UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
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SMR.780 - 14

FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(24 October - 11 November 1994)

"Addendum to Lecture Note No. 6: Two-species Interactions, Stage Structure and Environmental Factors"

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These are preliminary lecture notes, intended only for distribution to participants.

Table 3. Summary of model equations

Balance class i $dN_i(t)/dt = R_i(t) - M_i(t) - D_i(t)$

REPRODUCTIVE

Recruitment eggs $R_0(t) = F_0(C_2(t))\ H(n(t)/N_2(t))\ [1-Sw(C_2(t))]\ N_2(t) + I(t)$

Switching fraction $Sw(C_2(t)) = 1/[1+\exp((-C_2(t)+a\ Cmax_2)/(b\ Cmax_2))]$

Mating factor $H(n/N_2) = (n(t)/N_2(t))/(h+n(t)/N_2(t))$

Recruitment female neonates $R_1(t) = F_1(C_2(t))\ Sw(C_2(t))\ N_2(t) + M_0(t)$

Recruitment male neonates $I_1(t) = F_1(C_2(t))\ Fm\ [1-Sw(C_2(t))]\ N_2(t)$

Fertility j=0, j=1 $F_j(C_2(t)) = Fmax_j/[1+\exp((-C_2(t)+c_j aCmax_2)/(gCmax_2))]$

HATCHING

Hatching rate $M_0(t) = GF_0[T,P]\ R_0(t-\tau_0(t))\ S_0(t)$

Accumulated temperature $T_a = \int_{t-\tau_f}^{t} (T(\sigma)-T_b)\,d\sigma \quad for \quad T>T_b$

Accumulated photoperiod $P_a = \int_{t-\tau_f}^{t} (P(\sigma)-P_b)\,d\sigma \quad for \quad P>P_b$

Hatching fraction $GF_0(T,P) = \begin{cases} 1 & if \quad Ta>Th \wedge Pa>Ph \\ 0 & otherwise \end{cases}$

MORTALITY

Death rates class i $D_i(t)=\delta_i(t)\ N_i(t)$

Mortality increase class i $\gamma_i(t)=\gamma_{max}/[1+\exp((v\ Gmax_i-u_i(t))/(\zeta Gmax_i))]$

Accumulated starvation class i $u_i=\int_{t-\tau_0}^{t}(a\ Gmax_i-G_i(\sigma))\,d\sigma$ *for* $a\ Gmax_i>G_i(\sigma)$

Survival class i $dS_i(t)/dt=S_i(t)\,[G_i(t)\,\delta_i(t-\tau_i(t))/(G_i(t-\tau_i(t)))-\delta_i(t)]$

MATURATION, INGESTION, GROWTH

Max length, Max growth class i $L_i=\int_{t-\tau_i(t)}^{t}G_i(\sigma)\,d\sigma$, $Gmax_i=L_i/\tau_i(0)$

Maturation female neonates $M_1(t)=[G_1(t)/G_1(t-\tau_1(t))]\,R_1(t-\tau_1(t))\,S_1(t)$

Maturation delay class i $d\tau_i(t)/dt=1-G_i(t)/G_i(t-\tau_i(t))$

Growth rate class i $G_i(t)=\epsilon_i C_i(t)\ (\ q_1\ \alpha\ +\ q_2\ (1-\alpha))$

Ingestion rate class i $C_i(t)=Cmax_i\ Qf(t)\ QT(t)\ QP(t)\ QX(t)$

Food limiting factor $Qf(t)=f(t)/(f(t)+K_h)$

Temperature limiting factor $QT(t)=4\,[(T(t)-Tmin)\,(Tmax-T(t))]/(Tmax-Tmin)^2$

Photoperiod limiting factor $QP(t)=4\,[(P(t)-Pmin)\,(Pmax-P(t))]/(Pmax-Pmin)^2$

Stress limiting factor $QX(t)=1/[1+\exp((X(t)-x)/\zeta)]$

FOOD AND ENVIRONMENTAL

Food dynamics item 1 $df_1(t)/dt = fs_1(t) - \alpha[(C_1N_1+C_2N_2)+k\ (C_1n_1+C_2n_2)]$

