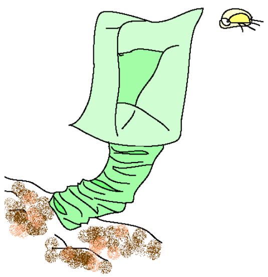
Optimal life history strategy and sperm competition of dwarf males of barnacles

○Sachi Yamaguchi*, Yuki Ozaki, Yoichi Yusa, Satoshi Takahashi

(Nara Women's University)

*e-mail: sachi@lisboa.ics.nara-wu.ac.jp



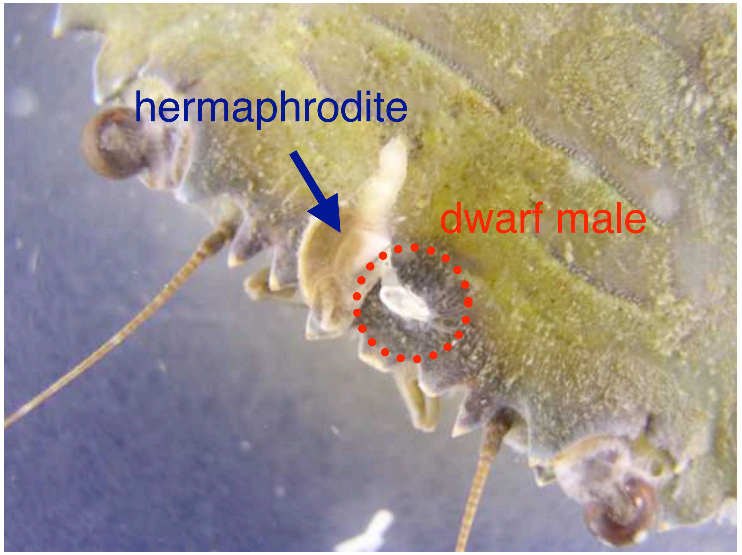
Barnacles' Biology (1)

- Barnacles are crustaceans that distribute widely in seas worldwide.

Octolasmis warwicki

Large hermaphrodite + dwarf ♂

attaches to crab



Scalpellum stearnsii

large ♀ + dwarf ♂

lives in deep sea

↑ We can not see dwarf males in this picture.

Barnacles' Biology (2)

- Barnacles have three patterns of sexuality depending on the species. (Darwin, 1851)
    - (a) Simultaneous hermaphrodite only
    - (b) Large hermaphrodite + Dwarf male (Androdioecy)
    - (c) Large female + Dwarf male (Dioecy)

- Males are very small! ---> "dwarf male"
    - --- Males attach to a large female or hermaphrodite.
    - --- Males living in shallow sea are larger than ones living in deep sea (Pilsbry, 1908).
    - --- Males grow up in some species, they do not in the others.
    - --- Males of androdioecious species tend to be larger than dioecious ones (Yusa and Yamato, unpublished).

Research Purpose

Dwarf males' body size varies depending on species.

