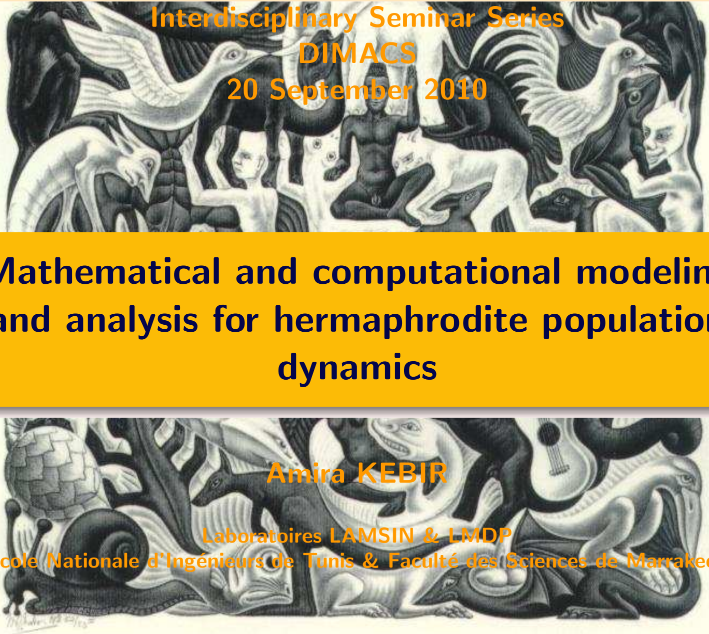

Interdisciplinary Seminar Series
DIMACS
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Mathematical and computational modeling and analysis for hermaphrodite population dynamics

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Although mammals have a relatively limited repertoire of reproductive patterns, in many other organism's gender is more flexible affair.

- Hermaphrodite: sex changing organisms.

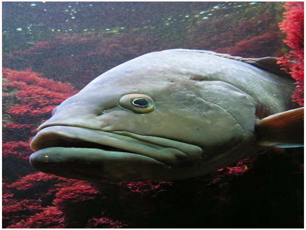
Vocabulary:

- Gonochoristic (dioecious): An organism with two separate sexes.
- Hermaphrodite "simultaneous": An organism that functions both as male and female.
- Sex change / Sequential Hermaphroditism: An organism that functions as one sex and then switches to the other sex.

The sex-ratio

Main questions

1. For sequential hermaphrodite, what is the first sex (♂or ♀)? When and how does sex change?
2. For simultaneous hermaphrodite: under what conditions does selection favor the ability of an individual to alter its allocation to male versus female function in response to particular environmental condition.



Models

The answers to these questions can be divided in two main area, a proximate and an evolutionary studies:

- The proximate point of view answer the following question, for a reproduction type, dioecy or hermaphrodite, what stabilize the sex-ratio?

This can be modelled by:

- Popuation dynamics response to a variable environment:
    - Physical environment: temperature,... .
    - Size distribution of the population.
    - Sexual competition.

Models

The answers to these questions can be divided in two main area, a proximate and an evolutionary studies:

- The evolutionary point of view answer the following question: in which case hermaphrodism can be evolutionary stable in a native population of dioecy.

This can be modelled by:

- Optimality or Adaptive dynamics: Sex allocation models [Ghiselin(1969), Charnov(1982)].

Sex allocation models [Ghiselin(1969), Charnov(1982)]

How best to divide a fixed investment between male and female components of fitness?

$\Downarrow$

Let Φ the *sex allocation* function: is the function that gives the ♀proportion of the total population number.

Sex allocation function (Φ) depends on:

Sex allocation models [Ghiselin(1969), Charnov(1982)]

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Sex allocation function (Φ) depends on:

1. **Evolutionary process:** Trade-off between the production of male and female reproductive structures: The fitness-gain curve (Sex allocation models [Charnov(1982), Charnov1979]) .

Sex allocation models [Ghiselin(1969), Charnov(1982)]

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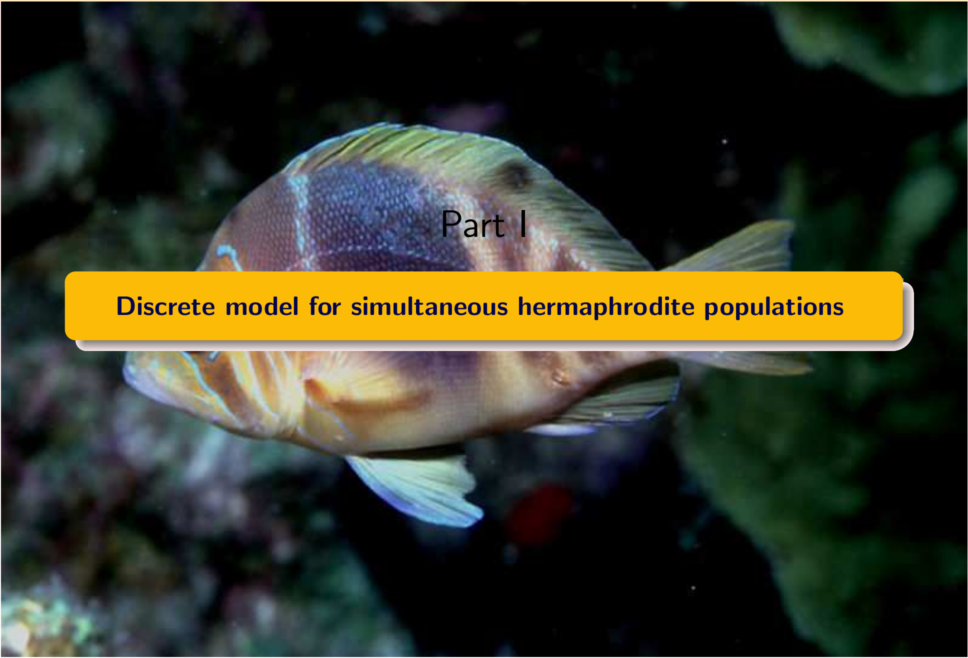
Sex allocation function (Φ) depends on:

