

Hydrodynamics Constraints and the Origin of Complexity and Cellular Differentiation in Volvocales

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Abstract

The transition from unicellular, to colonial, to larger multicellular organisms has benefits, costs, and requirements. Here we present a model that explains the dynamics involved in the unicellular-multicellular transition using life-history theory and allometry. We model the two fitness components (fecundity and viability) and compare the fitness of hypothetical colonies of different sizes with varying degrees of cellular differentiation to understand the general principles that underlie the evolution of multicellularity. We argue that germ-soma separation may have evolved to counteract the increasing costs and requirements of larger multicellular colonies. The model shows that the cost of investing in soma decreases with size. To illustrate the model we use some allometric relationships measured in Volvocales. Our analysis shows that the cost of reproducing an increasingly larger group has likely played an important role in the transition to multicellularity and cellular differentiation.

Trade-offs of germ-soma differentiation

Somatic cells specialize in survival functions
Germ cells specialize in reproductive functions

Somatic cells: ↑ Viability ↓ Fecundity
Specialized germ cells: ↑ Fecundity ↓ Viability

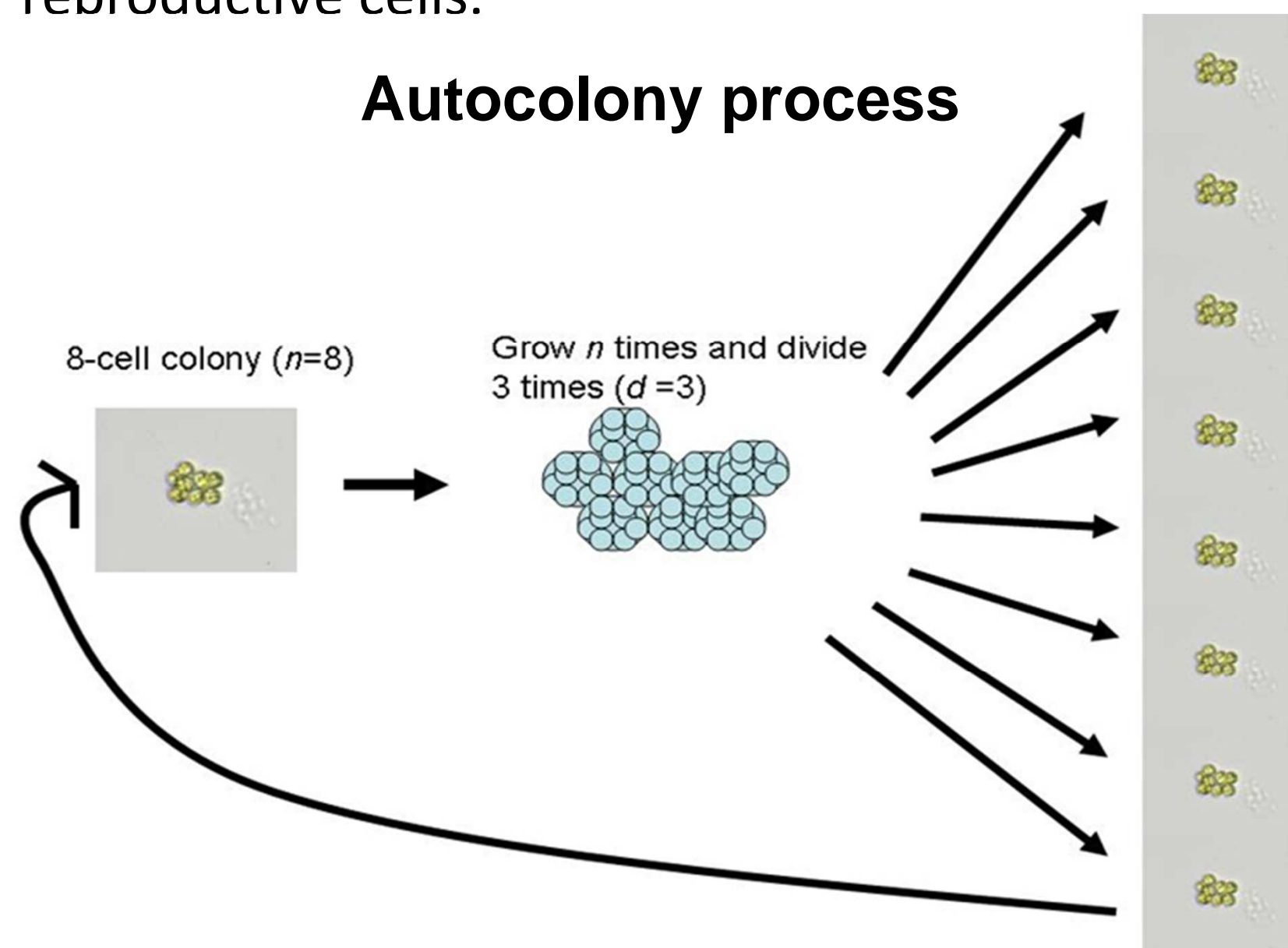
Reproduction costs: Larger size can be beneficial for the fitness of the colony, but can become costly, both in terms of survival and fecundity.