↓

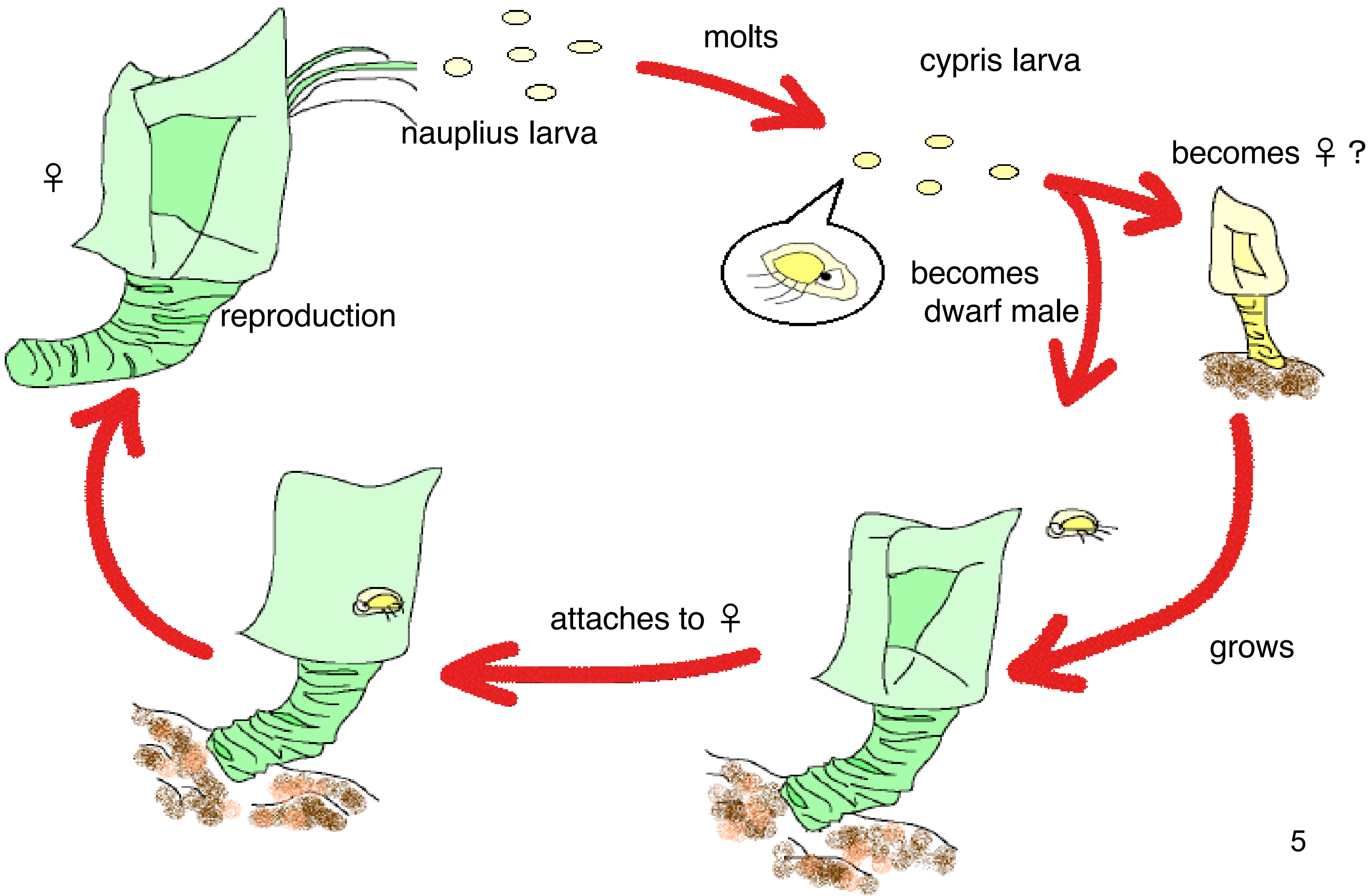
Differences of dwarf males' life histories such as their growth rate

Differences in size of dwarf males among species are caused by two factors.

1. The amount of sperm of large individuals, α
2. Food availability, β

To explain inter-specific differences in body size of dwarf males, we calculate the optimal life history strategy that maximize lifetime reproductive success using Pontryagin's maximum principle.

Life history of barnacles
Ex. *Scalpellum stearnsii*



Model

Life history strategy of barnacles' males: $(u(t), c(t))$

- The proportion of the resources allocated to reproduction, $u(t)$

  to growth, $1-u(t)$

- The consumption speed of initial energy storage, $c(t)$

- Assume that n dwarf males attach to a large individual.

- The resource flow (resource usage per unit time) $r(t)$ is obtained by $c(t)$ and $p(t)$.

$$r(t) = \underbrace{c(t)}_{\text{Consumption speed of energy storage}} + \underbrace{p(t)}_{\text{Feeding rate}}$$

-The resource flow $r(t)$ is divided for two usages.

$$\begin{cases} \text{Resources allocated to reproduction: } u(t)r(t) \\ \text{Resources allocated to growth: } (1-u(t))r(t) \end{cases}$$

- The consumption speed ***c*(*t*)** is larger, the energy storage remainder ***e*(*t*)** becomes smaller.

$$\underbrace{\frac{de}{dt} = -c(t)}_{\text{Consumption speed of energy storage}}$$

- As resource allocated to growth is larger, body size ***s*(*t*)** becomes larger.

$$\frac{ds}{dt} = \underbrace{(1 - u(t))r(t)}_{\text{Resource allocated to growth}}$$

- The feeding rate ***p*(*t*)** is proportional to the area of body size.

$$\underbrace{p(t)}_{\text{Feeding rate}} = \beta s^{\frac{2}{3}}(t)$$

Feeding efficiency

- Instantaneous reproductive success of the dwarf male, $\phi(t)$,

Number of eggs of a large individual

The amount of sperm of the dwarf male

$$\phi(t) = F \times \boxed{\frac{u(t)r(t)}{A(t) + \alpha}}$$

Sperm competition

The amount of sperm of all the dwarf males

The amount of sperm of surrounding large individuals

If large individuals are females, α equals 0.

