# Supplementary equations

## 1 Fitness expression

### 1.1 Fecundity

In the palintomic life cycle, a cell grows untill it reaches several times its initial size, and then a series of n rapid divisions occurs, leading to the production of $2^n$ daughter cells of size $\frac{\text{Finalsize}}{2^n}$. Fecundity can be approximated by $\frac{\text{Finalsize}}{c_0}$ .
We use a power-law growth model, assuming that $\frac{\partial V}{\partial t} = kV^b$ , where $V$ is the volume of the cell and $b$ and $k$ are constants, allowing us capture the slowing of relative growth rate as an organism's size increases over time [1]. We thus have:

$$\partial_t V(t) = kV(t)^b$$

which leads to

$$V(t_0 + t) = \Big((1 - b)kt + V(t_0)^{1-b}\Big)^{\frac{1}{1-b}}$$

For a cell first growing in a group (growth rate $k\alpha$) for a time $p \times t_g$ and then alone (growth rate $k$) for a time $(1 - p) \times t_g$, the final size is

$$c_0(1 + K(1 - p(1 - \alpha))t_{\text{gr}})^{\frac{1}{1-b}}, \text{ where } K = \frac{(1 - b)k}{c_0^{1-b}}$$

### 1.2 Mortality

The mortality rate is assumed to be constant, so the probability of survival $S$ is

$$S(t_0 + t) = S(t_0)e^{-mt}$$

For a cell first growing in a group (death rate $m\beta$) for a time $p \times t_{\text{gr}}$ and then alone (death rate $m$) for a time $(1 - p) \times t_{\text{gr}}$, the probability to survive until reproduction is

$$e^{-m(1-p(1-\beta))t_{\text{gr}}}$$

We do not consider the mortality ocuring during life events other than growth, yet as their duration is considered to be the same for every particle, this would not change the values of the traits for which the fitness is maximal.

### 1.3 Fitness

The fitness is thus

$$r(p, t_{\text{gr}}) = \frac{\ln(\text{fecundity} \times \text{survival})}{\text{generationtime}} \quad = \frac{1}{1 - b}\frac{\ln(1 + K(1 - p(1 - \alpha))t_{\text{gr}})}{t_{\text{gr}} + t_{\text{sw}}} - m(1 - p(1 - \beta))\frac{t_{\text{gr}}}{t_{\text{gr}} + t_{\text{sw}}}$$

## 2 Fitness maxima

The fitness expression is:

$$r(p,g) = \frac{1}{1-b}\frac{\ln(1+K(1-p(1-\alpha))t_{\mathrm{gr}})}{t_{\mathrm{gr}}+t_{\mathrm{sw}}} - m(1-p(1-\beta))\frac{t_{\mathrm{gr}}}{t_{\mathrm{gr}}+t_{\mathrm{sw}}}$$