Food dynamics item 2 $df_2(t)/dt = fs_2(t) - (1-\alpha)[(C_1N_1+C_2N_2)+k\ (C_1n_1+C_2n_2)]$

Staggered food supply item 1 $fs_1(t) = fsmax_1 \sin(2\pi t/ls)$

Staggered food supply item 2 $fs_2(t) = fsmax_2 \sin(2\pi(t-td_{12})/ls)$

Algae growth item j $fs_j(t) = fg_j^{max} QR(t)\, QTT_j(t)\, f_j(t)$

Light limiting factor $QR(t) = (e/\theta z)[\exp(-(SR/SR_{opt})\theta z)) - \exp(-SR/SR_{opt})]$

Light extinction factor $\theta = 0.0088\ f(t) f_c/f_{chl} + 0.053[f(t) f_c/f_{chl}]^{2/3} + k_{ext}$

Thermal factor algae j $QTT_j(t) = 4[(T(t)-Tf_j^{min})(Tf_j^{max}-T(t))]/(Tf_j^{max}-Tf_j^{min})^2$

Temperature $T(t) = Tm+Tp \sin[(2\pi/365)(t-Td)]$

Light $SR(t) = SRm+SRp \sin[(2\pi/365)(t-SRd)]$

Solar declination $\omega(t) = 0.4093+\sin[(2\pi/365)(t-82.2)]$

Photoperiod $P(t) = 7.639 acos[(-\sin(\frac{\pi}{180} lat)\sin\omega - 0.1047)/(\cos(\frac{\pi}{180} lat)\cos\omega)]$

Table 4. Summary of food and environmental conditions

LABORATORY AT CONSTANT FOOD SUPPLY, PHOTOPERIOD, TEMPERATURE AND STRESS

I_0	Inoculation rate	eggs/ml day^{-1}	0.05
fc_1	Constant food supply rate	Mcells ml^{-1}day-1	0.10
fc_2	Constant food supply rate	Mcells ml^{-1}day-1	0.10
$f_1(0)$	Initial food density item 1	Mcells ml^{-1}	0.001
$f_2(0)$	Initial food density item 2	Mcells ml^{-1}	0.001
$fmax_1$	Maximum food density item 1	Mcells ml^{-1}	0.50
$fmax_2$	Maximum food density item 2	Mcells ml^{-1}	0.50
q_1	Relative quality of food1	adimensional	1.00
q_2	Relative quality of food2	adimensional	1.00
T	Temperature	°C	20.0
P	Photoperiod	hrs	14.0
X	Stress level	µg/l	0.0

LABORATORY AT CONSTANT PHOTOPERIOD, TEMPERATURE AND STRESS; BUT WITH VARIABLE FOOD SUPPLY

I_0	Inoculation rate	eggs/ml day^{-1}	0.05
ls	Length of emulated season	days	90.0
fs_{max1}	Max supply for food 1	$Mcellml^{-1}day^{-1}$	0.10
fs_{max2}	Max supply for food 2	$Mcellml^{-1}day^{-1}$	0.10
td_{12}	Time delay between peaks	days	20.0
$f_1(0)$	Initial food density item 1	Mcells ml^{-1}	0.001
$f_2(0)$	Initial food density item 2	Mcells ml^{-1}	0.001
$fmax_1$	Maximum food density item 1	Mcells ml^{-1}	0.50
$fmax_2$	Maximum food density item 2	Mcells ml^{-1}	0.50
q_1	Relative quality of food1	adimensional	1.00
q_2	Relative quality of food2	adimensional	1.00
T	Temperature	°C	20.0
P	Photoperiod	hrs	14.0
X	Stress level	µg/l	0.0