If large individuals are hermaphrodites, α is positive.

Which $\boldsymbol{u(t)}$ and $\boldsymbol{c(t)}$ maximize the lifetime reproductive success of the dwarf male?

➡ Optimal strategy $(\boldsymbol{u}_{\mathrm{opt}}(t), \boldsymbol{c}_{\mathrm{opt}}(t))$ is calculated by Pontryagin's maximum principle.

Pontryagin's maximum principle (1)

- We define Hamiltonian function.

$$H(e,s,v,p_e,p_s,p_v,u,c) = p_e(t)\frac{de}{dt} + p_s(t)\frac{ds}{dt} + p_v(t)\frac{dv}{dt}$$

Where $v(t)$ is reproductive success until time t.

$$v(t) = \int_0^t \phi(\tau)d\tau$$

- Adjoint variables $p_e(t)$, $p_s(t)$ and $p_v(t)$ follow the equations below.

$$\frac{dp_e}{dt} = -\frac{\partial H}{\partial e} = 0,$$

$$\frac{dp_s}{dt} = -\frac{\partial H}{\partial s} = -\frac{2}{3}\beta s^{-\frac{1}{3}}\left[p_s(1-u) + \frac{p_v F u(A+\alpha)}{(u(c+\beta s^{\frac{2}{3}})+A+\alpha)^2}\right]$$

$$\frac{dp_v}{dt} = -\frac{\partial H}{\partial v} = 0.$$

- Conditions

$e(t)>0$, $e(T)=0$, $v(0)=0$, $p_e(T)=0$, $p_s(T)=0$, $p_v(T)=1$

boundary condition

Pontryagin's maximum principle (2)

- The optimal strategy ($u_{opt}(t)$, $c_{opt}(t)$) maximizes Hamiltonian at any time t.

$$H(e, s, v, p_e, p_s, p_v, u_{\mathrm{opt}}, c_{\mathrm{opt}}) \geq H(e, s, v, p_e, p_s, p_v, u, c)$$

$$0 \leqq u_{opt} \leqq 1, \; 0 \leqq c_{opt} \leqq C_{max}$$

- We solve simultaneous differential equations by Runge-Kutta method.

- We calculate ESS where the optimal life history strategy ($u_{opt}(t)$, $c_{opt}(t)$) coincides with the strategies of the other dwarf males and denote it by ($u^*(t)$, $c^*(t)$).

Optimization with boundary condition

The method of Lagrange multipliers

$G = v(T)$: Objective function = Lifetime reproductive success

$$\left.\begin{array}{l}\text{Control interval: } 0 \leqq t \leqq T \\ \text{Initial state: } (e(0), s(0), v(0)) = (E, s_0, 0)\end{array}\right\} \text{given}$$

