Laboratory 7 Solutions
Three State Variable Models

Biol534 Fundamentals of Ecological Modeling

Task 7.1: Linear Chain

Task 7.1.1: Forrester Diagram

Figure 1 is a Forrester diagram of the system described in the laboratory handout.

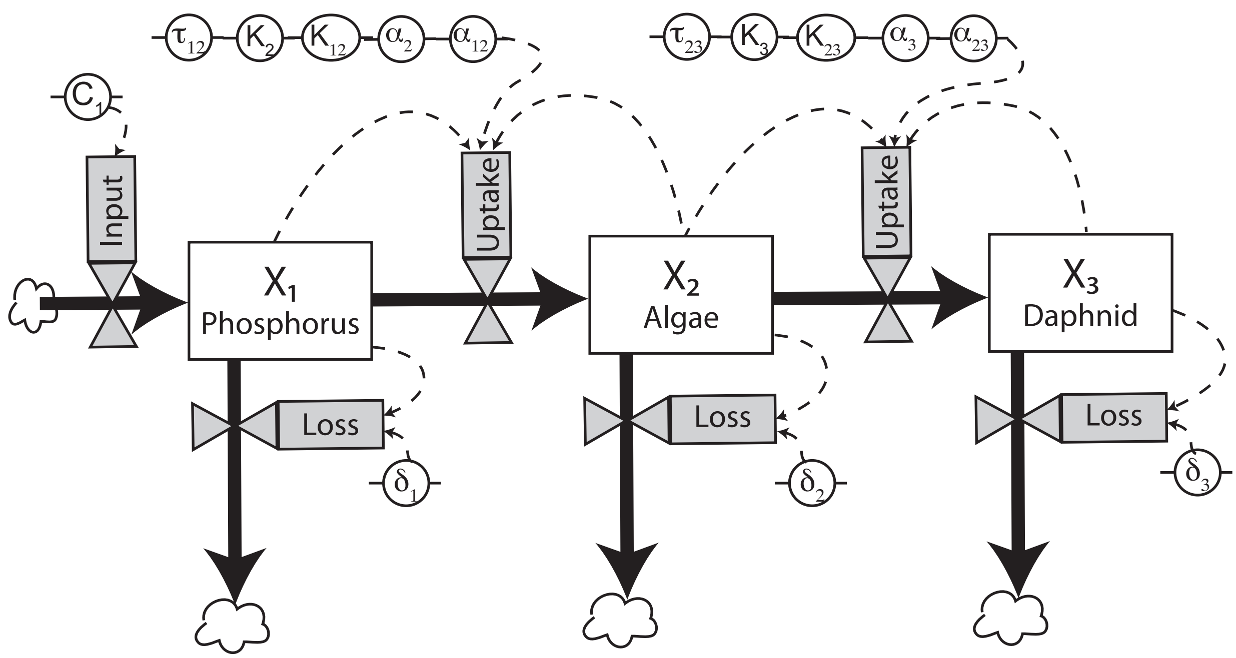

Figure 1: Forrester diagram of linear chain system.

Task 7.1.2: Nominal Dynamics

The system dynamics shown in Figure 2 are the nominal system dynamics using the parameters shown in Table 1. The Algae initially drop as they are consumed by the Daphnids faster than they can increase one the available phosphorus. As the phosphorus increases and daphnids decrease, the algae are able to grow. After a period of transient dynamics, the model stabalizes with both X_2 and X_3 below their carrying capacities and the phosphorus X_1 at a constant value. Thus, the algae must be taking up the phosphorus as fast as it comes in. The algae are limited by the phosphorus and the daphnid predation pressure, but there are not enough algae to fully support the daphnid population.