Model Assumptions

Within colony variation is negligible.
Variation exists only at the group level

- Asexual reproduction.
- Discrete generation time.
- Extra-cellular material is not taken into account.
- Only one somatic cell type.
- Cell number is fixed throughout development.
- Intrinsic growth rate of a unicell is the maximum rate.
- Initial cell size is the same for both somatic and reproductive cells.

Autocolony process



If we use a standard exponential growth model for the growth of cells in a colony and assume discrete generation time:

$$m = m_0 e^{rt}$$

r = cell growth rate
 t = generation time
 m and m_0 = final and initial mass

If mother colonies produce daughter colonies of the same type:

$$m = n m_0 \text{ or } n = m/m_0$$

n = colony cell number

$$n = e^{rt} \text{ or } t = \text{Ln}(n)/r$$

-Increasing colony cell number (n) increases generation time (t).

-Increasing the growth rate (r) decreases generation time (t).

Assuming colonies have discrete generation time, the per-generation fecundity of colonies composed of undifferentiated cells:

$$R_0 = n$$

R_0 can be also written as,

$$R_0 = \lambda^t$$

λ = fecundity rate

Since $n = e^{rt}$ and $R_0 = n$, then

$$\lambda^t = e^{rt}, \text{ or } \lambda = e^r$$

If r is constant and not size dependant, the fecundity rate for colonies composed of undifferentiated cells is the same regardless of size.

