E_1(t),\\
&\vdots\\
S_n(t+1) &= a_n(t)E_n(t),\\
R_1(t+1) &= R_1(t)+s_1(t)S_1(t),\\
&\vdots\\
R_n(t+1) &= R_n(t)+s_n(t)S_n(t),\\
D(t+1) &= D(t)+d_P(t)P(t)+\sum_{j=1}^{n}(1-s_j(t))S_j(t).
\end{aligned}$$

At time t, we call this system of equations $\mathcal{B}(t)$.

We modify $\mathcal{B}(t)$ by enforcing that larvae that have not settled by some predetermined "length of life," ℓ, will die. This reflects the condition that larvae that run out of stored energy before settling will not survive to complete their metamorphosis.

Consider the following system:

$$\begin{aligned}
P(t+1) &= 0,\\
E_1(t+1) &= 0,\\
&\vdots\\
E_n(t+1) &= 0,\\
S_1(t+1) &= a_1(t)E_1(t),\\
&\vdots\\
S_n(t+1) &= a_n(t)E_n(t),\\
R_1(t+1) &= R_1(t)+s_1(t)S_1(t),\\
&\vdots\\
R_n(t+1) &= R_n(t)+s_n(t)S_n(t),\\
D(t+1) &= D(t)+P(\ell)+\sum_{j=1}^{n} E_j(\ell)+\sum_{j=1}^{n}(1-s_j(t))S_j(t).
\end{aligned}$$

At time t, we call this system of equations $\bar{\mathcal{B}}(t)$.

At time $t=\ell$, all larvae not settled will die. We define the following system:

$$\begin{cases} \mathcal{B}(t) & \text{if } t \le \ell; \\ \bar{\mathcal{B}}(t) & \text{if } t > \ell. \end{cases} \tag{1}$$

We will call Eq. 1 the *basic model* or BM.

1.2 Reproductive Model

The Reproductive Model (RM) incorporates the potential for larvae that have metamorphosed into adults to reproduce. Larvae can reproduce after settling on a substrate or can metamorphose in the plankton. In this model, we follow the larvae only for one generation, meaning that juvenile larvae do not re-enter the system and settle or reproduce.

We define the following system of $4n+4$ equations:

$$
\begin{aligned}
P(t+1) &= (1-(d_P(t)+\sum_{j=1}^{n} e_j(t)+m(t)))P(t)+\sum_{j=1}^{n}(1-a_j(t))E_j(t),\\
E_1(t+1) &= e_1(t)P(t),\\
&\vdots\\
E_n(t+1) &= e_n(t)P(t),\\
S_1(t+1) &= a_1(t)E_1(t),\\
&\vdots\\
S_n(t+1) &= a_n(t)E_n(t),\\
R_1(t+1) &= R_1(t)+s_1(t)S_1(t),\\
&\vdots\\
R_n(t+1) &= R_n(t)+s_n(t)S_n(t),\\
D(t+1) &= D(t)+d_P(t)(P(t)+M(t))+\sum_{j=1}^{n}(1-s_j(t))S_j(t),\\
M(t+1) &= M(t)+m(t)P(t)-d_P(t)M(t),\\
J_1(t+1) &= J_1(t)+r(R_1(t))R_1(t),\\
&\vdots\\
J_n(t+1) &= J_n(t)+r(R_n(t))R_n(t),\\
J_M(t+1) &= J_M(t)+r_M(t)M(t).
\end{aligned}
$$

At time t, we call this system of equations $\mathcal{R}(t)$.

As in the basic model, we modify $\mathcal{R}(t)$ by enforcing that larvae that have not settled by some predetermined "length of life," ℓ, will die.

Consider the following system:

$$
\begin{aligned}
P(t+1) &= 0, \\
E_1(t+1) &= 0, \\
&\vdots \\
E_n(t+1) &= 0, \\
S_1(t+1) &= a_1(t)E_1(t), \\
&\vdots \\
S_n(t+1) &= a_n(t)E_n(t), \\
R_1(t+1) &= R_1(t) + s_1(t)S_1(t), \\
&\vdots \\
R_n(t+1) &= R_n(t) + s_n(t)S_n(t), \\
M(t+1) &= 0, \\
D(t+1) &= D(t) + P(\ell) + \sum_{j=1}^{n} E_j(\ell) + \sum_{j=1}^{n}(1 - s_j(t))S_j(t) + M(\ell), \\
J_1(t+1) &= J_1(\ell) \\
&\vdots \\
J_n(t+1) &= J_n(\ell) \\
J_M(t+1) &= J_M(\ell).
\end{aligned}
$$

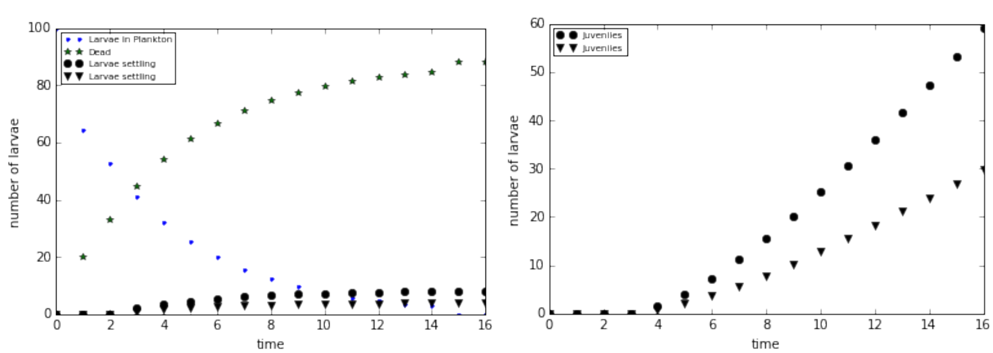
At time t, we call this system of equations $\bar{\mathcal{R}}(t)$.