1. **Evolutionary process:**
2. **Sexual competition:**
   - The body size of an individual and the size of distribution of the population (Size advantage models [Warner(1988)], [Ripoll(2007)]).
   - Population density, size (or age) distribution or the sex-ratio (our models).



Part I

Discrete model for simultaneous hermaphrodite populations

Goal

We are interested in the study of the proximate and ultimate factors affecting the gender choice of the simultaneous hermaphrodite and the way in which individuals respond to the variability of their environment.

How best to divide a fixed investment between male and female components of fitness?

$\Downarrow$ [Brauer(2007), Charnov(1982), Fischer(1981)]

A more female biased investment of reproductive resources when mating population density decreases

$\Downarrow$

$\Phi(?)$:

- the gender distribution of the population and $\Phi' \leq 0$

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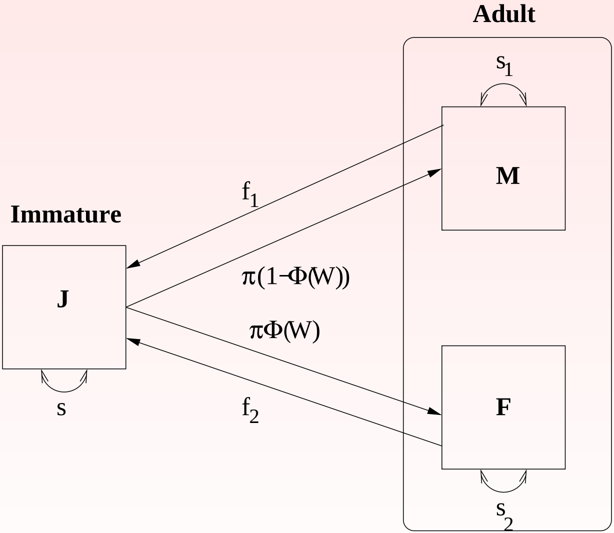

Figure: Conceptual model.

The Model

Mathematical formulation of the model leads to structured discrete system with a density-dependent form for immature sexual choice.

$$\begin{cases} J(t+1) = sJ(t) + f_1 M(t) + f_2 F(t) \\ M(t+1) = \pi(1 - \Phi(W(t)))J(t) + s_1 M(t) \\ F(t+1) = \pi\Phi(W(t))J(t) + s_2 F(t) \end{cases} \tag{1}$$

With $W(t) = J(t) + \beta_1 M(t) + \beta_2 F(t)$.

Φ verifies:

$$\Phi \in \mathbf{C}^1(\mathbf{R}_+, (0,1]), \ \Phi'(\mathbf{x}) \leq 0, \ \Phi(0) = 1 \text{ and } \lim_{\mathbf{x}\to+\infty} \Phi(\mathbf{x}) = 0.$$

System (1) is an example of nonlinear autonomous matrix equation [Cushing(1998)] ⇒ we follow the theory and methodology that can be found in [Cushing(1998)].

Model Analysis

We found that two parameters are the base of all the study

$$\begin{array}{ccc}
\swarrow & & \searrow \\
\Phi(\mathbf{W}) = 1 & & \Phi(\mathbf{W}) = 0 \\
\Downarrow & & \Downarrow \\
\begin{pmatrix} \mathbf{s} & \mathbf{f}_1 & \mathbf{f}_2 \\ 0 & \mathbf{s}_1 & 0 \\ \pi & 0 & \mathbf{s}_2 \end{pmatrix} & & \begin{pmatrix} \mathbf{s} & \mathbf{f}_1 & \mathbf{f}_2 \\ \pi & \mathbf{s}_1 & 0 \\ 0 & 0 & \mathbf{s}_2 \end{pmatrix} \\
\Downarrow & & \Downarrow \\
\eta_{\mathbf{F}} = \frac{\pi \mathbf{f}_2}{(1-\mathbf{s})(1-\mathbf{s}_2)} & & \eta_{\mathbf{M}} = \frac{\pi \mathbf{f}_1}{(1-\mathbf{s})(1-\mathbf{s}_1)}
\end{array}$$

that can be interpreted as the inherent net reproductive numbers when only the females reproduce and only the males reproduce respectively. Where, the net reproductive number of system 1 satisfies

$$\eta(\mathbf{W}) = \eta_{\mathbf{M}}(1 - \Phi(\mathbf{W})) + \eta_{\mathbf{F}}\Phi(\mathbf{W}) \tag{2}$$