If there is a fitness extremum at the point $(p^*, t^*_{\mathrm{gr}})$, then

$$\begin{aligned}
&\vec{\nabla} r(p^*, t^*_{\mathrm{gr}}) = \vec{0} \\
\iff &\begin{cases} \frac{1}{(1-b)(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})}\left(m(1-b)(1-\beta)t^*_{\mathrm{gr}} - \frac{K(1-\alpha)t^*_{\mathrm{gr}}}{1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}}\right) = 0 \\ \frac{1}{(1-b)(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})^2}\left(\frac{K(1-p^*(1-\alpha))(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})}{1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}} - \ln(1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}) - m(1-b)(1-p^*(1-\beta))t_{\mathrm{sw}}\right) = 0 \end{cases} \\
\iff &\begin{cases} m(1-b)(1-\beta) - \frac{K(1-\alpha)}{1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}} = 0 \\ \frac{K(1-p^*(1-\alpha))(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})}{1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}} - \ln(1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}) - m(1-b)(1-p^*(1-\beta))t_{\mathrm{sw}} = 0 \end{cases} \\
\iff &\begin{cases} m(1-b)(1-\beta)(1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}) - K(1-\alpha) = 0 \\ \frac{K(1-p^*(1-\alpha))(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})}{1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}} - \ln(1+K(1-p^*(1-\alpha))t^*_{\mathrm{gr}}) - m(1-b)(1-p^*(1-\beta))t_{\mathrm{sw}} = 0 \end{cases} \\
\iff &\begin{cases} p^* = \frac{1}{1-\alpha} + \frac{1}{K(1-\alpha)t^*_{\mathrm{gr}}}\left(1-\frac{1}{A}\right) \text{ where } A = \frac{m(1-b)(1-\beta)}{K(1-\alpha)} \\ \frac{\frac{1}{t^*_{\mathrm{gr}}}(\frac{1}{A}-1)(t^*_{\mathrm{gr}}+t_{\mathrm{sw}})}{\frac{1}{A}} + \ln(A) + m(1-b)t_{\mathrm{sw}}(\frac{1-\beta}{1-\alpha}-1) + \frac{A-1}{t^*_{\mathrm{gr}}}t_{\mathrm{sw}} = 0 \end{cases} \\
\iff &\begin{cases} p^* = \frac{1}{1-\alpha} + \frac{1}{K(1-\alpha)t^*_{\mathrm{gr}}}\left(1-\frac{1}{A}\right) \\ \begin{cases} t_{\mathrm{sw}} = \frac{1}{KA(1-\frac{1-\alpha}{1-\beta})}(A-1-\ln(A)) := t^*_{\mathrm{sw}} \text{ if } \alpha \neq \beta \\ \frac{m(1-b)}{K} = 1 \text{ if } \alpha = \beta \end{cases} \end{cases}
\end{aligned}$$

So there can be a fitness maximum for an intermediate value of $p$ only if $t_{\mathrm{sw}} = t^*_{\mathrm{sw}}$ or $\alpha = \beta$ and $m(1-b) = K$. Since it is very unlikely that the value are exactly the good one, we assume neither of these conditions are verified.
In that case, the maximum can be reached only for $p = 0$, $p = 1$ or $t_{\mathrm{gr}} = 0$ (in the last case, it means the population cannot maintain).
To know when these situations are verified, we need to study the direction of the fitness gradient.

$$\begin{aligned}
\partial_p r(p, t_{\mathrm{gr}}) > 0 &\iff p < \frac{1}{1-\alpha} + \frac{1}{K(1-\alpha)t_{\mathrm{gr}}}\left(1-\frac{1}{A}\right) \\
&\iff t_{\mathrm{gr}} < \frac{1}{K(1-p(1-\alpha))}\left(\frac{1}{A}-1\right) := t^p_{\mathrm{gr}}(p)
\end{aligned}$$

Let I be $]\frac{K-(1-b)m}{K(1-\alpha)(1-A)}, 1] \cap [0,1]$ if $A > 1$, $[0, \frac{K-(1-b)m}{K(1-\alpha)(1-A)}[ \cap [0,1]$ if $A < 1$. For every $p \in I$, there is a unique solution $t^g_{\mathrm{gr}}(p) \in [0, +\infty[$ of $\partial_{t_{\mathrm{gr}}} r(p, t_{\mathrm{gr}}) = 0$

(Because $\partial_{t^2_{\mathrm{gr}}} r(p, t_{\mathrm{gr}}) < 0$, $\partial_{t_{\mathrm{gr}}} r(p, 0) = \frac{1}{(1-b)t_{\mathrm{sw}}}(K(1-p(1-\alpha)) - (1-b)m(1-p(1-\beta))) > 0$ and $\partial_{t_{\mathrm{gr}}} r(p, t_{\mathrm{gr}}) \underset{t_{\mathrm{gr}}\to\infty}{\sim} -\frac{\ln(K(1-p(1-\alpha))t_{\mathrm{gr}})}{t^2_{\mathrm{gr}}} < 0$.)