At time $t = \ell$, all larvae not settled will die. We define the following system:

$$
\begin{cases} \mathcal{R}(t) & \text{if } t \leq \ell; \\ \bar{\mathcal{R}}(t) & \text{if } t > \ell. \end{cases} \tag{2}
$$

We will call Eq. 2 the *reproductive model*.

An example of a single trial of the Basic and Reproductive Models is shown in Figure 1.



(a) Basic Model (b) Reproductive Model

Figure 1: A single trial of Eqs. 1 and 2 for $n = 2$ substrates.

1.3 Life History Functions

Our model, in its most general form, is a non-autonomous system, meaning that the terms governing the life history functions (LHF) of the larvae are not constant but can depend on time. We describe several choices for each function that we have implemented in this paper. However, other functions could easily be used within the model.

1.3.1 LHF 1: Larval survival in the plankton

The function $d_P(t)$ represents the death rate in the plankton due to predation. A higher value of $d_P(t)$ means that a larvae is more likely to die in the plankton due to predation. For simplicity, we have used a constant value of $d_P(t)$; i.e. $d_P(t) \equiv d_P$.

For the purpose of sensitivity analysis, we define three regimes for death in the plankton due to predation: no predation ($d_P = 0$), moderate predation ($d_P = 0.2$), and high predation ($d_P = 0.4$).

1.3.2 LHF 2: Larval substratum acceptance

The acceptance rate functions, $a_j(t)$, give a measure of how likely the larvae are to settle on a given substrate at time t. That this changes with time reflects the fact that the choosiness of a larvae may change depending on length of time in the plankton [3]. A high value of $a_j(t)$ indicates a greater willingness to accept a substrate, which indicates less choosiness of the larvae. We have implemented three possibilities for $a_j(t)$: constant, decreasing, and quadratic choosiness.

In the constant choosiness model, values of $a_j(t)$ are constant; i.e. $a_j(t) \equiv a_j$, where the a_j are randomly chosen values in the range $[a_{\min}, a_{\max}]$ [2]. The constant model for one choice of a_j is shown in Figure 2a.

For both the decreasing and quadratic choosiness models, initial values of acceptance rates are uniform random variables in the range $[a_{\min}, a_{\max}]$.

We denote the acceptance function for the decreasing choosiness model by $\hat{a}_j(t)$. In this model, the acceptance rate will increase linearly from 0 to $2\hat{a}_j(0)$ over the length of the larvae's life. This can be interpreted as the larvae being completely unwilling to settle at time $t = 0$ and having maximum willingness to settle at the end of their life. The acceptance function for substratum s_j is given by

$$\hat{a}_j(t) = \frac{2\hat{a}_j(0)}{\ell}t, \tag{3}$$

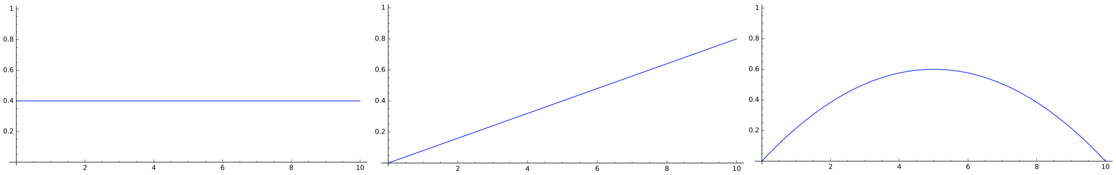
where ℓ is the length of life of the larvae. A graph of this function is given in Figure 2b.

We denote the acceptance function for the quadratic choosiness model by $\tilde{a}_j(t)$. In this model, the acceptance rate will be a quadratic function that starts and ends at 0, with a maximum at $\frac{\ell}{2}$. This can be interpreted as the larvae having maximum willingness to settle at the middle of their life, with complete unwillingness to settle at the beginning and a physiological inability to settle at the end of life. The acceptance function for substratum s_j is given by

$$\tilde{a}_j(t) = -\frac{6\tilde{a}_j(0)}{\ell^2}t^2 + \frac{6\tilde{a}_j(0)}{\ell}t. \tag{4}$$

A graph of this function is given in Figure 2c.

[2] Due to the variations we implemented, $a_{\max} \leq 0.5$.



(a) Constant choosiness (b) Decreasing choosiness (c) Quadratic choosiness

Figure 2: Three types of acceptance rate functions.

To keep the total likelihood of accepting a given substratum constant across all models, we enforce that the areas under the curves in Figure 2 be equal for each substrate.

Currently the survival rates, $s_j(t)$, are related to the initial acceptance rate values. Namely, $s_j(t) \equiv 2a_j(0)$. This could be easily modified to allow for more complicated substratum-dependent survival dynamics.

1.3.3 LHF 3: Larval substratum encounter

The encountering rate functions, $e_j(t)$, reflect the likelihood of the larvae encountering a given substrate at time t. This can be interpreted as an increase or decrease in swimming speed of larvae over time–the faster (or slower) a larva swims, the more (or less) likely it is to encounter a substratum. We have implemented three types of encountering models: constant, increasing, and decreasing speed.