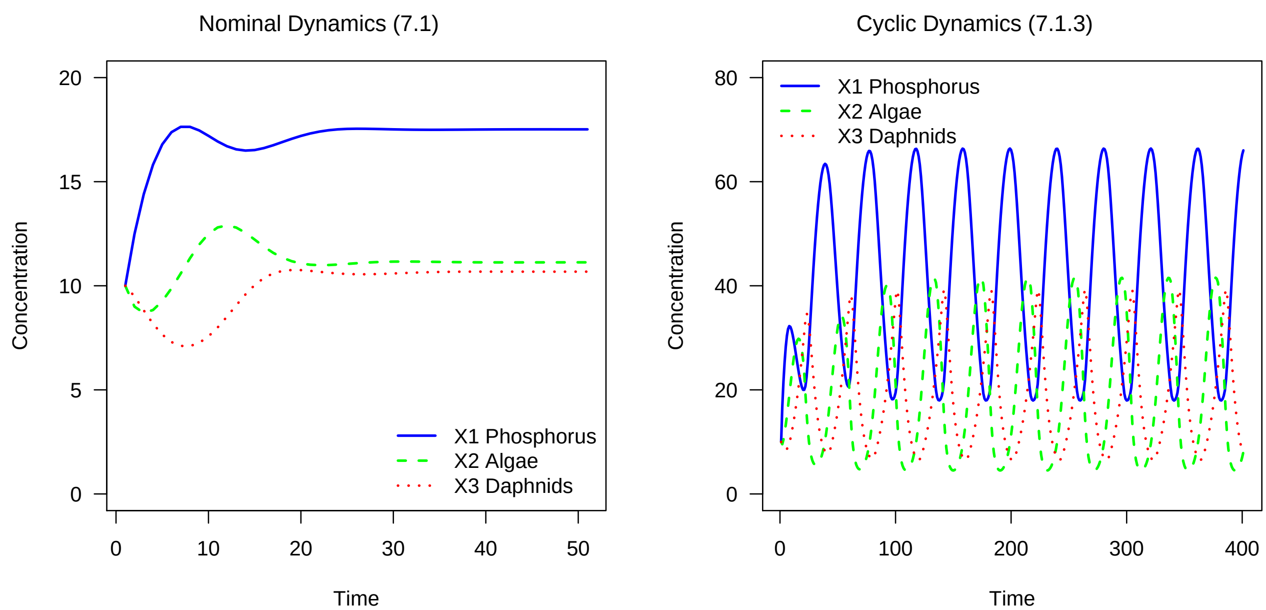

Figure 2: Chain dynamics. **Left** panel shows the nominal dynamics of the model given the original parameters and the **right** panel shows cyclic dynamics that were generated by altering the parameter values to $C_1 = 10$, $\tau_{12} = 0.35$, $\tau_{23} = 0.3$, $\alpha_{23} = 0.1$, and $K_3 = 100$.

Task 7.1.3: Stable Cycles

There are multiple ways to modify the parameter values to generate stable limit cycles in this model. The directions suggested that given enough enrichment C_1, altering τ_{12}, τ_{23}, α_{23}, and K_3 should generate stable cycles. I was able to generate cycles with the parameter values shown in Table 2, though this is not an exhaustive list.

Task 7.1.4: Alternative Stable States

Differences in the initial conditions for the linear chain model can generate two alternative stable states when the enrichment rate is elevated (Figure 3). In the first state, the steady state value of the algae is larger than that of daphnids ($X_2 > X_3$). The alternative state has the final magnitude of daphnids larger than algae ($X_3 > X_2$). The first stable state occurs because early algal growth ($t = 1$ to about $t = 6$) escapes predator control and are thus primarily limited by resource availability. In contrast, when daphnids start more abundant than the algae, the algae always experience predator control.

Table 1: Variables and Parameters for Task 8.1

Name & Description	Symbol	Value
State Variables		
Phosphorus	X_1	10
Algae	X_2	10
Daphnids	X_3	10
Constant Rates		
Input of available phosphorus	C_1	5
Rate Parameters		
Max uptake of X_1 by X_2	τ_{12}	0.35
Max uptake of X_2 by X_3	τ_{23}	0.5
Loss rate from X_1	δ_1	0.1
Loss rate from X_2	δ_2	0.1
Loss rate from X_3	δ_3	0.2
Control Parameters		
Refuge of X_1	α_{12}	5
Threshold response density of X_2	α_2	20
Refuge of X_2	α_{23}	5
Threshold response density of X_3	α_3	10
X_2 satiation concentration of X_1	K_{12}	20
Carrying Capacity of X_2	K_2	70
X_3 satiation concentration of X_2	K_{23}	20
Carrying Capacity of X_3	K_3	30

Table 2: Parameter combinations that generate stable limit cycles. Only parameters different from those in Table 1 are shown.