FIELD CONDITIONS: VARIABLE TEMPERATURE, PHOTOPERIOD, FOOD SUPPLY BUT WITH CONSTANT STRESS

I_0	Emergence rate	eggs/ml day^{-1}	0.05
fg_1^{max}	Max growth rate of algae sp 1	day^{-1}	0.60
fg_2^{max}	Max growth rate of algae sp 2	day^{-1}	0.60
$f_1(0)$	Initial food density algae 1	Mcells ml^{-1}	0.001
$f_2(0)$	Initial food density algae 2	Mcells ml^{-1}	0.001
SR_{opt}	Opt surface solar radiation	W m^{-2}	145
z	Depth of the euphotic zone	m	2.00
f_c	Carbon content of algae cells	pgC/cell	20.00
f_{chl}	Carbon to chlorophyll ratio	mgC/mg Chl	50.0
k_{ext}	Light extinction coeff. other fact.	m^{-1}	4.00
Tf_1^{max}	Maximum temperature growth algae 1	°C	20.0
Tf_1^{min}	Minimum temperature growth algae 1	°C	10.0
Tf_2^{max}	Maximum temperature growth algae 2	°C	30.0
Tf_2^{min}	Minimum temperature growth algae 2	°C	15.0
q_1	Relative quality of food1	adimensional	1.00
q_2	Relative quality of food2	adimensional	1.00
Tm	Mean temperature	°C	12.5
Tp	Temperature range	°C	7.5
Td	Temperature delay	days	150
SRm	Surface solar radiation (mean)	W m^{-2}	145
SRp	Surface solar radiation (range)	W m^{2}	145
SRd	Surface solar radiation (delay)	days	130
lat	Latitude	degrees	30
X	Stress level	µg/l	0.0

Table 1. Summary of Parameters

Parameter	Description	Units	Value
REPRODUCTIVE			
$Fmax_0$	Maximum sexual fertility rate	$eggs.day^{-1}.ind^{-1}$	0.10
$Fmax_1$	Maximum asexual fertility rate	$neonates.day^{-1}ind^{-1}$	4.00
Fm	Male productivity farction	adimensional	0.01
a	Switch fraction of ingestion rate	adimensional	0.30
b	Switch sensitivity	adimensional	0.01
h	Half mating rate sex ratio	adimensional	0.01
c_0	Half sexual fertility decrease	adimensional	0.90
c_1	Half asexual fertility decrease	adimensional	1.10
g	Fertility sensitivity to ingestion	adimensional	0.20
HATCHING			
Tr	Low temperature for egg hatching	°C	9.00
Tb	Temperature base value	°C	15.0
Pb	Photoperiod base value	hrs	12.0
Th	Threshold for thermal accumulation	°C.days	17.0
Ph	Threshold for photoperiodic accum	hrs.day	3.00
τ_0	Minimum epphipia development delay	days	2.00
MORTALITY			
y_0	Non-stress. develop.eggs death rate	day^{-1}	0.07
y_{ess}	Non-stress. resting eggs death rate	day^{-1}	0.001
y_1	Non-stressed neonates death rate	day^{-1}	0.10
y_2	Non-stressed adults death rate	day^{-1}	0.05
Y_{max}	Maximum stress mortality increase	adimensional	4.00
v	Half fraction for stress mortality	days	1.00
ξ	Lethal sensitivity to stress	days	0.10
GROWTH AND INGESTION			
L_1	Carapace length interval (neonates)	mm	0.45
L_2	Carapace length interval (adults)	mm	0.15
$\tau_1(0)$	Minimum neonate develop. delay	days	4.00
$\tau_2(0)$	Minimum post-reproductive delay	days	10.0
Cmax1	Max female ingestion rate	$Mcells.day^{-1}.ind$	0.50
Cmax2	Max female ingestion rate	$Mcells.day^{-1}.ind$	5.00
k	Male ingestion/female ingestion	adimensional	0.50
Kh	Half rate food density	$Mcells.ml^{-1}$	0.20
Tmax	Maximum temperature tolerance range	°C	30.0
Tmin	Minimum temperature tolerance range	°C	10.0
Pmax	Maximum photoperiod tolerance range	hrs	16.0
Pmin	Minimum photoperiod tolerance range	hrs	10.0
x	Half rate threshold stress level	μg/l	10.0
ζ	Non-lethal sensitivity to stress	μg/l	0.10