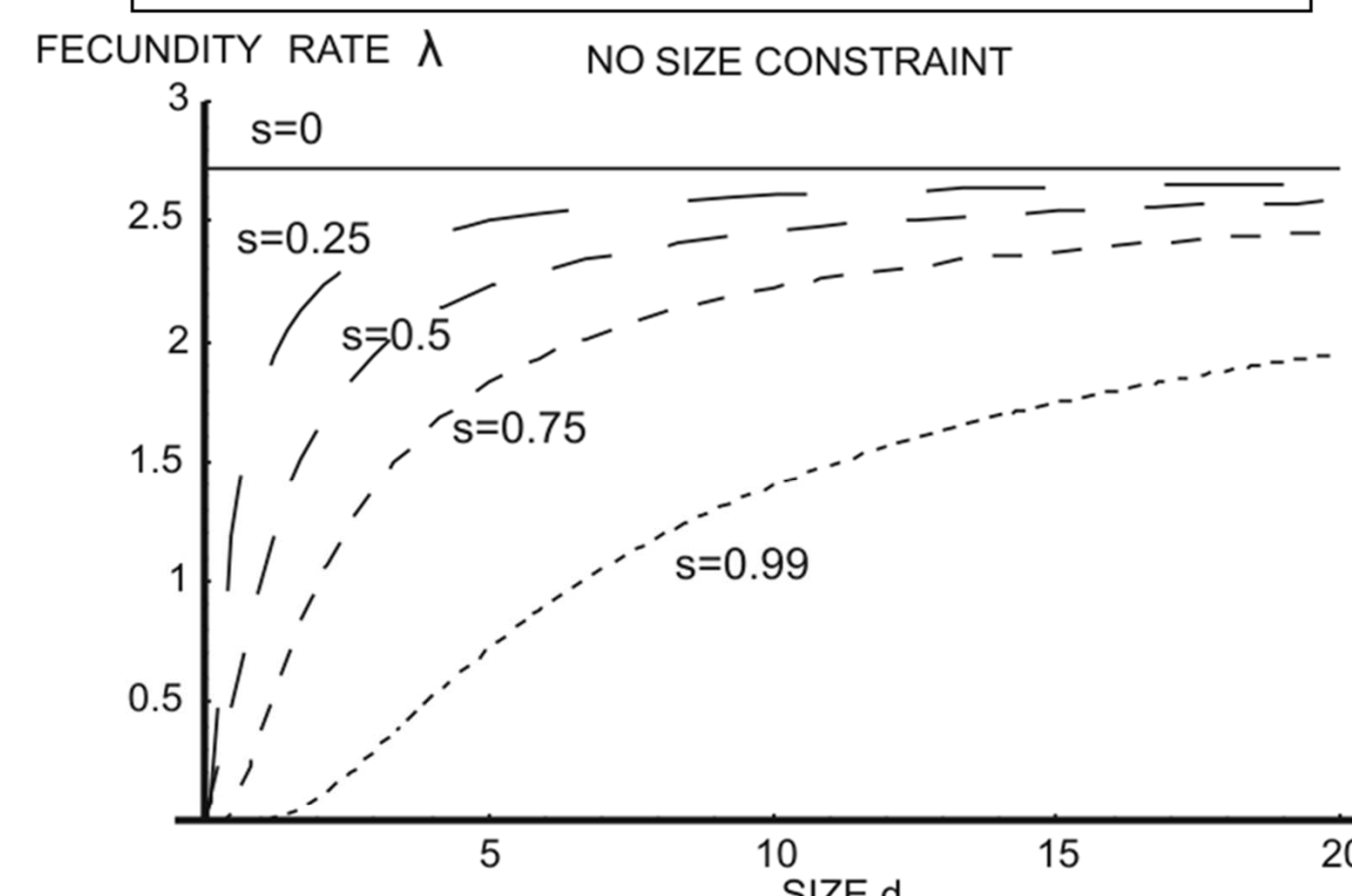
In an ideal world with no size constraints or benefits, size does not matter.

If colonies invest in soma and a proportion s of cells become sterile and do not reproduce:

$$R_0 = n(1-s)$$

since $1/t = r/\text{Ln}(n)$

$$\lambda^t = e^{rt}(1-s) \text{ or } \lambda = e^r(1-s)/\text{Ln} n$$



Investing in a proportion of somatic cells decreases the fecundity rate since somatic cells do not reproduce, but this negative effect dilutes as colony size (d) increases regardless of a cost or benefit of size to the fecundity rate.

But, r depends on the Supply B and Demand C of resources to the colony, which depend on size and cellular differentiation

$$\lambda = e^r(1-s)/\text{Ln} n$$

The demand C depends on the total number of cells (n) and to the proportion of somatic cells (s) which determines how much a colony has to grow to produce daughter colonies of the same type.

The Model

Demand

Total Cost of Reproduction

$$C \sim n^2(1-s)$$

Production costs are lowered as colonies invest in soma

Supply

The vegetative functions B needed to acquire resources to grow and reproduce are performed by the undifferentiated reproductive cells that retain those functions and soma:

$$B \sim ns + n(1-s)(1-g)$$

g = germ specialization parameter (we assume an additive contribution between the two cell types)