	A	B	C	D	E	F	G
C_1	10		10	10			10
τ_{23}	0.30	0.35			0.25	1	
α_{12}							0
α_{23}	0.1	0.1	0	0	0	0	0
K_2		100	20				
K_{23}		5					
K_3	100	20					
α_2			20				
α_3			20	20		0	20
K_{12}			20				

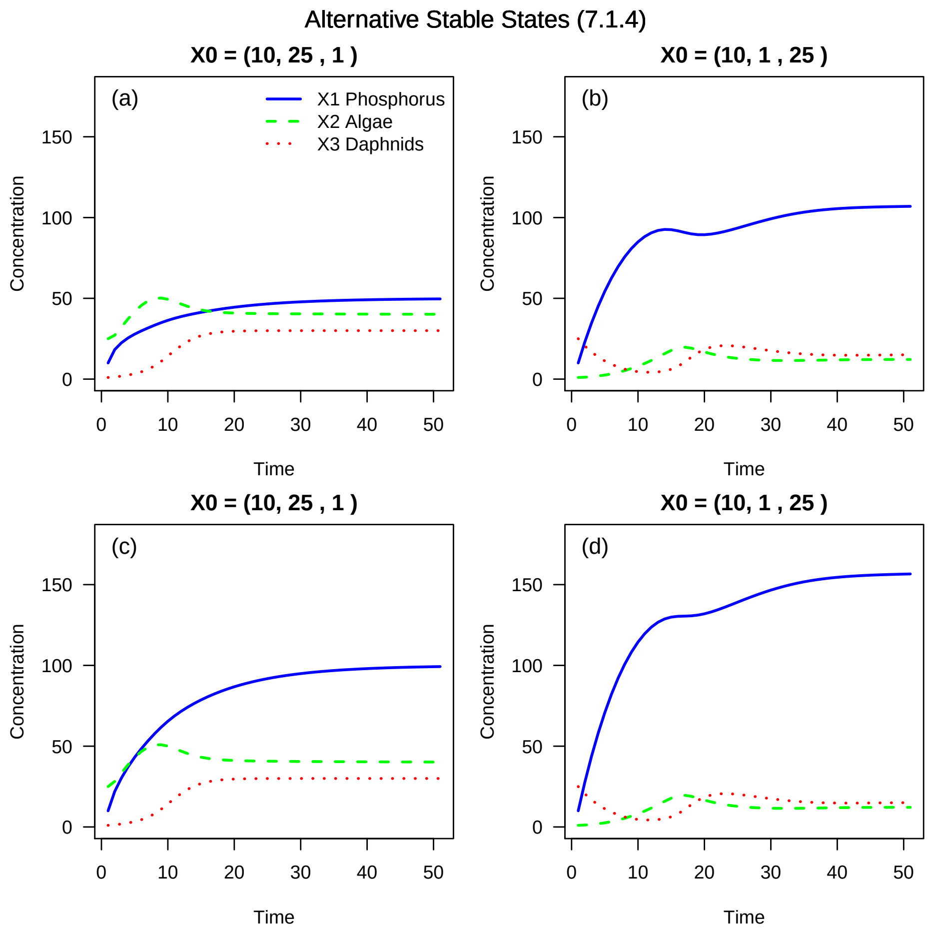

Figure 3: Alternative Stable States. In (a) and (b) the enrichment level $C_1 = 15$ while in (c) and (d) $C_1 = 20$. (a) and (c) illustrate the state that occurs when algae start larger than daphnids and (b) and (d) show the opposite.

Task 7.2: Resource Competition

Task 7.2.1: Forrester Diagram

A simplified Forrester Diagram for this model is presented as Figure 4.