In the constant speed model, values of $e_j(t)$ are constant; i.e. $e_j(t) \equiv e_j$, where the e_j are randomly chosen in the range $[e_{\min}, e_{\max}]$ [3]. Figure 3a shows the constant encounter rate parameter for a given e_j.

For both the increasing and decreasing speed models, initial values of encounter rates are uniform random variables in the range $[e_{\min}, e_{\max}]$.

We denote the increasing speed function by $\hat{e}_j(t)$. In this model, the encounter rate will increase linearly from $\frac{\hat{e}_j(0)}{4}$ to $\frac{7\hat{e}_j(0)}{4}$ from $t = 0$ to $t = \ell$. This reflects an increasing swimming speed of the larvae over time. The encounter function for substratum s_j is given by

$$\hat{e_j}(t) = \frac{3\hat{e}_j(0)}{2\ell}t + \frac{\hat{e}_j(0)}{4}. \tag{5}$$

This function can be seen in Figure 3b.

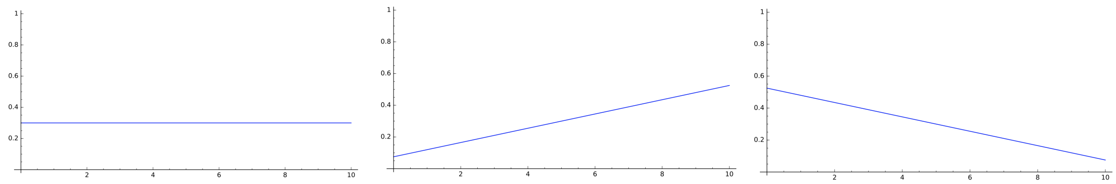
We denote the decreasing speed function by $\tilde{e}_j(t)$. In this model, the encounter rate will decrease linearly from $\frac{7\tilde{e}_j(0)}{4}$ to $\frac{\tilde{e}_j(0)}{4}$ from $t = 0$ to $t = \ell$. This can be interpreted as a decrease in larval speed over time. The encounter function for substratum s_j is given by

$$\tilde{e_j}(t) = -\frac{3\tilde{e}_j(0)}{2\ell}t + \frac{7\tilde{e}_j(0)}{4}. \tag{6}$$

This function can be seen in Figure 3c.

To keep the total likelihood of encountering a given substratum constant across all models, we enforce that the areas under the curves in Figure 3 be equal for each substrate.

[3] Because of the particular variations we employ, $e_{\max} \leq \frac{4(1-d_p)}{7n}$.



(a) Constant speed (b) Increasing speed (c) Decreasing speed

Figure 3: Three types of encountering rate functions.

1.3.4 LHF 4: Larval reproduction

LHF 4a: Substrate-dependent reproduction

To model dependencies of reproductive fitness on the quality and availability of the substrate, we model two scenarios: positive and negative. In both scenarios, two substrates are of average quality substrate, with parameter values as follows: $0.06 \le e_i \le 0.09$ and $0.2 \le a_i \le 0.3$.

In the positive scenario, we assume that there is a single highly desirable substrate and two moderately desirable substrates. Specifically, we let the highly desirable substrate (substrate 1) have parameter values as follows: $0 \le e_1 \le 0.015$ and $0.45 \le a_1 \le 0.5$.

In the negative scenario, we assume that there is a single undesirable substrate and two moderately desirable substrates. However, the parameter values make the undesirable substrate more plentiful. Specifically, we let the undesirable substrate (substrate 1) have parameter values as follows: $0.135 \le e_1 \le 0.15$ and $0 \le a_1 \le 0.05$.

LHF 4b: Density-dependent reproduction

In this variation, the reproductive functions, $r(S_j(t))$, may depend on the density of larvae that have settled on substrate j. We have implemented three reproductive models: constant, synergistic, and competitive reproduction.

Each substrate has two randomly chosen reproductive parameters associated with it: $r_{\min}$ and $r_{\max}$. These numbers are meant to represent the minimum and maximum number of offspring a larvae can have during their lifetime. Let T be the number of time steps over which our model will be run.

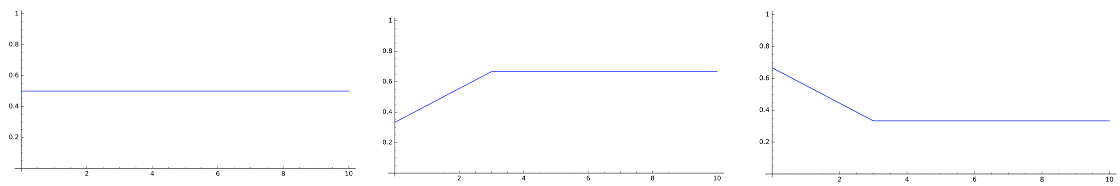
In the constant reproduction model, $r(S_j(t)) \equiv r_j$, where $r_j = \frac{r_{\max}+r_{\min}}{2T}$.