Proposition

Let $\mathbf{0} = (0, 0, 0)$ *be the trivial equilibrium of system (1). If* $\eta_{\mathsf{F}} < 1$*, then* $\mathbf{0}$ *is asymptotically stable and if* $\eta_{\mathsf{F}} > 1$, $\mathbf{0}$ *is unstable.*

Proposition

Let $\mathsf{s}_1 \leq \mathsf{s}_2$*. If* $\eta_{\mathsf{F}} < 1$ *then equilibrium* $\mathbf{0}$ *of system (1) is globally asymptotically stable.*

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Proposition

System (1) has a positive equilibrium point $\mathbf{X}^* = (\mathbf{J}^*, \mathbf{M}^*, \mathbf{F}^*)$

1. *either* $\eta_\mathbf{M} < 1$ *and* $\eta_\mathbf{F} > 1$: $\mathbf{X}^*$ *is asymptotically stable for values of* $\eta_\mathbf{F} > 1$ *close enough to* 1.
2. *or* $\eta_\mathbf{M} > 1$ *and* $\eta_\mathbf{F} < 1$: $\mathbf{X}^*$ *is unstable for values of* $\eta_\mathbf{F} < 1$ *close enough to* 1.

The positive equilibrium, in both cases, can be explicitly calculated:

$$\mathbf{X}^* = (\mathbf{J}^*, \frac{\pi(1-\kappa)}{1-\mathbf{s}_1}\mathbf{J}^*, \frac{\pi\kappa}{1-\mathbf{s}_2}\mathbf{J}^*), \tag{3}$$

where $\mathbf{J}^* = \Phi^{-1}(\kappa)/(1 + \beta_1 \frac{\pi(1-\kappa)}{1-\mathbf{s}_1} + \beta_2 \frac{\pi\kappa}{1-\mathbf{s}_2})$ and $\kappa = (1-\eta_\mathbf{M})/(\eta_\mathbf{F} - \eta_\mathbf{M})$.

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Unbounded solutions of system (1)

Proposition

Let $\mathbf{s}_1 \leq \mathbf{s}_2$ *and* $\eta_{\mathbf{M}} > 1$*. If* $(\mathbf{J}(\mathbf{t}), \mathbf{M}(\mathbf{t}), \mathbf{F}(\mathbf{t}))$ *is the solution of system (1) associated to the non-negative initial condition* $(\mathbf{J}(0), \mathbf{M}(0), \mathbf{F}(0)) \neq (0, 0, 0)$ *then* $\{(\mathbf{J}(\mathbf{t}), \mathbf{M}(\mathbf{t}), \mathbf{F}(\mathbf{t})) : \mathbf{t} \in \mathbb{N}\}$ *is unbounded.*

Sufficient condition for the permanence of the system (1)

To prove the permanence of system (1) we apply theorem 3 in [Kon et al.(2004)]; for that we need system (1) to be dissipative,

Proposition

Let $\eta_{\mathbf{M}} < 1$. *If* $\mathbf{x}\Phi(\mathbf{x})$ *is bounded on* $[0, \infty)$ *then system (1) is dissipative.*

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Numerical results

- We use particular forms of function Φ. Here we adapt the so-called generalized Ricker function as presented in [Getz(1996)], $\Phi_{R_\gamma}(x) = e^{-x^\gamma}$.
- We study how γ, the abruptness parameter, s_1 and s_2, the adult survival rates, and β_1 and β_2, the competition coefficients, affect the stability of the system.

For this, we look for η_F, the female inherent reproductive number:

1. Where the positive equilibrium point $X^* = (J^*, M^*, F^*)$ loses its stability.
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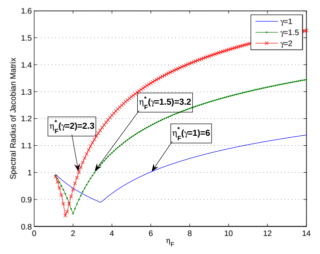
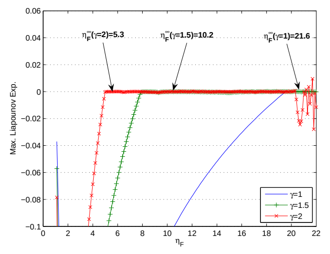
The Effect of the abruptness parameter γ

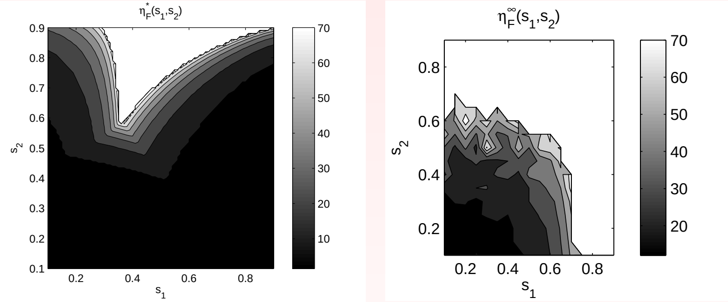


(a) The spectral radius of the Jacobian matrix associated to the equilibrium point $X^* = (J^*, M^*, F^*)$ of system (1). η_F^* represents the bifurcation value where X^* loses its stability.



(b) The largest Lyapunov exponents (LLE) of the orbit of system (1). η_F^∞ represents the largest value of η_F such that the LLE of the orbit is negative for $\eta_F \leq \eta_F^\infty$.