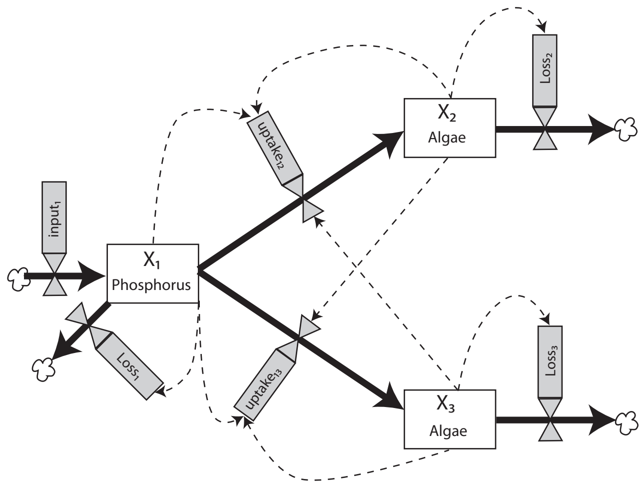

Figure 4: Simplified Forrester diagram for resource competition model.

The equations for this model were as follows.

Differential Equations

$$\dot{X}_1 = C_1 - \delta_1 X_1 - \tau_{12} X_2 \cdot f(X_2, X_3) \cdot f(X_1)_a - \tau_{13} X_3 \cdot f(X_3, X_2) \cdot f(X_1)_b \quad (1)$$

$$\dot{X}_2 = \tau_{12} X_2 \cdot f(X_2, X_3) \cdot f(X_1)_a - \delta_2 X_2 \quad (2)$$

$$\dot{X}_3 = \tau_{13} X_3 \cdot f(X_3, X_2) \cdot f(X_1)_b - \delta_3 X_3 \quad (3)$$

Resource Controls

$$f(X_1)_a = \left[1 - \left(\frac{K_{12} - X_1}{K_{12} - \alpha_{12}}\right)_+\right]_+ \quad (4)$$

$$f(X_1)_b = \left[1 - \left(\frac{K_{13} - X_1}{K_{13} - \alpha_{13}}\right)_+\right]_+ \quad (5)$$

Space Control with Intraspecific Competition

$$f(X_2, X_3) = \left[1 - w_2\left(\frac{X_2 + \beta_3 X_3 - \alpha_2}{K_2 - \alpha_2}\right)_+\right]_+ \quad (6)$$

$$f(X_3, X_2) = \left[1 - w_3\left(\frac{X_3 + \beta_2 X_2 - \alpha_3}{K_3 - \alpha_3}\right)_+\right]_+ \quad (7)$$

Task 7.2.2: Modes of Control

When the system is *optimally enriched system* where $X_1 > K_{12}$ and K_{13}, the resource controls in equations (1–3) equal unity and effectively drop out of the equations. Thus, we can use graphical analysis to determine the *zero net growth isoclines* (ZNGI) to determine the possible behavior of the system when intra- and inter-specific competition for space are the determining modes of control.

Figure 5a shows the isoclines for the nominal parameters supplied for this exercise. This diagram suggests that X_3 will win the competition, regardless of the starting densities of X_2 or X_3. This is why the model cannot exhibit a locally stable state for both X_2 and X_3 when interference competition is the driving factor. We are not in the parameter space for the special case of intraspecific competition where the species coexist.