In the synergistic reproduction model, we assume that there is a positive correlation between settled population and reproduction rate. Let S be the critical density level. Then we assume that the reproductive function is a piecewise-defined function that grows linearly between $(0, \frac{r_{\min}}{T})$ and $(S, \frac{r_{\max}}{T})$ and is constant for inputs larger than S, as shown in Figure 4. The function becomes:

$$r(x) = \begin{cases} \frac{r_{\max}-r_{\min}}{T\cdot S}x + \frac{r_{\min}}{T} & \text{if } x \le S; \\ \frac{r_{\max}}{T} & \text{if } x \ge S. \end{cases} \tag{7}$$

In the competitive reproduction model, we assume that there is a negative correlation between settled population and reproduction rate. Let S be the critical density level. Then we assume that the reproductive function is a piecewise-defined function that decreases linearly between $(0, \frac{r_{\max}}{T})$ and $(S, \frac{r_{\min}}{T})$ and is constant for inputs larger than S, as shown in Figure 4. In this case, the function becomes:

$$r(x) = \begin{cases} \frac{r_{\min} - r_{\max}}{T \cdot S} x + \frac{r_{\max}}{T} & \text{if } x \leq S; \\ \frac{r_{\min}}{T} & \text{if } x \geq S. \end{cases} \quad (8)$$



(a) Constant reproduction (b) Synergistic reproduction (c) Competitive reproduction

Figure 4: Three types of density-dependent reproductive functions.

Notice that the three density-dependent reproductive functions intersect at $\frac{S}{2}$, as shown in Figure 5. On a given substrate, if there are fewer than $\frac{S}{2}$ larvae settled, the competitive reproduction function will be largest. Once there are more than $\frac{S}{2}$ larvae settled, the synergistic reproduction function will be the largest.

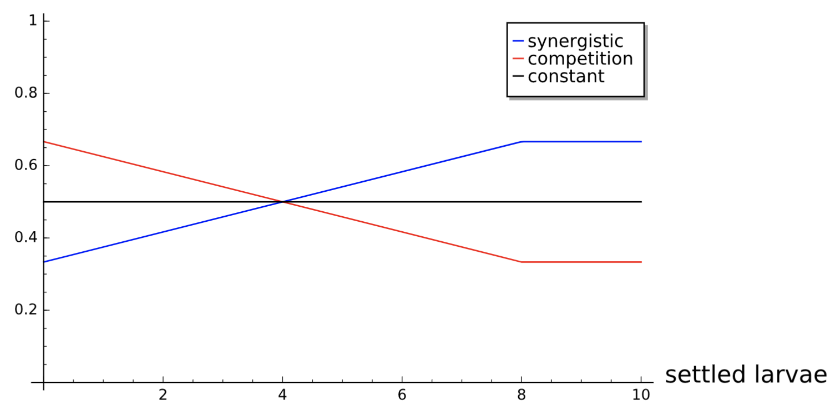


Figure 5: Intersection of three density-dependent reproductive functions ($S = 8$).

1.3.5 LHF 5: Larval abandonment of substratum selection behavior

The metamorphosis rate function, $m(t)$, represents the rate at which larvae metamorphose in the plankton. A higher value of $m(t)$ means that a larvae is more likely to metamorphose in the plankton. Currently the model is implemented with a constant value of $m(t)$; i.e. $m(t) \equiv m$.

The reproductive rate in the plankton function, $r_M(t)$, represents the rate at which larvae reproduce in the plankton. The model uses a constant value for this function; i.e. $r_M(t) \equiv r_M$.

In most of the analysis, we let $m = 0$. However, in Section 4, we explore the effects of varying m.

1.4 Naming Conventions

Because the model has not been parametrized with real world data, we cannot use the actual fitness values returned by the model for the purposes of prediction. However, we can use these values to compare the quality of different mechanisms (choosiness, speed, and reproduction) under different environmental conditions.

In what follows, we will use codes for the various mechanisms employed. They are as follows:

- **Choosiness**:
  - A for autonomous (constant),
  - D for decreasing,
  - Q for quadratic.
- **Encounter**:
  - A for autonomous (constant),
  - I for increasing,
  - D for decreasing.
- **Reproduction**:
  - A for autonomous (constant),
  - S for synergistic,
  - C for competitive.

Our naming convention is that a mechanism in the basic model will have two letters, with the first representing the choosiness and the second representing the encounter rate. For example, QD would be the mechanism with quadratic choosiness and decreasing speed.

In the reproductive model, a mechanism will have three letters, with the first representing the choosiness, the second representing the encounter rate, and the third representing the reproductive function. For example, AIC would be the mechanism with constant choosiness, increasing speed, and competitive reproduction.

2 Analysis of the basic model

2.1 Results

For the basic model, we have three choices of life history functions governing the choosiness of larvae: constant, decreasing, and quadratic, and we have three choices of life history functions governing the speed of larvae: constant, increasing, decreasing. Under the same environmental conditions, we can compare the fitness of each of the nine combinations. These results are for a simulation with 10 000 trials.

As shown in Main Document, Table 2, under moderate predation and medium value of ℓ, the fitness ranges from 6.7% to 17.5%. Nearly all of the pairwise combinations (except for one) were significantly different ($p < 0.001$), meaning that the model demonstrates a clear ranking of fitness of different mechanisms. The mechanisms that had the highest fitness were ones with constant or quadratic choosiness and decreasing speed. The mechanisms that had the lowest fitness were ones with decreasing or constant choosiness and increasing speed.

2.2 Sensitivity Analysis

To test the robustness of our model under different environmental conditions, we performed a sensitivity analysis on various parameters [2]. The two parameters that yielded the most significant behavior changes were the level of predation (d_P) and the length of life (ℓ). The dependence on d_P appears to be due to beginning of life behavior, while the dependence on ℓ appears to be due to end of life behavior. For the analysis in this section, all fitness values reflect a simulation with 1000 trials.