The effect of the adult survival rates



(c) value of η_F for which the positive equilibrium point $X^* = (J^*, M^*, F^*)$ of system (1) loses its stability

(d) smallest value of η_F starting from which the corresponding orbit has a positive LLE

Conclusion

- The population dynamics shows a sensibility to changes in life history parameters and in sex allocation patterns [Higgins et al.(1997)].
- Numerical simulations reveal the existence of chaotic-like long-term behavior of the population dynamics for certain domains of parameters values:
  In this sense iteroparity and abruptness parameter have opposite effects. The latter is prone to imply chaotic behavior whereas the former promotes stability.

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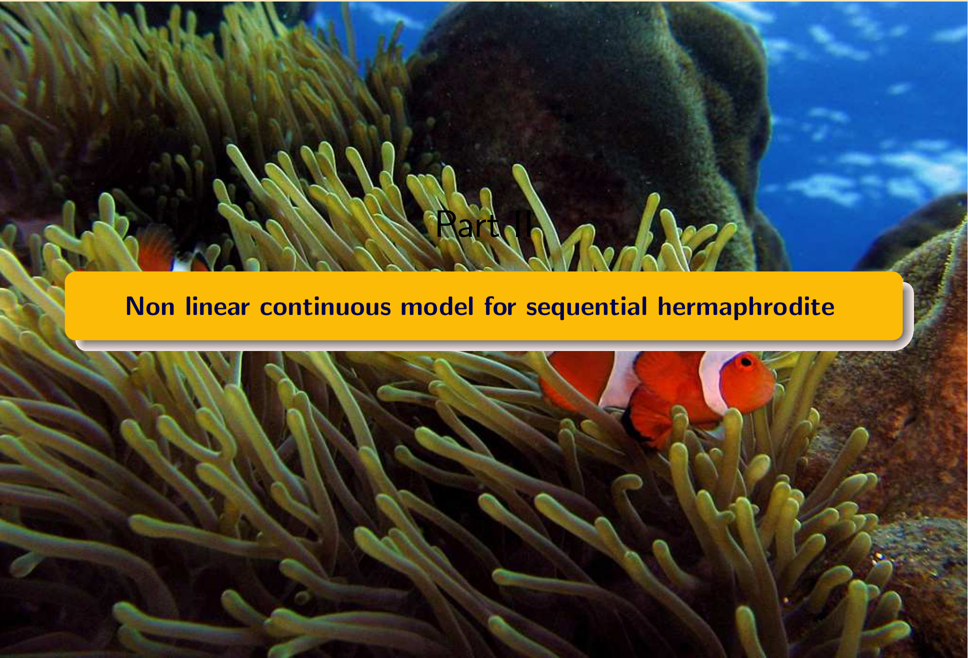

Part II

Non linear continuous model for sequential hermaphrodite

Biological context

For many sequential hermaphrodite species, experiments have confirmed:

The sexual inversion is not really a spontaneous mechanism
ectogenic

but rather

A plastic trait depending on social group like population density, size (or age) distribution or the sex-ratio [Liu and Sadovy(2004), Warner(1996), Shapiro et al.(1984), Munday(2002)]

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Goal

1. **Modelling point of view:** This work is devoted to a general model that describes the dynamics of a sequential hermaphrodite species, like grouper:
2. **Biologically:** We are interesting to study the evolution of sex ratio in the population and the influence of density dependence in population dynamics.
3. **Mathematically:** To analyze a continuously structured population model by Partial Differential Equations approach.

Goal

1. **Modelling point of view:** This work is devoted to a general model that describes the dynamics of a sequential hermaphrodite species, like grouper:
    - The gender change may be induced by environmental or social factors, like size and gender structure of population.
    - The transition from Juvenile to adult state occurs an a random way, when individual attain a specific size.
    - Mortality of an adult is density dependant.
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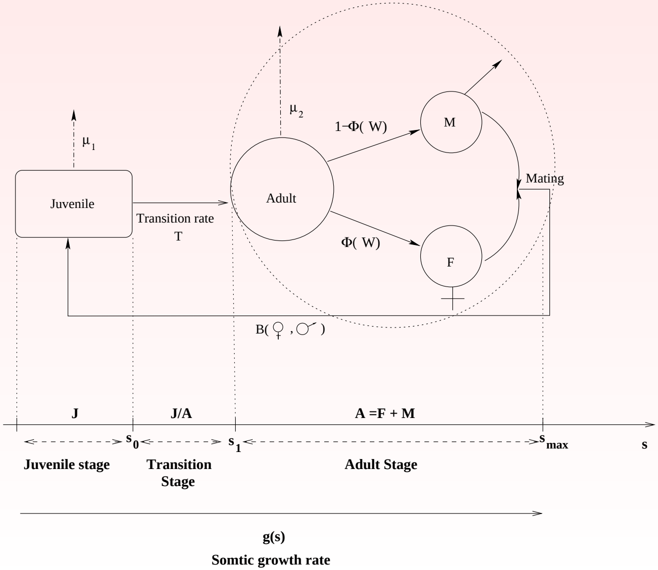
Model Description