Table 2. Summary of Variables

Variable	**Description**	**Units**
DENSITIES		
N_i	Female density in class i	ind.ml^{-1}
n_i	Male density in class i	ind.ml^{-1}
n	Total male density	ind.ml^{-1}
NET RATES		
R_i	Female recruitment rate to class i	ind.day^{-1}.ml^{-1}
M_i	Female maturation rate out of class i	ind.day^{-1}.ml^{-1}
D_i	Female mortality rate in class i	ind.day^{-1}.ml^{-1}
r_i	Male recruitment rate to class i	ind.day^{-1}.ml^{-1}
m_i	Male maturation rate out of class i	ind.day^{-1}.ml^{-1}
d_i	Male mortality rate in class i	ind.day^{-1}.ml^{-1}
I	Sexual eggs inoculation/emergence rate	eggs.ml^{-1}.day^{-1}
REPRODUCTIVE		
F_0	Sexual fertility rate	eggs.day^{-1}.ind^{-1}
F_1	Asexual fertility rate	neonates.day^{-1}.ind^{-1}
H	Mating rate	adimensional
Sw	Switching fraction	adimensional
HATCHING		
GF_0	Ephippial eggs hatching fraction	adimensional
τ_f	Ephippial eggs hatching delay	days
τ_0	Ephippial eggs development delay	days
Ta	Thermal accumulation for hatching	°C.days
Pa	Photoperiod accumulation for hatching	hrs.days
MORTALITY		
S_i	Survival fraction in class i	adimensional
δ_i	Stressed per capita death rate in class i	day^{-1}
γ_i	Relative increase of mortality in class i	adimensional
u_i	Accumulated growth deficit in class i	mm
GROWTH AND INGESTION		
τ_i	Delay class i	days
C_i	Female ingestion rate in class i	Mcells.day^{-1}.ind^{-1}
G_i	Growth rate in class i	mm.day^{-1}
GF_i	Growing fraction in class i	adimensional
$Gmax_i$	Maximum Growth rate in class i	mm.day^{-1}
ϵ_i	Efficiency of food in class i	mm/Mcell
Qf	Food limiting factor	adimensional
QT	Thermal limiting factor	adimensional
QP	Photoperiodic limiting factor	adimensional
QX	Stress limiting factor	adimensional
FOOD AND ENVIRONMENTAL		
α	ratio of food item 1 to total food	adimensional
f_j	Food density item j	Mcells.ml^{-1}
f	Total food density	Mcells.ml^{-1}
fs_j	Food supply rate item j	Mcells ml^{-1}day^{-1}
T	Mean daily water emperature	°C
QR	Solar radiation factor	adimensional
QTT_j	Thermal factor item j	adimensional
P	Photoperiod	hrs
SR	Surface solar radiation	W m^{-2}
θ	Light extinction factor	m^{-1}
X	Stress level	μg/l
ω	Solar declination	rad