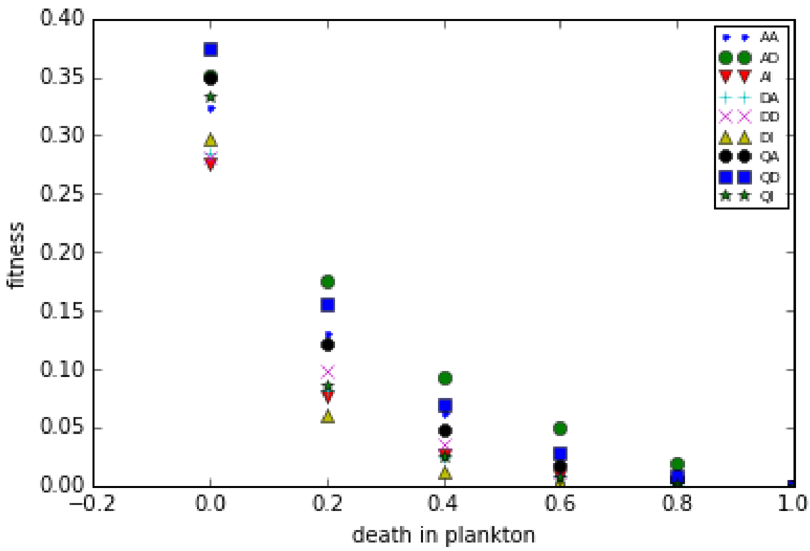


Figure 6: Fitness of different mechanisms as a function of larval death in the plankton.

As we see in Figure 6, the mechanisms having the highest fitness are those with decreasing speed and either constant or quadratic choosiness. However, the overall rankings depend on the value of d_P. For ease of discussion, we consider three regimes: no predation ($d_P = 0$), moderate predation ($d_p = 0.2$), and high predation ($d_p = 0.4$). The rankings are shown in Table 3.

Maximum fitness always occurred for mechanisms with decreasing speed. Perhaps this is unsurprising because larvae with higher initial speed can encounter substrata more quickly and have a higher probability of settling before falling prey to predators. However, it is interesting to note that the QD mechanism performed best when there is no predation, while under moderate and high predation conditions, the AD mechanism was optimal. The AD mechanism yielded better performance with moderate to high predation, at least in part, due to the fact that larvae with this behavior settle more quickly than those with any other behavior, as shown in Figure 7.

We can quantify those trends by examining the percentage of surviving larvae (i.e., larvae that will eventually settle) that have settled by a certain time. For example, at time $\frac{\ell}{2}$ with moderate predation, 69% of larvae with the AD mechanism have settled, as compared to 59% for QD, 56% for AA, and only 16% for DI.

Table 3: Basic model rankings under different predation levels.

No predation	Moderate predation	High predation
QD	AD	AD
AD	QD	QD
QA	QA	AA
DI	AA	QA
DA	DD	DD
AA	DA	DA
QI	QI	QI
DD	AI	AI
AI	DI	DI

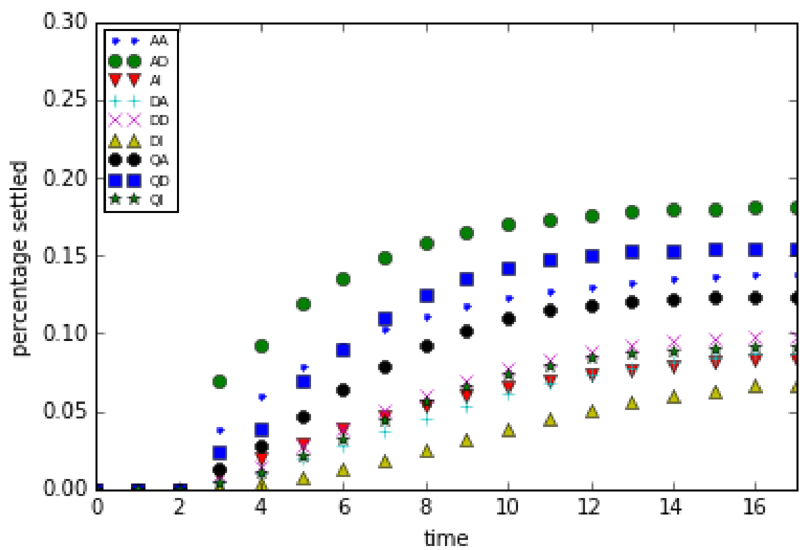


Figure 7: Percentage of larvae settled at a given time with moderate predation.

It is also interesting to note that the DI mechanism performed fairly well (ranked fourth) in the no predation condition, while it dropped to last with moderate and high predation. This is due to the number of larvae that settle towards the end of their life. In models with moderate or high predation, larvae displaying DI behaviors will not tend to survive in the plankton long enough to settle.

As we vary the length of life parameter, ℓ (Figure 8), AD and QD are still the mechanisms with the highest fitness. Interestingly, QD yields the highest fitness for small values of ℓ, whereas AD yields the highest fitness for moderate to large values of ℓ. We defined three regimes for ℓ: short ($\ell = 5$), medium ($\ell = 15$), and long ($\ell = 25$). The rankings in each regime are given in Table 4.