Model

The model consists of the two following systems of non-linear first order hyperbolic partial differential equations with their initial and boundary conditions:

$$\left\{\begin{array}{lcl} \frac{\partial}{\partial t}J(s,t) + \frac{\partial}{\partial s}(g(s)J(s,t)) & = & -\mu_1(s)J(s,t) - T(s)J(s,t) \\ J(0,t) & = & \mathcal{B}(\Phi(.,P_2(t))A(.,t),(1-\Phi(.,P_2(t)))A(.,t)) \\ J(s,0) & = & J^0(s) \end{array}\right. \tag{4}$$

$$\left\{\begin{array}{lcl} \frac{\partial}{\partial t}A(s,t) + \frac{\partial}{\partial s}(g(s)A(s,t)) & = & -\mu_2(s,P_2(t))A(s,t) + T(s)J(s,t) \\ A(0,t) & = & 0 \\ A(s,0) & = & A^0(s) \end{array}\right. \tag{5}$$

Whereas for almost all $s > s_1$, where s_1 is the upper threshold, $J(s,t) = 0$ and for almost all $s < s_0$, where s_0 is the lower threshold, $A(s,t) = 0$.

Where:

- the superscript 0 refer to the boundary condition ($s = 0$) and the initial condition ($t = 0$).
- $T(s)$ is the transition rate from immature to mature class.
- $\mu_1(s)$ is the immature mortality rate.
- $\mu_2(s, P_2(t))$ is the mature mortality rate which depends on the size s, and on the mature total population $P_2(t)$.

and

- $g(s)$ is the somatic growth rate for the juvenile and adult subclass biomass.
- $\mathcal{B}(\Phi(., P_2(t))A(., t), (1 - \Phi(., P_2(t)))A(., t))$ is the non-linear birth function giving the influx of newborns.

$$\begin{aligned} B(A(., t)) &= \mathcal{B}(\Phi(., P_2(t))A(., t), (1 - \Phi(., P_2(t)))A(., t)) \\ &= f \int_0^\infty \Phi(s, P_2)A(s, t)ds \frac{\int_0^\infty (1 - \Phi(s, P_2))A(s, t)ds}{1 + \int_0^\infty (1 - \Phi(s, P_2))A(s, t)ds} \end{aligned} \tag{6}$$

Webb [Webb(1985)] methodology

Integrating (4), (5) along the characteristic curves $(1, s(t))$, the system is transformed into the following integral equation:

$$
\begin{aligned}
&\text{if } a(s) \geq t \text{ then,}\\
&\begin{cases}
J(s,t) = J^0(S(a(s)-t))Q_1(s, S(a(s)-t)\dfrac{g(S(a(s)-t))}{g(s)}\\[2ex]
A(s,t) = (J^0(S(a(s)-t))Q_2(s,t,S(a(s)-t);P_2) + A^0(S(a(s)-t))\Pi_2(s,t,S(a(s)-t);P_2))\dfrac{g(S(a(s)-t))}{g(s)}
\end{cases}\\
&\text{if } a(s) < t \text{ then,}\\
&\begin{cases}
J(s,t) = B(A(.,t-a(s)))Q_1(s,0)\dfrac{g(0)}{g(s)}\\[2ex]
A(s,t) = B(A(.,t-a(s)))Q_2(s,t,0;P_2)\dfrac{g(0)}{g(s)}
\end{cases}
\end{aligned}
\tag{7}
$$

Remark

Notice that each column vector above has entries in $[0,1]$ *and which sums* ≤ 1.

1. We prove that (7) is a well posdness problem: The proof is based on a fixed point argument in some suitable banach space: We suppose that:
    1. The functional B fulfills a local Lipschitz condition.
    2. The function μ_2 fulfills a local Lipschitz condition with respect to adult population size p_2 uniformly in size s.
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- Let the product space $L^1 \times L^1 \cong L^1(0,\infty; R^2)$ equipped with norm $\|(\phi,\psi)\|_1 = \|\phi\|_1 + \|\psi\|_1$.
- For $T > 0$, let $L_T := C([0,T]; L^1 \times L^1)$ be the Banach space when $L^1 \times L^1$ is equipped with the norm: $\|(\phi,\psi)\|_{L_T} = \sup_{0 \le t \le T} \|(\phi(.,t),\psi(.,t))\|_1$.

Definition

We say that (J, A) is a solution of (4,5) on $[0, T]$ provided that $(J(.,t), A(.,t))$ satisfies (7) for all $t \in [0, T]$.

Assumptions of the model

Let Ψ, $\overline{\Psi} \in L^1 \times L^1$ and p, $\overline{p} \in \mathbb{R}$ and assume that

Hypothesis

For all $r > 0$ *there exists* $c_1(r) > 0$ *such that if* $\|\Psi\|_1$ *and* $\|\overline{\Psi}\|_1 \leq r$ *then*
$|B(\Psi) - B(\overline{\Psi})| \leq c_1(r)\|\Psi - \overline{\Psi}\|_1.$

Hypothesis

For all $r > 0$ *there exists* $c_2(r) > 0$ *such that if* $|p|$ *and* $|\overline{p}| \leq r$ *then*
$|\mu_2(s, p) - \mu_2(s, \overline{p})| \leq c_2(r)|p - \overline{p}|.$

Theorem

(Local existence and uniqueness) *Under hypotheses 12.1 and 12.2 there exist* $T > 0$ *such that the system (7) has a unique solution* $(J, A) \in L_{T,+}$ *where* $L_{T,+} := C([0, T]; L^1_+ \times L^1_+)$

The proof is based on a fixed point argument in L_T

Global existence and uniqueness

Theorem

Under Hypotheses 12.1 and 12.2, the solutions of system (7), given by Theorem (12.3), are defined for all $t \geq 0$.