Final state: $(e(T), s(T), v(T))$

- without boundary condition

$$G = \eta_e e(T) + \eta_s s(T) + \eta_v v(T)$$

$$(p_e(T), p_s(T), p_v(T)) = (\eta_e, \eta_s, \eta_v) = (0, 0, 1)$$

- with boundary condition

$$G = \eta_e e(T) + \eta_s s(T) + \eta_v v(T) + \lambda e(T)$$

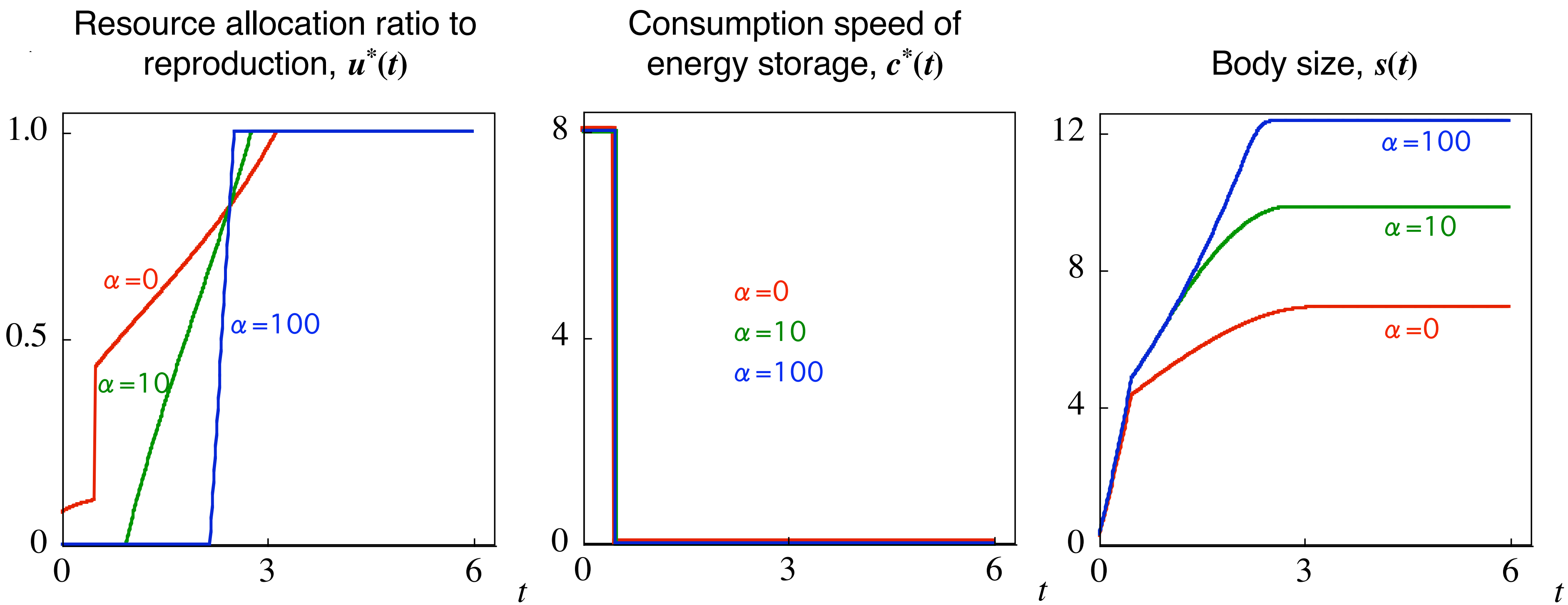
$$(p_e(T), p_s(T), p_v(T)) = (\eta_e + \lambda, \eta_s, \eta_v) = (\lambda, 0, 1)$$

Lagrange multiplier

Result (1)

Effect of the sperm amount of large individuals, α

In food-rich environments (β =1.00)