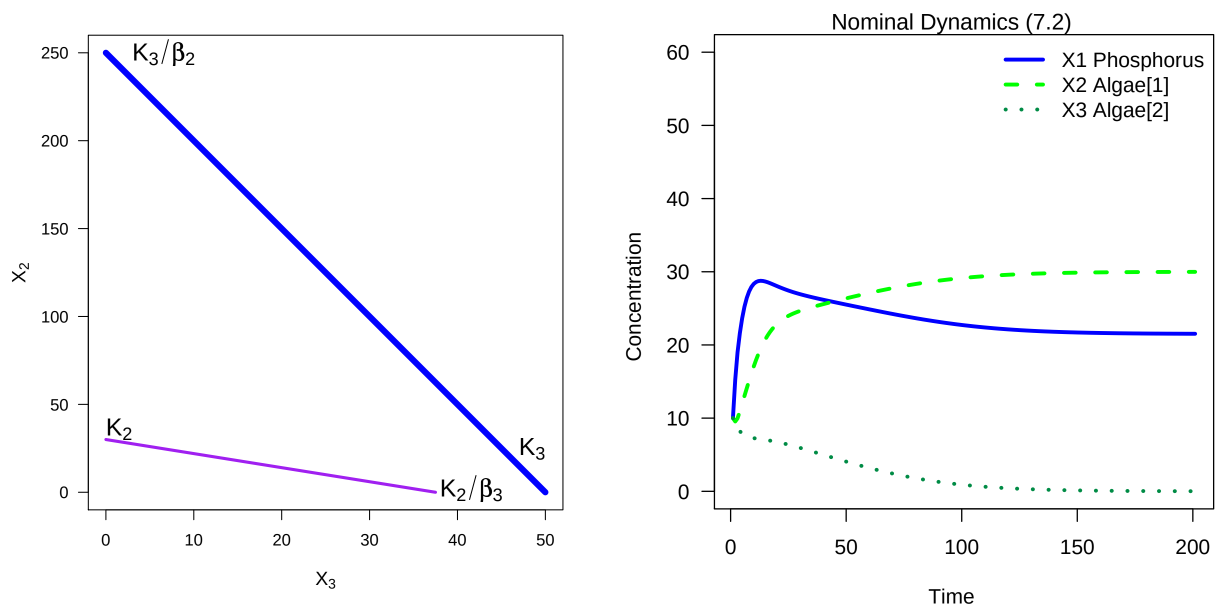

Figure 5: Nominal results of resource competition model. (a) Graphical analysis of resource competition system using nominal parameter values. (b) Nominal simulation.

Why does the isocline analysis prediction not match the nominal dynamics shown in Figure 5b? It does not match because the system is not optimally enriched, so the better exploitative competator wins (X_2, see Task 7.2.4).

Task 7.2.3: Algae Adaptations

The first algae (X_2) grows faster than the second (X_3) as reflected in the τ_{1j} values, but it is less tolerant to competition based on its lower carrying capacity and the larger coefficient of interspecific competition β_3. This implies that when there is plenty of resource, X_3 should win the competition. This is consistent with the isocline analysis shown in Figure 5a.

Task 7.2.4: Nominal Behavior

Figure 5b shows the nominal behavior of the model. Notice that the nominal dynamics do **NOT** match the predictions of the ZNGI analysis and consideration of the algae adaptations. This is because the system is not optimally enriched, so the phosphorus resource controls are active in the specified nominal dynamics.

To better understand the dynamics of the model, I explored the effect of changing the phosphorus enrichment rate (C_1), which is shown in Figure 6. Notice that when $C_1 < 9$, nutrient resources limit the growth of the algae. Further, X_2 has a competitive advantage in this situation because it can take up the phosphorus faster. When $C_1 \geq 9$, phosphorus is no longer limiting and X_3 wins because it is the superior competitor.