Remark

Indeed, by the Gronwall inequality, we obtain the following a priori bound of the L^1*-norm of the solutions of 7:*

$$\|I(.,t)\|_1 \leq \|I^0\|_1 e^{nf(0)t} \;\; t \in [0, T_{max(I0)})$$

We look for steady states of the system (4), *i.e.* solutions independent of time in ${L^1}_+ \times {L^1}_+$. So, stationary solutions $I(s,t) = (J(s,t), A(s,t)) = (J^*(s), A^*(s)) = I^*(s)$ must satisfy,

$$\left\{ \begin{array}{lcl} \frac{d}{ds}(g(s)J^*(s)) & = & -\mu_1(s)J^*(s) - T(s)J^*(s) \\ J^*(0) & = & B(A^*(.)) = \mathcal{B}(\Phi(., {P^*}_2)A^*(.), (1-\Phi(., {P^*}_2))A^*(.)) \end{array} \right. \tag{8}$$

and

$$\left\{ \begin{array}{lcl} \frac{d}{ds}(g(s)A^*(s)) & = & -\mu_2(s, {P^*}_2)A^*(s) + T(s)J^*(s) \\ A^*(0) & = & 0 \end{array} \right. \tag{9}$$

We found that ${P^*}_2$ the total biomass of adult, verifies the following scalar non-linear equation:

$$\int_0^\infty (1 + {P^*}_2(1 - \Phi(s, {P^*}_2))){Q^*}_2(s, {P^*}_2)ds = f{P^*}_2 \int_0^\infty \Phi(s, {P^*}_2){Q^*}_2(s, {P^*}_2)ds \times \int_0^\infty (1 - \Phi(s, {P^*}_2)){Q^*}_2(s, {P^*}_2)ds \tag{10}$$

where, ${Q^*}_2(s, {P^*}_2)$ is the adult survival probability at equilibrium point,
Therefore for each solution ${P^*}_2 \geq 0$ of 10 there exist a steady state $\overline{I} = (\overline{J}, \overline{A}) \in {L^1}_+ \times {L^1}_+$ of 4 and 5.

Remark

This equation depends in the form of the sex allocation function. Therefore, Sex allocation term plays a very important role in the existence and on the asymptotic behavior of equilibrium solutions.

Proposition

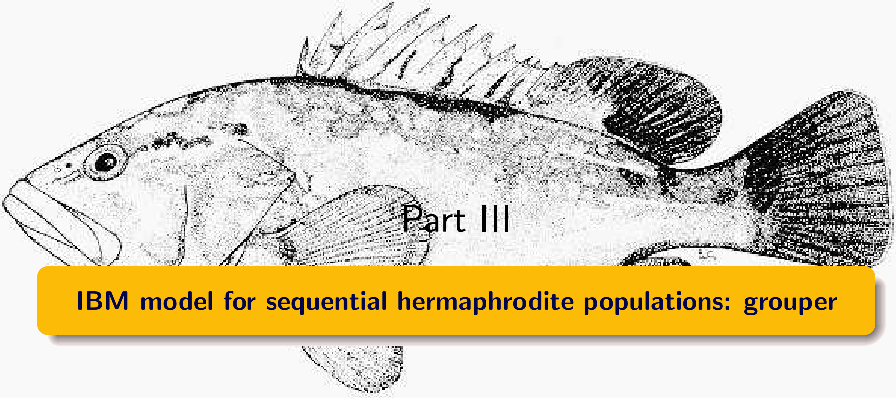
Let Hypotheses 12.1 and 12.2 hold.

1. *If* $P(0) < \frac{\mu_0}{fg(0)}$ *then the trivial equilibrium of (4) and (5) is locally asymptotically stable.*
2. *If* $fg(0) < \mu_0$ *then the trivial equilibrium of (4) and (5) is globally asymptotically stable.*

Remark

An initially low population density produces that the extinction equilibrium is always locally asymptotically stable, displaying the Allee effect ([Allee(1951)] and [(Allee)1931]). On the other hand, we have determined a sufficient condition to have a global extinction this result is a classical statement in population dynamics which means that if the minimum mortality exceeds the maximum fertility then there is no possibility of non-trivial dynamics.

- Study the model by computational analysis and in some statement like without competition effects on adult mortality or size effect on sex allocation function what will facilitate theoretical analysis.
- find the unbeatable strategy or the evolutionarily stable strategy (ESS): by using the same technique developed in [Diekmann et al.(1995)] named convex analysis.



Part III

IBM model for sequential hermaphrodite populations: grouper

FAO

Environmental Contexts

- In the Mediterranean sea, the *Epinephelus marginatus* grouper was indexed in **the red list** of The World Conservation Union (IUCN) as endangered species (www.iucn.org).
- For this protogynous fish, most fishing techniques tend to target the larger individuals.

Aim

Goal

Define an approach that represents the physiological complexities of this species and to

- study the effect of density dependence sex allocation on population by comparing dynamics population for different scenarios and simulations.
- investigate the relative contribution of the adult stages to population persistence and also analyze the effect of their interaction on population dynamics.