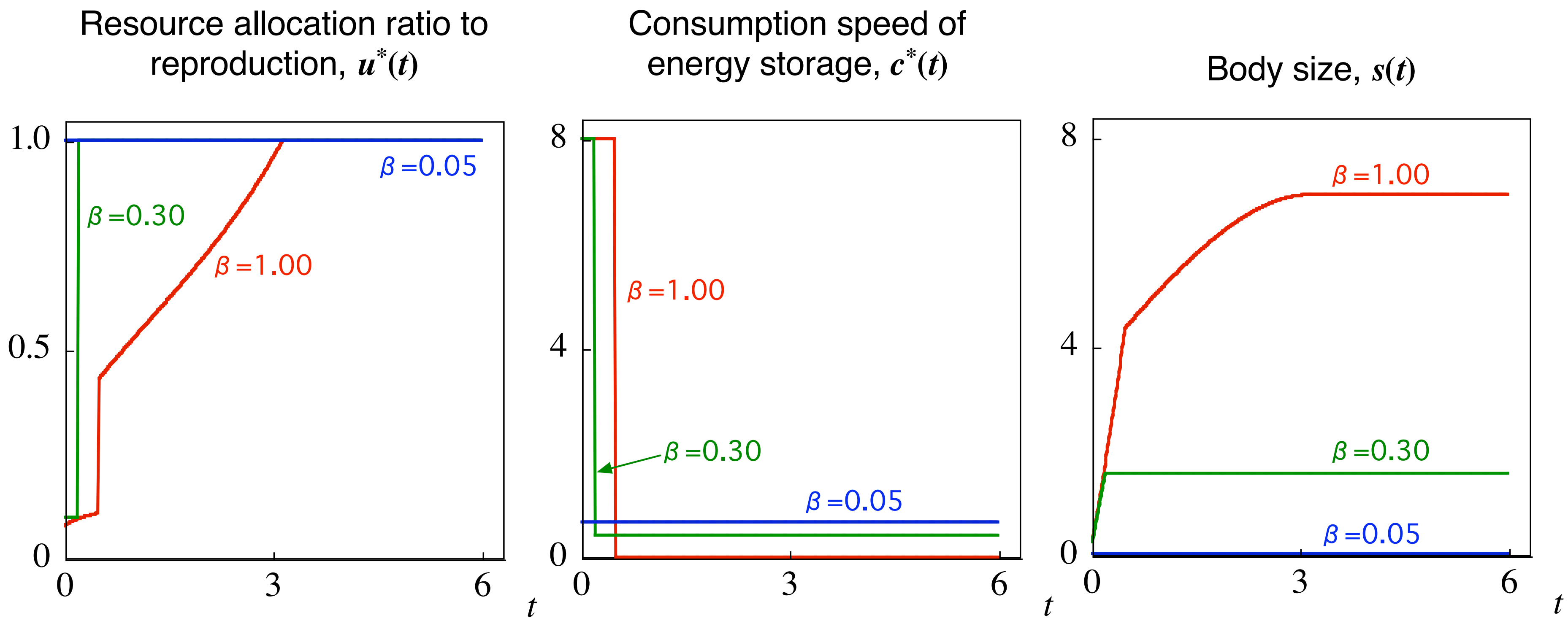


- Dwarf males use up energy storage as fast as possible.
- Body size increases with α.
- Strategy $u^*(t)$ tends to "bang-bang control" as α becomes large.

Result (2)

Effect of the feeding efficiency, β

In dioecious species (α =0)

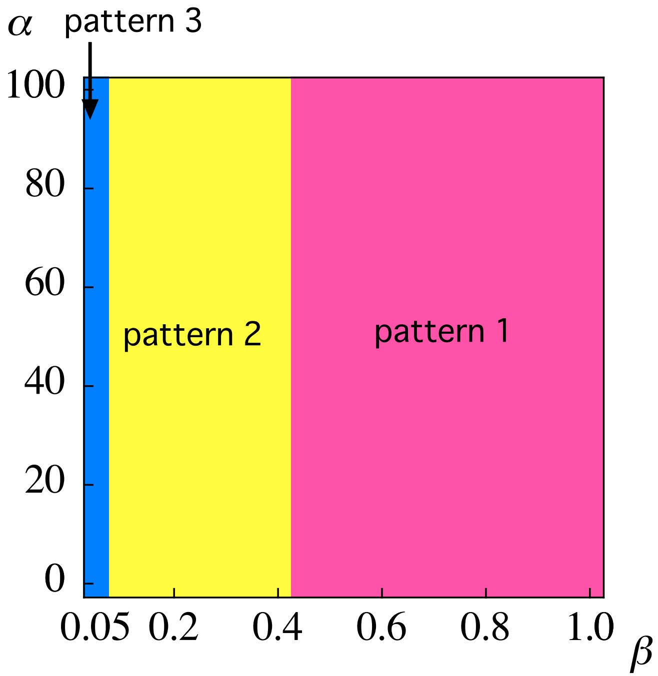


- Dwarf males grow in shorter time when β becomes smaller.
- They do not grow and use all the resources to reproduction when β is very small.

Result (3-1)

Compound effect of the amount of sperm of large individuals, α, and the feeding efficiency, β