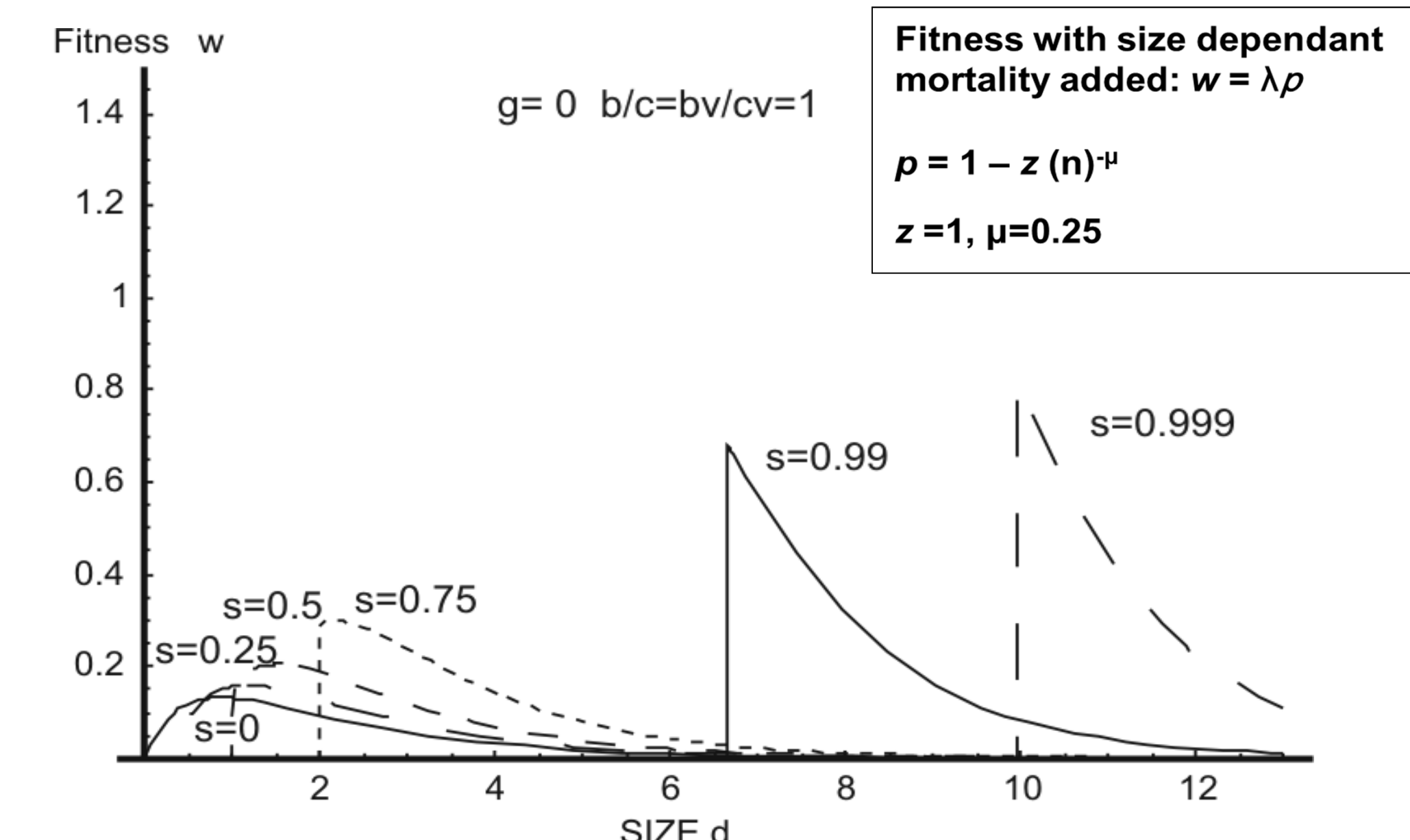
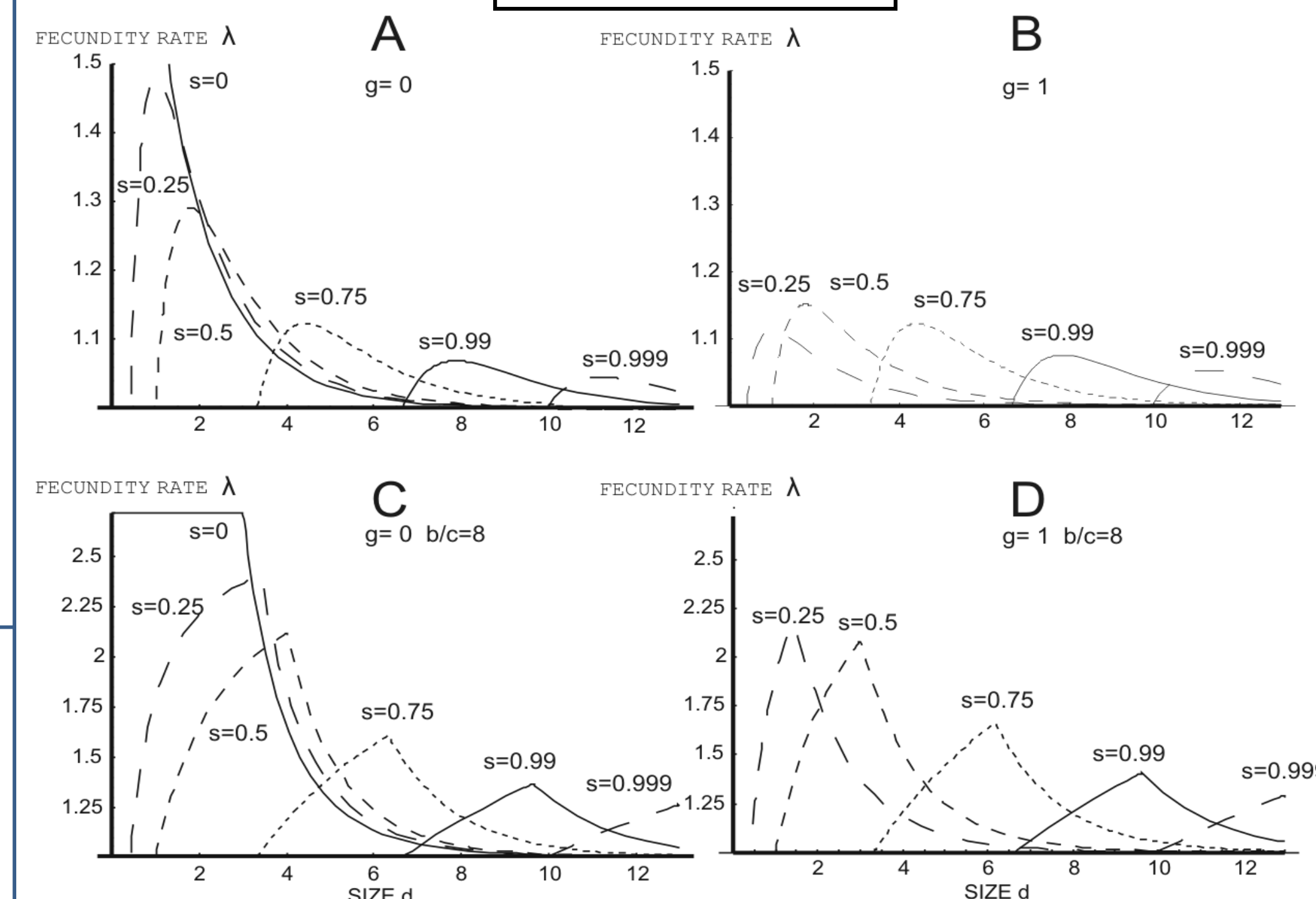
We use the ratio between the supply B and demand C of resources as the factor that may limit the intrinsic growth rate r :