Moreover, $\forall p \in I, \partial_{t^2_{\mathrm{gr}}} r(p, t_{\mathrm{gr}}) \neq 0$, so the implicit fuction theorem says that $t^g_{\mathrm{gr}}$ is continuous in every $p \in I$.

$\forall p \in [0,1] \setminus I$, $\max_{p, t_{\mathrm{gr}}>0} r(p, t_{\mathrm{gr}}) = r(p, 0) = 0$ which means that a population of individuals with this value of $p$ cannot maintain.

The population cannot maintain $\iff I = \emptyset$.

$$
\begin{aligned}
p = 0 \text{ is optimal} &\iff \begin{cases} 0 \in I \\ \partial_p r(0, t_{\mathrm{gr}}^{g}(0)) < 0 ( \iff t_{\mathrm{gr}}^{g}(0) < t_{\mathrm{gr}}^{p}(0) \iff (t_{\mathrm{gr}}^{p}(0) > 0 \text{ and } \partial_{t_{\mathrm{gr}}} r(0, t_{\mathrm{gr}}^{p}(0)) < 0)) \end{cases} \\
&\iff \begin{cases} \begin{cases} A < 1 \text{ and } K - (1-b)m > 0 \\ \text{or} \\ K - (1-b)m > 0 \end{cases} \\ \begin{cases} A(\frac{1}{A} - 1) + KAt_{\mathrm{sw}} + \ln(A) - (1-b)mt_{\mathrm{sw}} < 0 \\ A < 1 \end{cases} \qquad \text{because } t_{\mathrm{gr}}^{p}(0) = \frac{1}{K}(\frac{1}{A} - 1) \end{cases} \\
&\iff \begin{cases} \frac{(1-b)m}{K} < 1 \text{ (condition for the unicell population to be able to maintain)} \\ A < 1 ( \iff \frac{m(1-b)}{K} < \frac{1-\alpha}{1-\beta}) \\ \begin{cases} t_{\mathrm{sw}} < t_{\mathrm{sw}}^{*} \text{ if } \frac{1-\alpha}{1-\beta} < 1 \\ t_{\mathrm{sw}} > t_{\mathrm{sw}}^{*} \text{ if } \frac{1-\alpha}{1-\beta} > 1 \text{ (and this is always true because in that case } t_{\mathrm{sw}}^{*} < 0) \end{cases} \end{cases} \\
&\iff \begin{cases} \frac{(1-b)m}{K} < 1 \text{ if } \alpha < \beta \\ t_{\mathrm{sw}} < t_{\mathrm{sw}}^{*} \text{ if } \alpha > \beta \end{cases}
\end{aligned}
$$

$$
\begin{aligned}
p = 1 \text{ is optimal} &\iff \begin{cases} 1 \in I \\ p = 0 \text{ is not optimal} \end{cases} \\
&\iff \begin{cases} \frac{(1-b)m}{K} < \frac{\alpha}{\beta} \\ t_{\mathrm{sw}} > t_{\mathrm{sw}}^{*} \\ \alpha > \beta \end{cases}
\end{aligned}
$$

## 3 Results

The effects of the parameters value on the optimal $p$ value are illustrated in figure S1.