It is also interesting to note that for most of the mechanisms, there appears to be a global maximum for fitness values as a function of ℓ under moderate to high predation. Specifically, the mechanisms with quadratic and decreasing choosiness display this behavior, whereas the trend for mechanisms with constant choosiness is less clear. In Figure 9, we fix the speed mechanism to be increasing and compare the three choosiness mechanisms. For mechanisms with quadratic and decreasing choosiness, there is a value such that the length of life, which

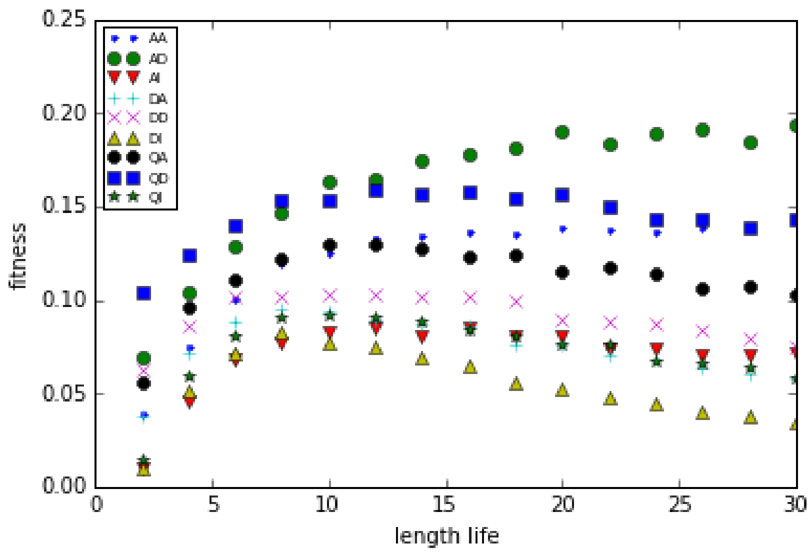


Figure 8: Fitness of different mechanisms as a function of length of life.

Table 4: Basic model rankings under length of life values.

Short ℓ	Medium ℓ	Large ℓ
QD	AD	AD
AD	QD	QD
QA	AA	AA
DD	QA	QA
AA	DD	DD
DA	QI	AI
QI	AI	QI
DI	DA	DA
AI	DI	DI

governs the time larvae have to search for acceptable substrate, has a diminishing return as it means more opportunity to die due to predation.

3 Analysis of the reproductive model

As a base case, we consider the reproductive model with constant reproductive rates. In Main Document, Table 3, we show that the reproductive fitness values are between 0.48 and 1.85 and that the relative fitness rankings are the same as for the basic model. The rankings are unsurprising, given that in this model, reproduction is constant and therefore depends only upon the settling behavior. The reproductive model also employs two varieties of reproductive mechanisms: substratum-dependent reproduction (LHF 4a) and density-dependent reproduction (LHF 4b).

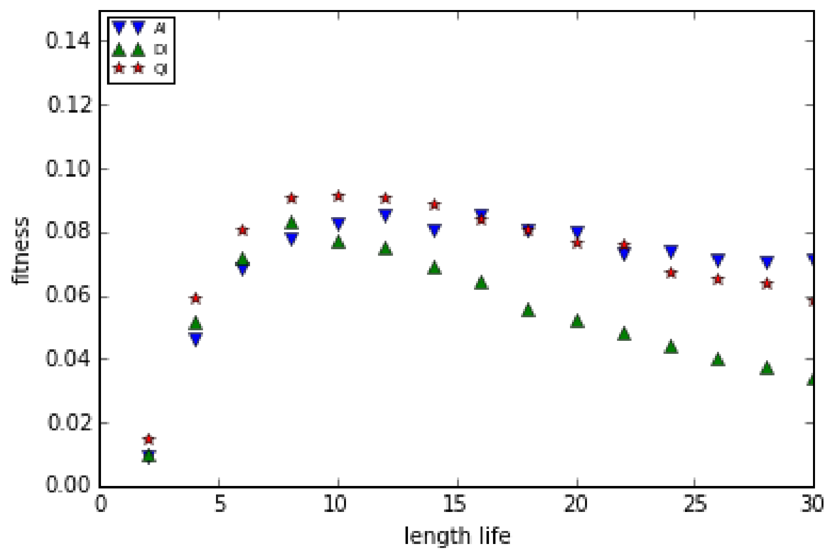


Figure 9: Fitness of mechanisms with increasing speed as a function of length of life with moderate predation.

3.1 Results of substratum-dependent reproduction model

As shown in Main Document, Table 3, both the positive and negative substratum-dependent conditions yields lower reproductive fitness than the autonomous model, with the negative condition yielding the lowest reproductive fitness. This is not surprising as the more restrictive conditions on substrates yields lower fitness (or percentage of settled larvae): between 4% and 12% for the positive condition and between 4% and 10% for the negative condition. These results are for a simulation with 10 000 trials.

3.2 Sensitivity analysis of substratum-dependent reproduction model

The relative fitness of different mechanisms do not appear to be dependent on changing the encounter or acceptance rates. For the analysis in this section, all fitness values reflect a simulation with 1000 trials.