$$B/C_r = bB^\beta/cC^\alpha$$

b = supply of resources of the unicell basal to the lineage
 c = demand of resources of the unicell basal to the lineage
 α and β = scaling exponents for the demand and supply

if $B/C_r \geq 1 \rightarrow r = (1 + u_g g)r_0 \rightarrow$ Supply meets Demand
if $B/C_r < 1 \rightarrow r = (1 + u_g g)r_0 B/C_r$
 r_0 = growth rate of the unicell
 u_g = germ specialization benefit

$$\lambda = e^r(1-s)/\text{Ln} n$$

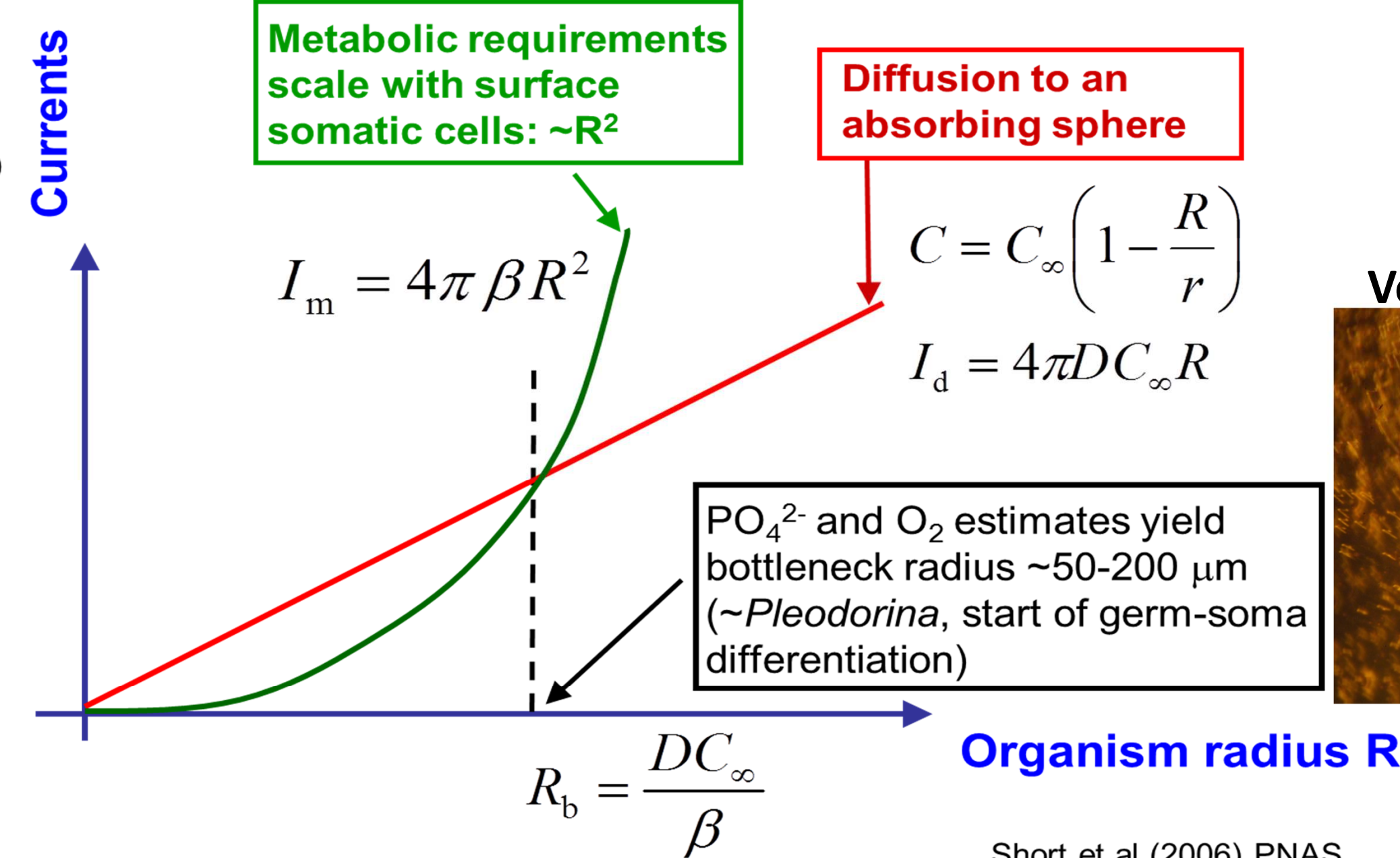


Fecundity rate and fitness curves of hypothetical colonies form peaks that shift to larger size as the proportion of somatic cells s increases. For a fixed proportion of somatic cell s there is a colony size that optimizes the fecundity rate, this optimal size increasing as s increases.

Volvocales are freshwater green algae that comprise a group of closely related lineages with different degrees of cell specialization which seem to represent "alternative stable states" (Larson et al 1992)