3-1. Three patterns of the consumption speed of energy storage, $c^*(t)$



Pattern 1: $c^*(t) = C_{max} \rightarrow 0$

Pattern 2: $c^*(t) = C_{max} \rightarrow \text{Const.}(>0)$

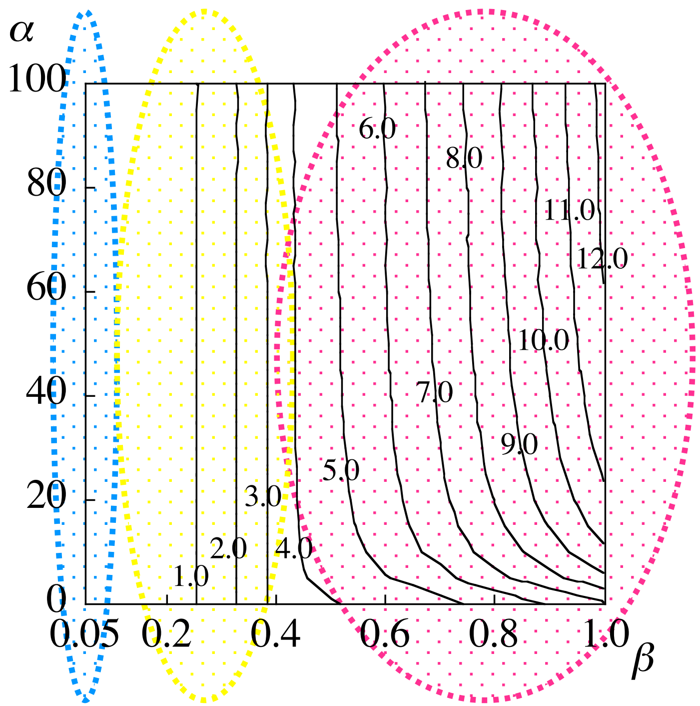
Pattern 3: $c^*(t) = E/T$

- The temporal pattern of the consumption speed of energy storage substantially depends on the feeding efficiency, β .

Result (3-2)

Compound effect of the amount of sperm of large individuals, α, and the feeding efficiency, β

3-2. Contour graph of the final body size, s(T)



- When β is large, the final body size increases with α and β.

- When β is at an intermediate level, the final body size depends only on β.

- When β is very small, dwarf males do not grow at all.

Summary

- small β, all α
  - -- No growth.
  - -- Dwarf males use all the resources to reproduction.

- large β, $\alpha=0$
  - -- Simultaneous growth and reproduction (“intermediate growth”)

- large β, $\alpha>0$
  - -- Comparing to $\alpha=0$, dwarf males grow larger.
  - -- They stop growth earlier.
  - -- Strategy $\boldsymbol{u}^*(\boldsymbol{t})$ tends to “bang-bang control” as α becomes large.

- Males’ body size becomes larger at large β than at small β.

Discussion (1)

- small β, all α : *Food-poor environments*
  - -- Dwarf males attain higher reproductive success by investing all the resources to reproduction than growth.

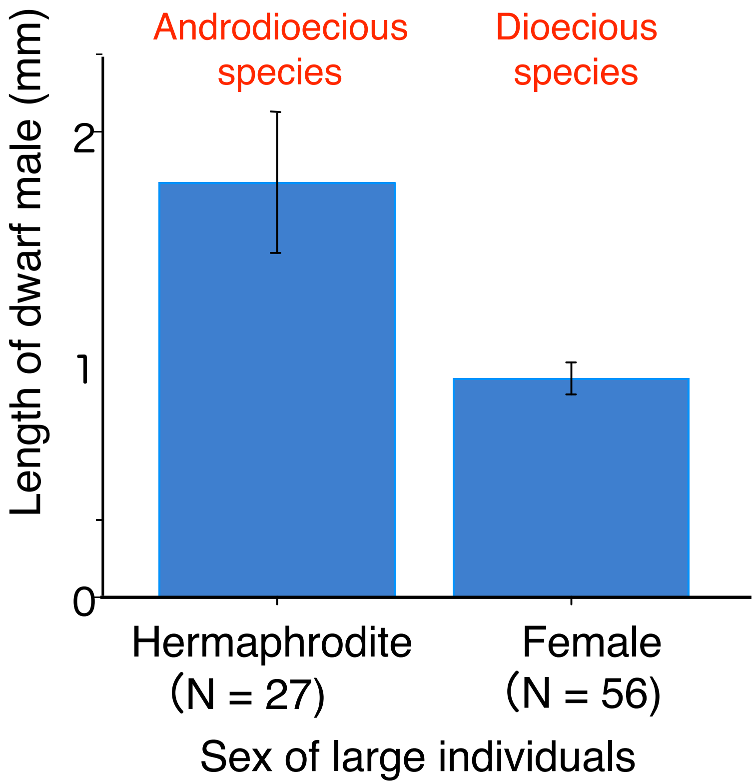
- large β, α=0: *Food-rich environments, Dioecious species*
  - -- Sperm competition is weak for dwarf males.
  - -- Dwarf males have advantage to fertilize eggs for a longer time.
  - -- Large amount of sperm lowers efficiency.
  - ---> “intermediate growth” (simultaneous growth and reproduction)

- large β, α>0: *Food-rich environments, Androdioecious species*
  - -- Sperm competition is severe for dwarf males.
  - -- To counter large hermaphrodites, dwarf males have advantage in making many sperm after becoming larger quickly.
  - ---> approaches to “bang-bang control” (all $(u=1)$ or none $(u=0)$ strategy)

Discussion (2)

Compared between the field data and our model's result…

Yusa and Yamato, unpublished data



---> Our model explains the field data that dwarf males in androdioecious barnacles are larger than dioecious ones.