We perform a two-dimensional sensitivity analysis on the acceptance rate, a_1, and the encounter rate, e_1, of the special substrate. We define three encounter regimes: low encounter ($e_1 = 0.05$), medium encounter ($e_1 = 0.1$), and high encounter ($e_1 = 0.15$). We then let a_1 vary between 0 and 0.5. As we see in Figure 10, there is no change in the rankings under the changing a_1 values. The results are similar for medium and high encounter rates. The percentage increase in fitness due to increasing a_1 is roughly the same among mechanisms as well.

3.3 Results of density-dependent reproduction model

In the density-dependent model, the mechanisms with the highest reproductive fitness are those with the highest fitness from the basic model, coupled with synergistic or constant reproduction. As shown in Main Document, Table 4, the highest reproductive fitness has a value of 2.23 and is for the mechanism with constant choosiness, decreasing speed, and

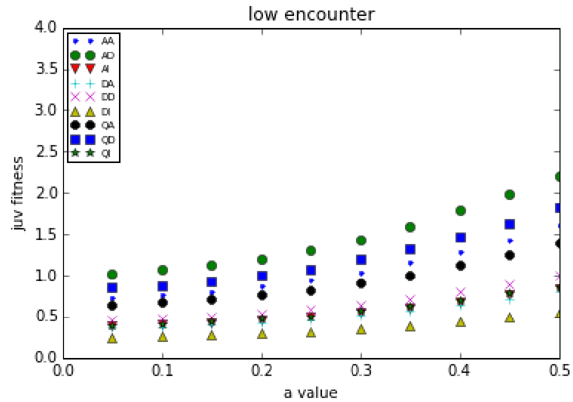


Figure 10: Dependence of different mechanisms on changing encounter and acceptance rates with a low encounter rate.

synergistic reproduction (ADS). With the same condition, the lowest reproductive fitness value that occurred is 0.43 and is for the mechanism with decreasing choosiness, increasing speed, and synergistic reproduction (DIS). These results are for a simulation with 10,000 trials.

3.4 Sensitivity analysis of density-dependent reproduction model

We perform sensitivity analyses of the reproductive model with respect to different parameters. The two that have the largest effects are the critical density value, S (see Section 1.3.4) and the number of available substrates. For the analysis in this section, all fitness values reflect a simulation with 1000 trials.

We define three regimes for the critical density value: low (S = 5), medium (S = 10), and high (S = 15). When there are three substrates available, we have the following highest and lowest ranking mechanisms with listed reproductive fitness values.

Table 5: Mechanisms with highest and lowest reproductive fitness with different critical densities.

Low S		Medium S		High S	
ADS	2.40	ADS	2.23	ADS	2.07
QDS	1.95	ADA	1.84	ADA	1.76
ADA	1.83	QDS	1.76	ADC	1.63
AAS	1.64	AAS	1.54	QDS	1.53
QDA	1.49	ADC	1.50	QDA	1.51
⋮		⋮		⋮	
QIC	0.59	DAA	0.65	AIS	0.66
DAC	0.57	DAS	0.65	DAS	0.62
DIS	0.51	DIC	0.50	DIC	0.52
DIA	0.46	DIA	0.48	DIA	0.46
DIC	0.42	DIS	0.42	DIS	0.39

It is perhaps not surprising that the ADS mechanism has the highest fitness under all critical density conditions, given that it consistently has one of the highest fitness levels in the basic model. However, what is surprising is that the fitness for ADS is 23%, 22%, and 18% (for low S, medium S, and high S, respectively) higher than the next highest mechanism. This is a much higher gap than exists between any other subsequently ranked pairs. For example, the second place mechanism has a fitness of only 7%, 4%, and 8% (for low S, medium S, and high S, respectively) higher than the third place mechanism. This enhanced performance can be explained, at least in part, due to the rapidity at which the AD mechanism settles as compared to other mechanisms. Figure 11 shows the total number of larvae settled on a single substrate, given three substrates, moderate predation, and medium S. The value $\frac{S}{2}$ is also shown. The AD mechanism crosses the value $\frac{S}{2}$ four time steps before the next before the mechanism, QD, does.

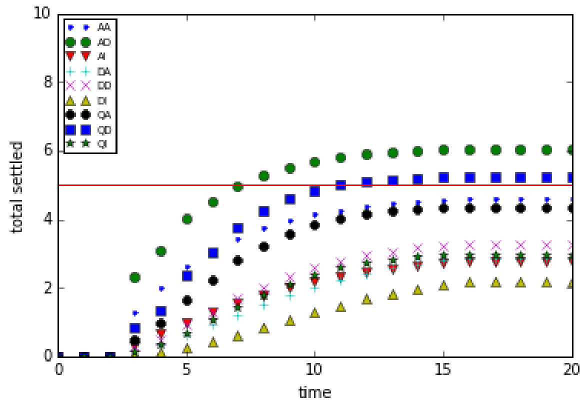


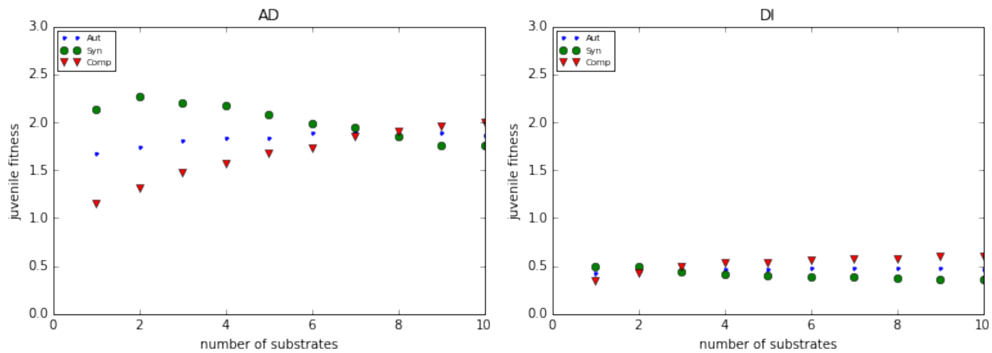
Figure 11: Total larvae settled on a single substrate for different mechanisms.