Tools

By using informatics stochastic approaches:

IBM.

$$\Downarrow$$

We develop here a **IBM model**, where population is treated as collections of individuals, each of which is represented by a set of variables:

1. Size,
2. Stage,
3. Sexual status.

These temporally variables characteristics change as a function of the individual current state and the interaction with other individuals.

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2. Stage,
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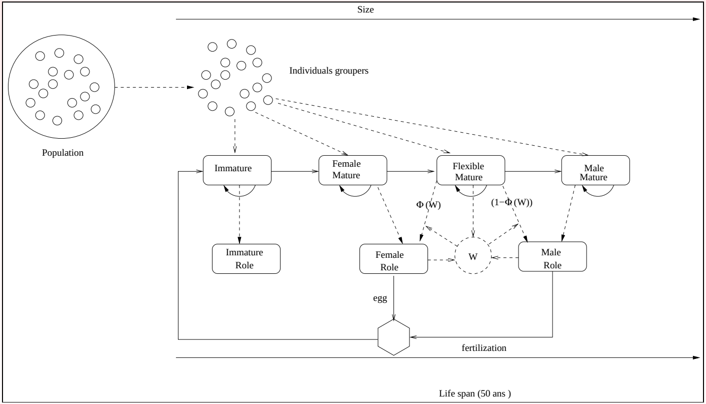
These temporally variables characteristics change as a function of the individual current state and the interaction with other individuals.

Each grouper was individually subjected to all demographic processes including:

1. growth,
2. mortality,
3. sexual status and
4. reproduction.

Using **stochastic** processes.

Description of different modular units used in our study system



Parameters values

Symbol	Value	Definition	Reference
s_m	49	Maturation size	[Renones et al.(2007), Chauvet(2007)]
s_{min}	59	Minimum size of sexual inversion	[Renones et al.(2007), Chauvet(2007)]
s_{max}	100	Maximum size of sexual inversion	[Renones et al.(2007), Chauvet(2007)]
S_∞	114.49	Maximum life size	[Chauvet(1981)]
	50	Maximum life span	[Chauvet(1981), Chauvet(2007)]
S_{inv}	79.51(10)	Fixed size of sexual inversion	[Chauvet(1981)]
k	0.093	Annual growth rate	[Chauvet(1981)]
t_0	-0.75	Initial time	[Chauvet(1981)]
Fr	$115\ 10^3(16\ 10^3)$	Relative fecundity (number of eggs per ovulation)	[Marino et al.(2003)]
ov	2(1)	Number of ovulation laid	[Marino et al.(2003)]
eg_h	0.3(0.2)	Rate of hatched eggs	[Marino et al.(2003)]
f	0.4	0ptimal fertilization rate	[Marino et al.(2003)]
a	$9\ 10^{-6}$	Constant	[Bouain and Siau(1983), Andrade et al.(2003)]
b	3.14	Constant	[Bouain and Siau(1983), Andrade et al.(2003)]
S_{ph}	10^{-5}	Egg post hatching survival	[Bouain and Siau(1983), Andrade et al.(2003)]
β_1, β_2	$4, 1.5$	Male and female competition coefficients	
m_1	0.25	Immature natural mortality rate	
m_2	0.16	Female natural mortality rate	
m_3	0.16	Flexible natural mortality rate	
m_4	0.1	Male natural mortality rate	

Function	Definition	Reference
$\mu_i(t) = S_\infty(1 - e^{-k(age(\mu_i(t-1))+1-t_0)})$	Von Bertalanffy function	[Bertalanffy(1934)]
$W_i(t) = Nb_{A_{fm}}(t) + \beta_1\ Nb_M(t) + \beta_2\ Nb_F(t)$	Weighted mature population size	[Cushing and Li(1992)]
$Wg_i(t) = a(S_i(t))^b$	Female weight	[Bouain and Siau(1983), Andrade et al.(2003)]

- The model starts with a defined numbers of individuals in the initial population.
- It then monitors the changes in each individual that occur through internal processes (biological).
- An annual time step was used as the period at which individuals were exposed to internal processes.
- The model was run in a 300 year horizon and each simulation was run 500 times.
- The simulation outputs correspond to the mean of the 500 simulation of the model

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Scenario1 We exclude the density dependence of the sexual status, in this case the sexual inversion, of each female individual, occurs at a given size, noted S_{inv}, with a certain individual variability given by the normal distribution.

Scenario2 We use the density dependence of sexual status as described, where the sexual inversion depend on the abundance of mature and on the flexible individual sizes and Φ the sex allocation function is Beverton-Holts function, where $\Phi(x) = \frac{1}{1+x}$.

Scenario3 Interaction between Scenario1 and Scenario2 $\Rightarrow$ Evolutionary study.

Remark

The mortality is fixed for each life stage.

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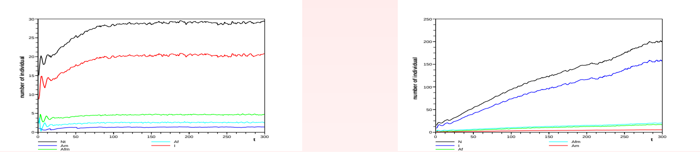
Population dynamical study

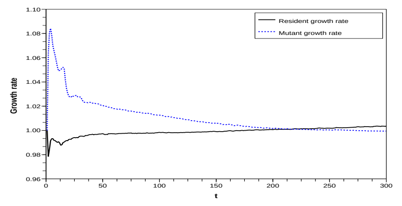


(e) scenario 1. (f) scenario 2.