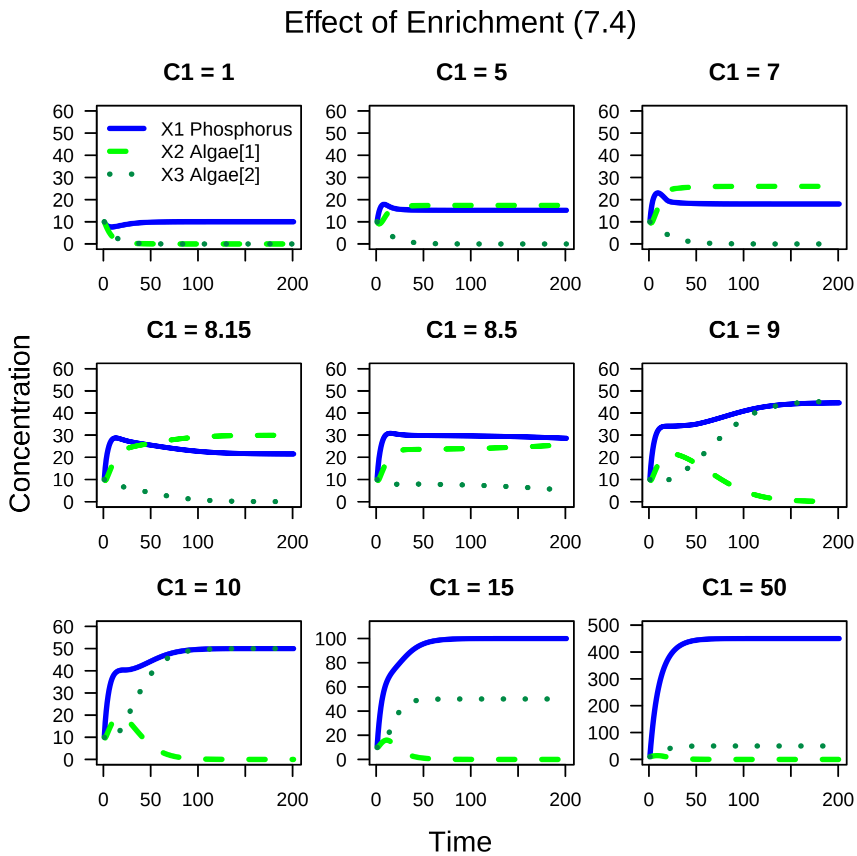

Figure 6: Dynamics of the prey competition model as enrichment C_1 increases.

Task 7.2.5: Experimentation

This was up to you to follow what you thought was interesting.

Appendix

7.1 Nominal Run

```
# Laboratory 7.1 -- Nominal Dynamisc
# Borrett, Nov. 2011
# this function contains the simplest case as well as some additional funcitonal responses
# ---------------------------------------------------------------------------
rm(list=ls())
library("deSolve")

# Model Function
model=function(t,state,parameters){
  with(as.list(c(state,parameters)), {
    # Aux. Var.
    fx1<-pmax(0,(1-pmax(0, (K12-X1)/(K12-alpha12)) )); # resource control

    wc2<- (1-delta2/tau12)
    fx2a<-pmax(0,(1-wc2*pmax(0,(X2-alpha2)/(K2-alpha2) ))); # space control
    fx2b<-pmax(0,(1-pmax(0,(K23-X2)/(K23-alpha23)))); # resource control

    wc3<- (1-delta3/tau23)
    fx3<-pmax(0,(1-wc3*pmax(0,(X3-alpha3)/(K3-alpha3)))); # space control

    phi1 = tau12 * X2 * fx1 * fx2a;
    phi2 = tau23 * X3 * fx3 * fx2b;

    # Diff Eqs.
    dX1 =  C1 - delta1 * X1 - phi1;
    dX2 =  phi1 - phi2 - delta2 * X2
    dX3 =  phi2 - delta3*X3

    return(list(c(dX1,dX2,dX3)))
  })
}

tspan=seq(0,50,by=1)
#
state = c(X1=10,
  X2=10,
  X3=10)
#
parameters = c(C1 = 5,        # enrichment rate
  delta1 =  0.1,  # max specific loss rate
  K1 =      0 ,   # carrying capcity
  alpha12 = 5,    #
    # species 2: Algae
  tau12 =   0.35,    # max consumption rate
  eps12 =   0,        # fraction egested
  delta2 =  0.1,      # max specific loss rate
  K2 =      70,       # carrying capacity
  alpha2  = 20,       # threshold reponse density of X2
  K12     = 20,       # satiation concentration of X2 on X1
  alpha23 = 5,       # Refuge of X2 from X3
```

```
    # species 3: Daphnids
  tau23 =   0.5,     # max consumption rate
  eps23 =   0,       # fraction egested
  delta3 =  0.2,     # max specific loss rate
  K3 =      30,      # carrying capacity
  alpha3  = 10,       # threshold reponse density of X2
  K23     = 20)       # satiation concentration of X2 on X1

out <- ode(state,times=tspan,func=model,parms=parameters)

### --- PLOT --- ####
fn <- "T71-nominal.pdf"
pdf(fn,height=5,width=5)
opar <- par(las=1,mar=c(4,4,1,1),oma=c(0,0,2,0))
#
matplot(out[,2:4],type="l",col=c("blue","green","red"),
        ylim=c(0,20),lty=c(1,2,3),lwd=2,
        xlab="Time",ylab="Concentration",
        )
legend("bottomright",legend=c("X1 Phosphorus","X2 Algae","X3 Daphnids"),
       lty=1:3,col=c("blue","green","red"),bty="n",lwd=2)
mtext("Nominal Dynamics (7.1)",side=3,line=0,outer=TRUE,cex=1.1)
#
dev.off()
cmd <- paste("open",fn)
system(cmd)
```