On the other hand, the DI mechanism with any reproductive function has the lowest juvenile fitness under all critical density conditions. As we see in Figure 11, the DI mechanism has the fewest larvae settled, and thus has the fewest adult larvae available to reproduce.

Additionally, the relative fitness of the different reproductive models is dependent on the number of substrates available. In Figure 12a, under the medium critical density condition, we show the dependence of the AD and DI mechanisms with each reproductive function on the number of substrates. In both cases, there is a number of substrates for which the competitive model outperformed both the synergistic and autonomous models. This is due to the fact that, with more substrate options available, the likelihood of more than $\frac{S}{2}$ larvae settling on a given substrate decreases. However, notice that for AD, the number of substrates needed to trigger this switch is large ($n = 8$) compared to that for DI ($n = 3$). This is due, again, to the higher speed and quantity of settling that occurs under the AD mechanism.

4 Metamorphosis in the Plankton

We would like to know when larvae choose to metamorphose in the plankton versus when they choose to search for and settle on substrate; i.e. when they are obligatorily or facultatively sessile (See Main Document). Our hypothesis is that the percentage of larvae metamorphosing in the plankton should depend on the quality and availability of substrate–namely, if there is readily available high quality substrate, larvae should be less likely to metamorphose



(a) AD mechanism

(b) DI mechanism

Figure 12: Dependence of different mechanisms on number of substrates.

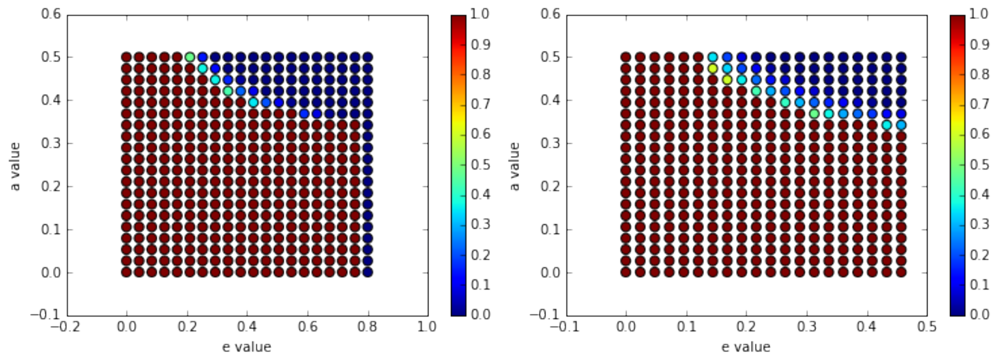
in the plankton, whereas if there is only poor quality substrate or small amounts of substrate available, larvae should be more likely to metamorphose in the plankton.

If we fix all other parameter values, we can search for which value of the metamorphosis parameter, m, yields the maximum fitness. In order to make our analysis computationally feasible and visually accessible, we assume that there is only one type of substrate available; i.e. $n = 1$. We then have one parameter, e, which governs the availability of the substrate, and one parameter, a, which governs the quality of the substrate.

For a given point in the ea-plane, we search for the value of m that yields the highest maximum fitness using the Scipy package in Python. We then use a color to show the maximum value of m, where the scale is shown on the right in Figure 13. A color indicating a large value of m shows that maximum fitness occurs when larvae do not settle on a substrate (always metamorphose in the plankton). In particular, a value of 1.0 (red dot) indicates that the maximum fitness occurs when larvae metamorphose in the plankton without attempting to settle. A small value of m indicates that maximum fitness occurs when larvae rarely metamorphose in the plankton. In particular, a value of 0.0 (blue dot) indicates that the maximum fitness occurs when the larvae never metamorphose in the plankton; i.e. they search for substrate or die trying. Other colors indicate a continuum between these two conditions; i.e. a value strictly between 0.0 and 1.0 indicates that the maximum fitness is achieved when some portion of the larvae settle on a substrate and some metamorphose in the plankton.

In Figure 13, we show the ea-plane for two different mechanisms (both with autonomous reproduction). In each of these pictures, we use the medium values of d_p, ℓ, and S from our preceding sensitivity analyses. We notice that for conditions with poor quality (as measured by a) and low quantity (as measured by e) substrate, the highest fitness is achieved when the larvae metamorphose in the plankton without searching for substrate. However, for conditions with high quality and high quantity substrate, the highest fitness is achieved when the larvae never metamorphose in the plankton. In other words, the likelihood of reproductive success on a substrate is so great, it is not worth the lower quality environment of metamorphosing in the plankton.

It is particularly interesting that there are boundary points between these two regions that yield a maximum fitness when some portion of the larvae settle and some metamorphose in the plankton. More analysis is needed to determine how to interpret the significance of these values.



(a) AA mechanism (b) AD mechanism

Figure 13: Metamorphosis parameter yielding highest fitness at different points in the *ea*-plane.

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