Primary productivity as a function of solar radiation

Maximum photosynthesis rate

$Pmax := .5$

Initial slope of photosynthesis rate

$\alpha := 0.02$

Solar radiation just below the surface

$I0 := 300$

Extinction coefficient

$k := 0.5$

Depth interval

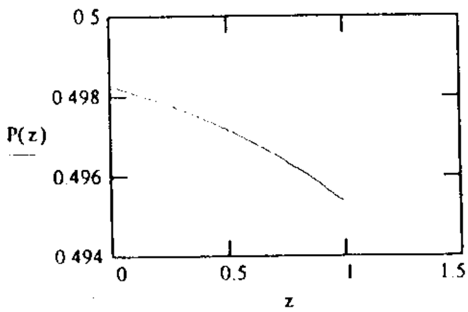
$z := 0.01, 0.02 .. 1$

Beer's law

$I(z) := I0 \cdot \exp(-k \cdot z)$

Smith's pp model

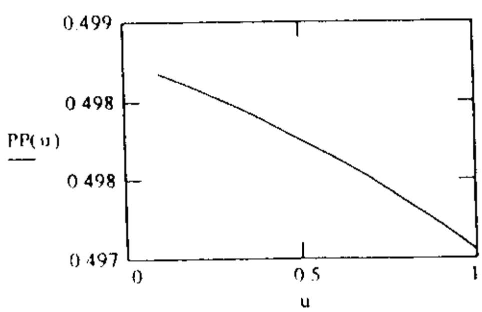
$$P(z) := Pmax \cdot \frac{I(z)}{\sqrt{\left(\frac{Pmax}{\alpha}\, I^{2}\right)^{2} + I(z)^{2}}}$$



Depth average

$u := 0.1, .2 .. 1$

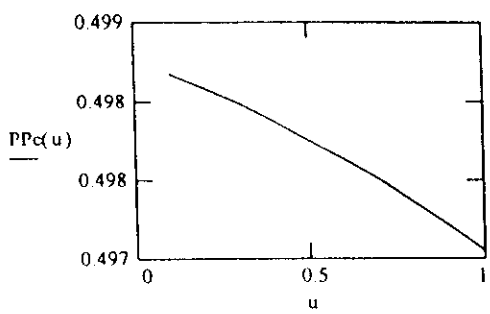
$$PP(u) := \frac{\int_0^u P(z)\, dz}{u}$$



Closed expression from Ginot-Herve (1994)

$$y := \left(\frac{Pmax}{\alpha}\right)^2 \qquad Id(u) := I0 \cdot \exp(-k \cdot u)$$

$$PPc(u) := \frac{Pmax}{k \cdot u} \cdot \ln\left(\frac{I0 + \sqrt{y + I0^2}}{Id(u) + \sqrt{y + Id(u)^2}}\right)$$



Primary productivity as a function of solar radiation

Maximum photosynthesis rate

$Pmax := .5$

Optimal light intensity in Steele's model

$Lo := 200$

Solar radiation just below the surface

$I0 := 300$

Extinction coefficient

$k := 0.5$

Depth interval

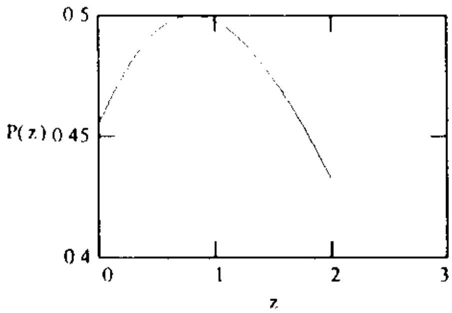
$z := 0.01, 0.02 .. 2.0$

Beer's law

$I(z) := I0 \cdot \exp(-k \cdot z)$

Steele's pp model

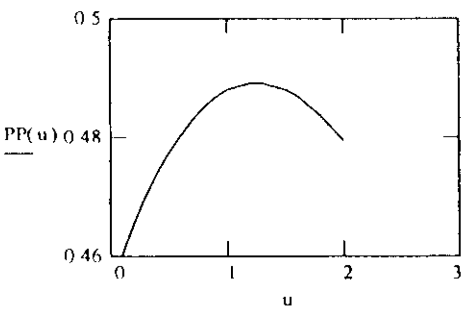
$$P(z) := Pmax \cdot \frac{I(z)}{Lo} \cdot \exp\left(1 - \frac{I(z)}{Lo}\right)$$



Depth average

$u := 0.1, .2 .. 2$

$$PP(u) := \frac{\int_0^u P(z)\, dz}{u}$$



Closed expression from Swartzman&Kaluzny

$Id(u) := I0 \cdot \exp(-k \cdot u)$

$$PPc(u) := \frac{Pmax \cdot \exp(1)}{k \cdot u} \cdot \left(\exp\left(\frac{-Id(u)}{Lo}\right) - \exp\left(\frac{-I0}{Lo}\right)\right)$$