Volvocine Green Algae as a Case Study

Advection Currents are Important to Circumvent the Diffusional Bottleneck



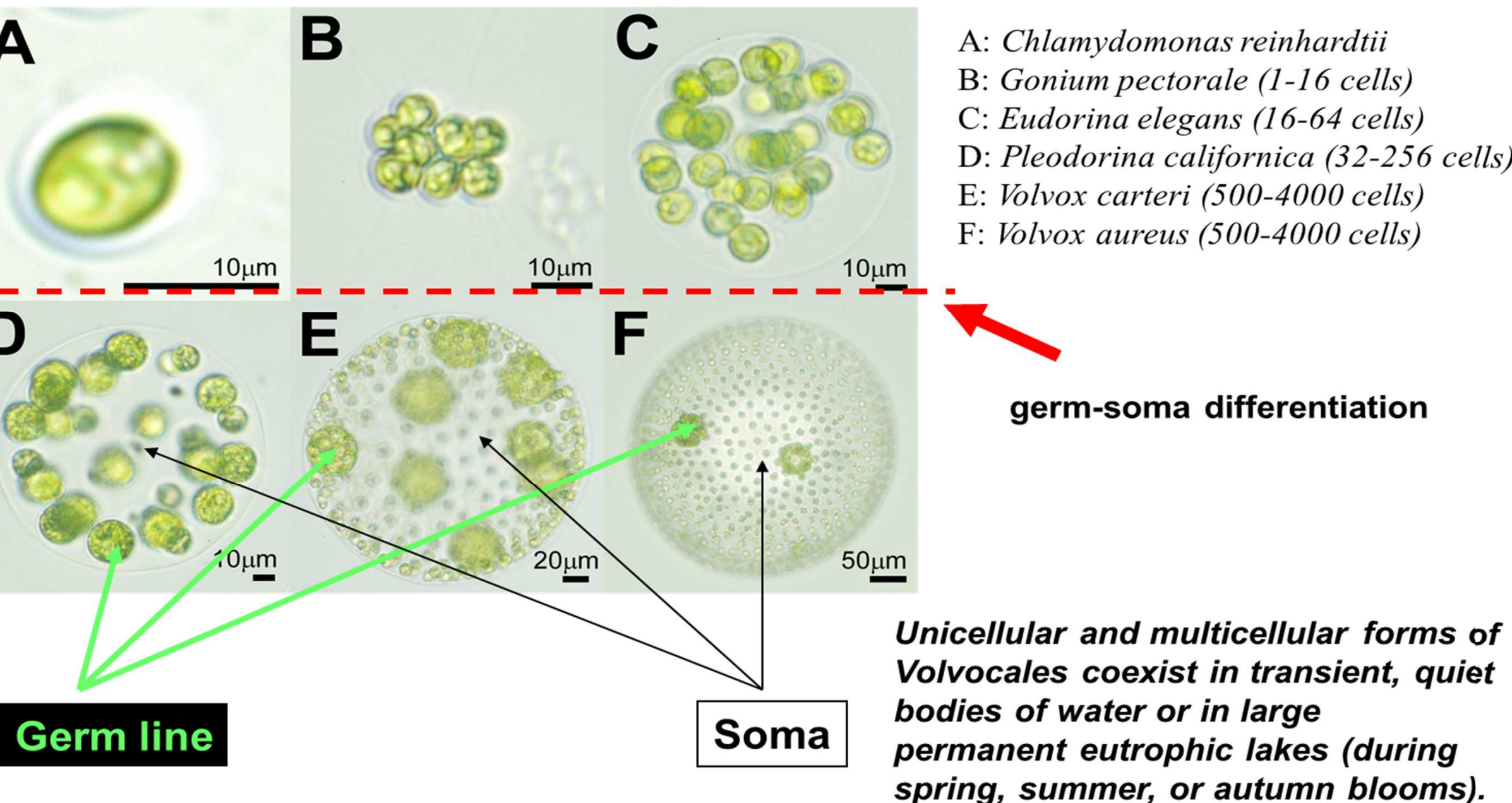
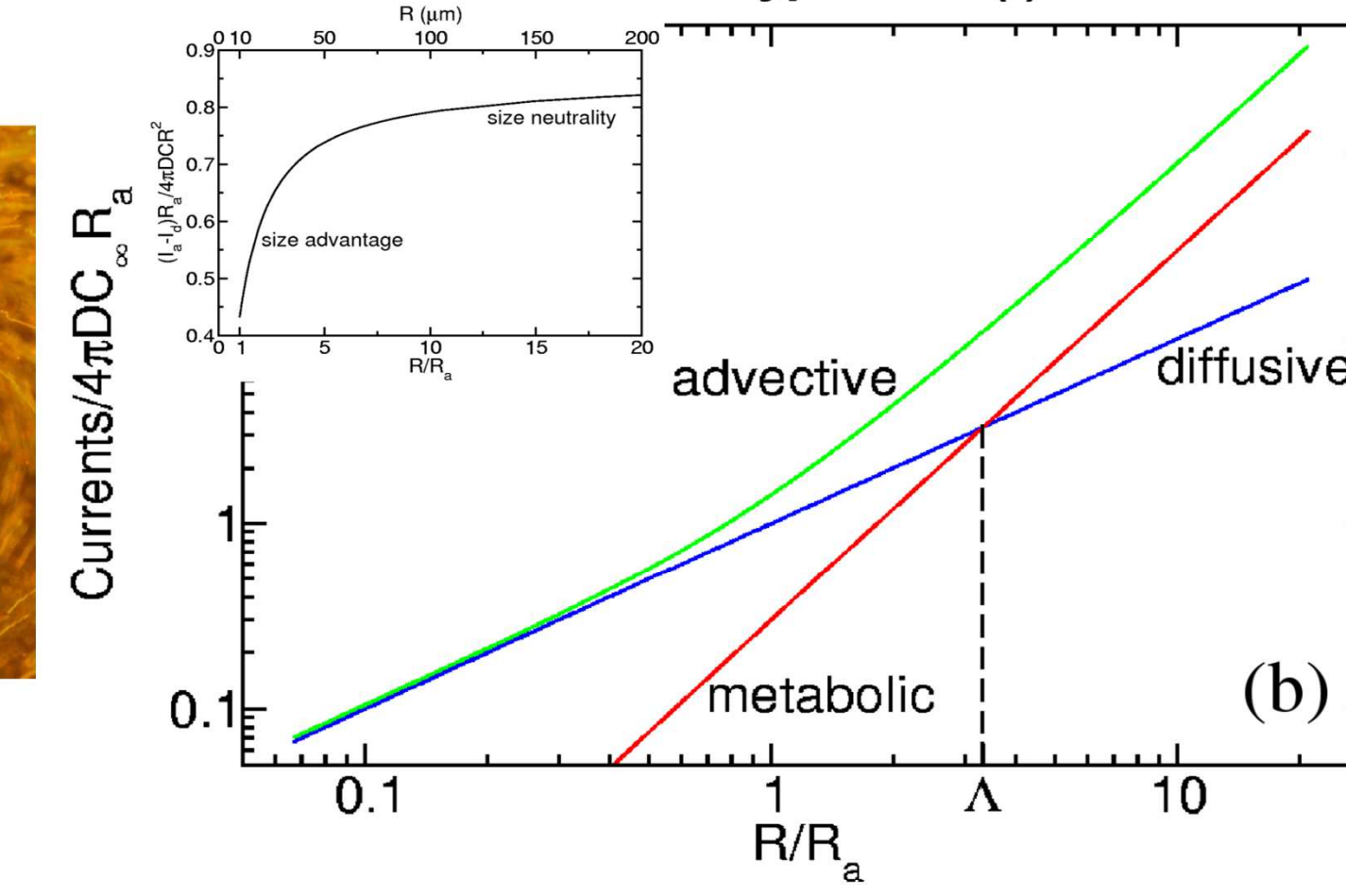
$$B \sim ns + n(1-s)(1-g)$$

$$I_a \sim R Pe^{1/2} \text{ (Short et al 2006)}$$

$$I_a \sim B^{1/2} (B^{1/2} B^{1/2})^{1/2} \sim B$$

$$B/C_r = bB/cC$$

Bottleneck Bypassed (!)



Unicellular and multicellular forms of Volvocales coexist in transient, quiet bodies of water or in large permanent eutrophic lakes (during spring, summer, or autumn blooms).

Conclusions

- Using life-history theory and allometry we produced a model that describes the dynamics of the emergence of germ-soma differentiation as size increases in multicellular organisms.
- The model shows that the cost of reproducing an increasingly larger group has likely played an important role in the evolution of complexity in the transition to multicellularity.
- The trade-offs between fecundity, viability, and size recently studied in Volvocales show in detail how metabolic and viability constraints as colonies increase in size might be strong enough to push the organism design to cellular specialization and higher complexity.

Selected References

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