(g) scenario 1. (h) scenario 2.

Figure: Population dynamics and growth rate dynamics under two different scenarios of sexual inversion through simulations time: (a), (c) "without density dependence effect" and (b), (d) "with density dependence effect". For (a), (b) we present dynamic of total population N and of different life stages : Immature I, female A_f, flexible A_{fm} and male A_m ; for (c), (d) we show the dynamics of the growth rate.

Evolutionary study



(a) growth rate for resident and mutant populations.

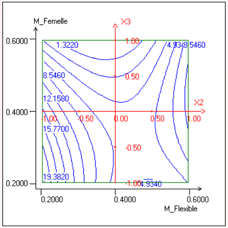
Figure: Evolution by time of the two sexual inversion strategies for sex change hermaphrodite : density dependent strategy and fixed size dependent strategy: we show the growth rate dynamics for resident and the total of mutant.

To perform our analysis we conducted several simulations with different combinations of mortality rates between all adult stages.

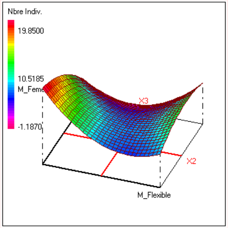
Definition

We computed extinction probability for a simulation set by dividing the number of replications that have resulted in an extinct population by the total number of replications performed (*i.e.* 500).

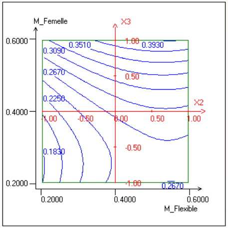
Adult mortality effect



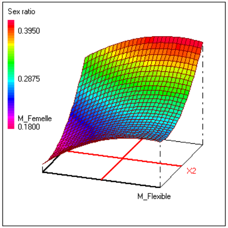
(a) number of individuals.



(b) number of individuals.

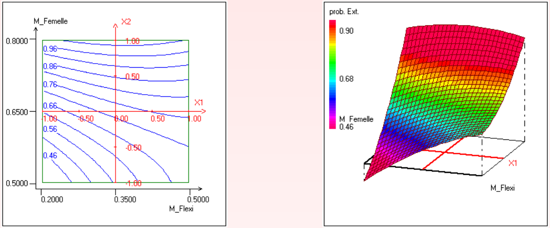


(c) sex-ratio.



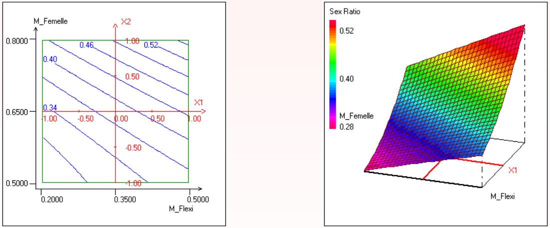
(d) sex-ratio.

Adult mortality effect



(a) Probability of extinction.

(b) Propability of extinction.



(c) sex-ratio.

(d) sex-ratio.

Figure: Propability of extinction ((a), (b)) and sex ratio ($M/(M+F)$) dynamics ((c), (d)) under density dependence scenarios at year 300 with increased female and flexible mortality rates.

Conclusion

- Following evolutionary argument [Maynard-Smith(1985)] the most appropriate strategy in term of *Evolutionary Stable Strategies* (ESS) is the one that maximize the fitness, so the one that presents a density dependent sex allocation.

$\Downarrow$

Social factors like density dependence cannot be isolated from the grouper dynamics. This strategy has the tendency to protect the population by manipulating the sex ratio.

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Conclusion

- Female mortality is recognized to be closely correlated with increased extinction probabilities and
- flexible mortality is a critical parameter that can leads unexpectedly population to total extinction. This response has been already observed in many protogynous fish like groupers [Munoz and Warner(2003)], in which large non-sex-changed females can predominate.

⇓

Then our analysis indicates a need for protection of the female and flexible marine stages. Reduction of moralities in these two stages can be considered a conservation priority.

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Conclusion

- the removal of big males, does not affect the population and not even the sex ratio dynamics.

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Density dependence of sex change mitigates the effect of continued removal of large males. This result was observed for many typical protogynous fish include for grouper species [Munoz and Warner(2003), Mark(1999)].

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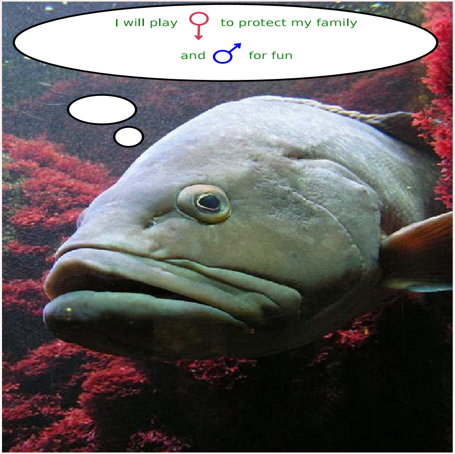

Thanks for your attention

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