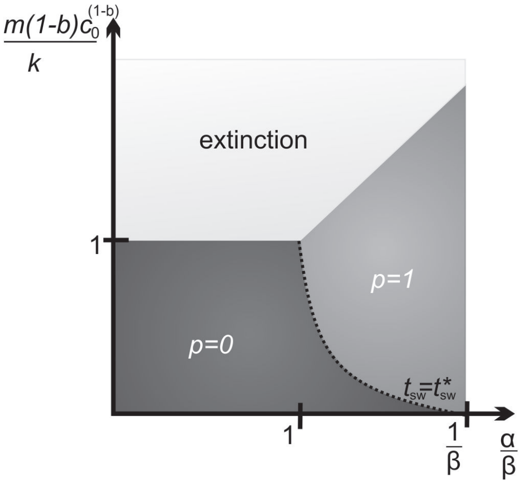

*Figure S1: Effect of the parameter values on the optimal p value. The vertical axis is a comparison between the cell death rate, $m$ , and the cell growth parameter, $k$ . (The $\frac{m}{k}$ ratio is also multiplied by $(1-b)c_0^{(1-b)}$ , which we assume is fixed.) The horizontal axis is a comparison between the group-living growth reduction factor, $\alpha$ , and the group-living mortality rate reduction factor, $\beta$ .*

There are 3 different cases depending on the parameter values. In the white zone , the death rate is too high and neither group nor unicellular populations can survive. In the dark grey zone, a unicellular population is advantaged over a group population and $p = 0$ is optimal. In the light grey zone, a group population is advantaged over a unicellular one and $p = 1$ is optimal. When we consider values of $\frac{m}{k} c_0^{(1-b)}$ that are higher than 1, we see that populations often go extinct. However, if groups are beneficial enough (i.e.,$\frac{\alpha}{\beta}$ is high enough), groups can escape extinction. Groups are able to persist under some conditions (i.e., $m$ and $k$ values) that preclude the possibility of viable unicellular populations. When we consider values of $\frac{m}{k} c_0^{(1-b)}$ that are lower than 1, we see that groups are optimal when they are beneficial enough (i.e., $\frac{\alpha}{\beta}$ is high enough). The benefit needed for groups to be optimal depends on the value of $\frac{m}{k} c_0^{(1-b)}$. For example, if there is no mortality ($m = 0$), groups will never be optimal. By extension, at low values of $\frac{m}{k} c_0^{(1-b)}$, groups must be highly advantageous (very high $\frac{\alpha}{\beta}$) if the group life cycle ($p = 1$) is to be optimal.
As we would expect, the evolution of a group life cycle (increase from zero to non-zero $p$) requires that the advantages associated with living in groups outweigh the detriments. In the parameter space where populations do not go extinct, unicellularity ( $p = 0$ ) is optimal (and the group life cycle will not evolve) when $\alpha < \beta$ or when $t_{sw} < t^*_{sw}$ and $\frac{m(1-b)}{K} < \frac{1-\alpha}{1-\beta}$. One may interpret the advantage of group living to survival, $\beta$, as coming from increased size perhaps lowering the predation risk. It has been shown that the presence of a predator may select for colonies in a small number of generations [2,3]. One may interpret the cost of group living to the growth rate, $\alpha$, as coming from the difficulty in a group of cells attaining resources and getting rid of waste [4]. High $\alpha$ may be associated with a high nutrient concentration [5]. We are particularly interested in cases where the benefit of groups is high (low $\beta$ ) and the cost is low (high $\alpha$) because these conditions would be favourable for the evolution of a group life cycle.

## References

1. Paine, C. E. T., Marthews, T. R., Fogt, D. R., Purves, D., Rees, M., Hector, A. & Turnbull, L. A., 2013, *How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists*, Methods in ecology and evolution 3, 245-256
2. Boraas, M. E., Seale, D. B. & Boxhorn, J. E., 1998, *Phagotropphy by a flagellate selects for colonial prey: A possible origin of multicellularity.* Evol. Ecol. 12, 153–164.
3. Becks, L., Ellner, S. P., Jones, L. E. & Hairston, N. G., 2010 *Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics.*, Ecol. Lett. 13, 989–97.
4. Nielsen, S. L., 2006, *Size-dependent growth rates in eukaryotic and prokaryotic algae exemplified by green algae and cyanobacteria: comparisons between unicells and colonial growth forms.* J. Plankton Res. 28, 489–498.
5. Dmitriew, C. M., 2011, *The evolution of growth trajectories: what limits growth rate?* Biol. Rev. Camb. Philos. Soc. 86, 97–116.