7.2 Nominal Run

```
# Laboratory 7.2 -- Nominal Dynamics
# Borrett, Nov. 2011
# this function contains the simplest case as well as some additional funcitonal responses
# ----------------------------------------------------------------------------
rm(list=ls())
library("deSolve")

# Model Function
model=function(t,state,parameters){
  with(as.list(c(state,parameters)), {

    # CONTROL EQUATIONS (Algebraic)
    fx1a = pmax(0, (1 - pmax(0, (K12 - X1)/(K12 - alpha12)))); # RESOURCE CONTROL
    fx1b = pmax(0, (1 - pmax(0, (K13 - X1)/(K13 - alpha13)))); # RESOURCE CONTROL

    w2 <- (1-delta2/tau12)
    fx2x3 = pmax(0, (1 - w2 * pmax(0,(X2 + beta3*X3 -alpha2)/(K2 - alpha2)))); # SPACE CONTROL
    w3 <- (1-delta3/tau13)
    fx3x2 = pmax(0, (1 - w3 * pmax(0,(X3 + beta2*X2 -alpha3)/(K3 - alpha3)))); # SPACE CONTROL

# PROCESS EQUATIONS (Algebraic)
    enrichment = C1;
    Loss1 =      delta1 * X1;
    Uptake12 =   tau12 * X2 * fx2x3 * fx1a;
    Loss2 =      delta2 * X2;
```

```
    Uptake13 =   tau13 * X3 * fx3x2 * fx1b;
    Loss3 =      delta3 * X3;

  # equations (ODE)
    dX1 =  enrichment - (Loss1 + Uptake12 + Uptake13);
    dX2 =  Uptake12 - Loss2;
    dX3 =  Uptake13 - Loss3;

    return(list(c(dX1,dX2,dX3)))
  })
}

tspan=seq(0,200,by=1)
#
state = c(X1=10,
  X2=10,
  X3=10)
#
parameters = c(C1 = 8.15,        # enrichment rate
  tau12 =   0.35,    # max consumption rate
  tau13 =   0.2,     # max consumption rate
  delta1 =  0.1,  # max specific loss rate
  delta2 =  0.2,      # max specific loss rate
  delta3 =  0.1,     # max specific loss rate
  K12     = 20,       # satiation concentration of X2 on X1
  K13     = 50,       # satiation concentration of X2 on X1
  K2 =      30,       # carrying capacity
  K3 =      50,      # carrying capacity
  alpha12 = 5,    #
  alpha13 = 10,       # Refuge of X2 from X3
  alpha2  = 10,       # threshold reponse density of X2
  alpha3  = 20,       # threshold reponse density of X2
  beta2 = 0.2,
  beta3 = 0.8)

out <- ode(state,times=tspan,func=model,parms=parameters)

### --- PLOT --- ####
fn = "../results/plot-L7t2-nominal.pdf"
pdf(fn,height=5,width=5)
opar <- par(las=1,mar=c(2,2,0,1),oma=c(2,2,2,0))
#
matplot(out[,2:4],type="l",col=c("blue","green","springgreen4"),
        ylim=c(0,max(60,out[,2]*1.1)),lty=c(1,2,3),lwd=3,
        xlab="Time",ylab="Concentration",
#        main=paste("C1 =",p.vec[i]),
        )
legend("topright",legend=c("X1 Phosphorus","X2 Algae[1]","X3 Algae[2]"),
       lty=1:3,col=c("blue","green","springgreen4"),bty="n",lwd=3)
mtext("Nominal Dynamics (7.2)",side=3,line=0,outer=TRUE,cex=1.1)
mtext("Time",side=1,line=1,outer=TRUE,cex=1)
mtext("Concentration",side=2,line=0.75,las=3,outer=TRUE,cex=1)
#
dev.off()
```

```
cmd <- paste("open",fn)
system(cmd)
```