Are ecosystem structures driven by maximizing resilience?

The reconstruction of food web fluxes provides information regarding ecosystem structure and energy transport through the system. Complex ecosystems are often simplified by compartmentalizing the system into trophic groups and studying the relationship among groups around equilibrium state. Optimization techniques have been used extensively to reconstruct food web fluxes by minimizing a measure of the system's performance. A widely used measure has been the sum of squared fluxes. However this does not have an obvious ecological basis. As an alternative we propose to maximize system resilience. Resilience is defined here as a measure of the rate at which a system returns to equilibrium state following a perturbation.

The basic structure of an ecosystem can be modeled using the concept of a food web and explored by methods which aim to quantify either energy or mass transport among species in the community (Vezina & Platt, 1988; Ulanowicz, 1989; Christensen & Pauly, 1992). Such a system can be described by a set of mass-balance equations that define the interactions between all compartments in the community at steady state. The interactions can then be constrained to lie within known bounds determined from observational data. Numerical techniques can then be used to find the solution that optimizes the desired component of the system's performance as measured by an appropriate objective function. Vezina & Platt (1988) adopted an objective function, (following Wunsch's (1978) application to problems in physical oceanography) that minimizes the sum of squared food web fluxes. This objective function has since been used widely in ecological food web modeling and was chosen based on its use in physical oceanography. However, Wunsch (1978) stated that the objective function was chosen partly for its parsimony rather than its scientific relevance. We present an alternative objective function which relates to the dynamics of the modeled system. The idea is linked to the concept of stability and a system's dynamical behavior following a perturbation. A system's response to perturbations can be characterized quantitatively by resilience (Pimm & Lawton, 1977) which measures the rate at which perturbations to a system, around equilibrium, decay.

Considering a general dynamic linear ecosystem model consisting of m trophic groups $\mathbf{X}(t) = \{X_1(t),...X_m(t)\}$ each with an unknown nitrogen content $X_i(t)$, $(i = 1,...,m)$. The dynamics of this simplified ecosystem model are described by the set of m rate equations in matrix notation as,
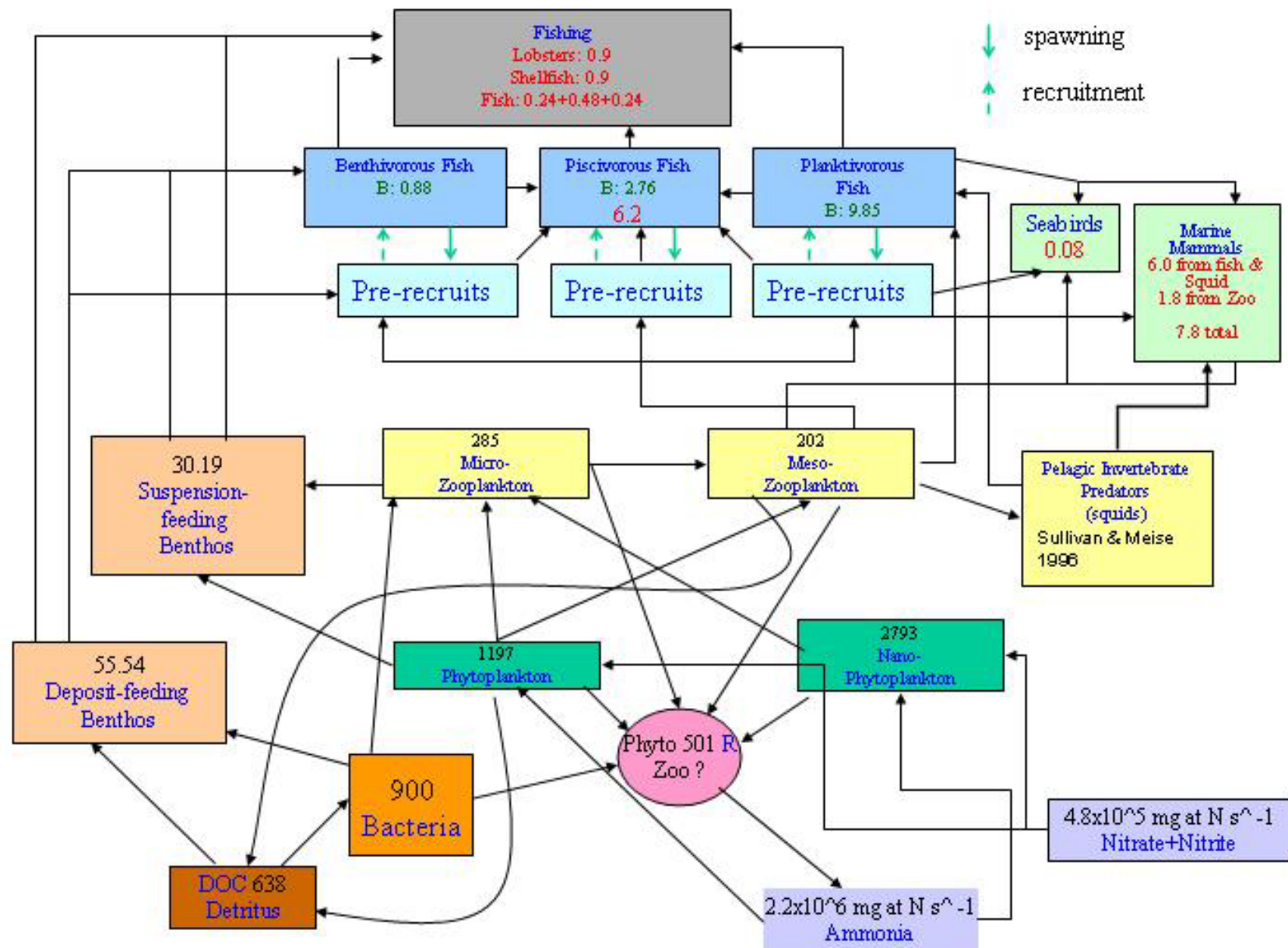
$$\frac{d\mathbf{X}(t)}{dt} = \mathbf{AX}(t) + \mathbf{k} \qquad 1$$

where $\mathbf{A}$ is an m by m matrix whose elements a_{ij} are the coefficients of the mass balance equations. As (1) is a linear system, $\mathbf{A}$ can also be interpreted as the community matrix where a_{ij} describe the effect of group j upon group i near equilibrium (May, 1973). $\mathbf{k}$ is a vector of known external net input/output terms. Resilience defined as

$$\text{Resilience} = -\operatorname{Re}(\lambda_1(\mathbf{A})) \qquad 2$$

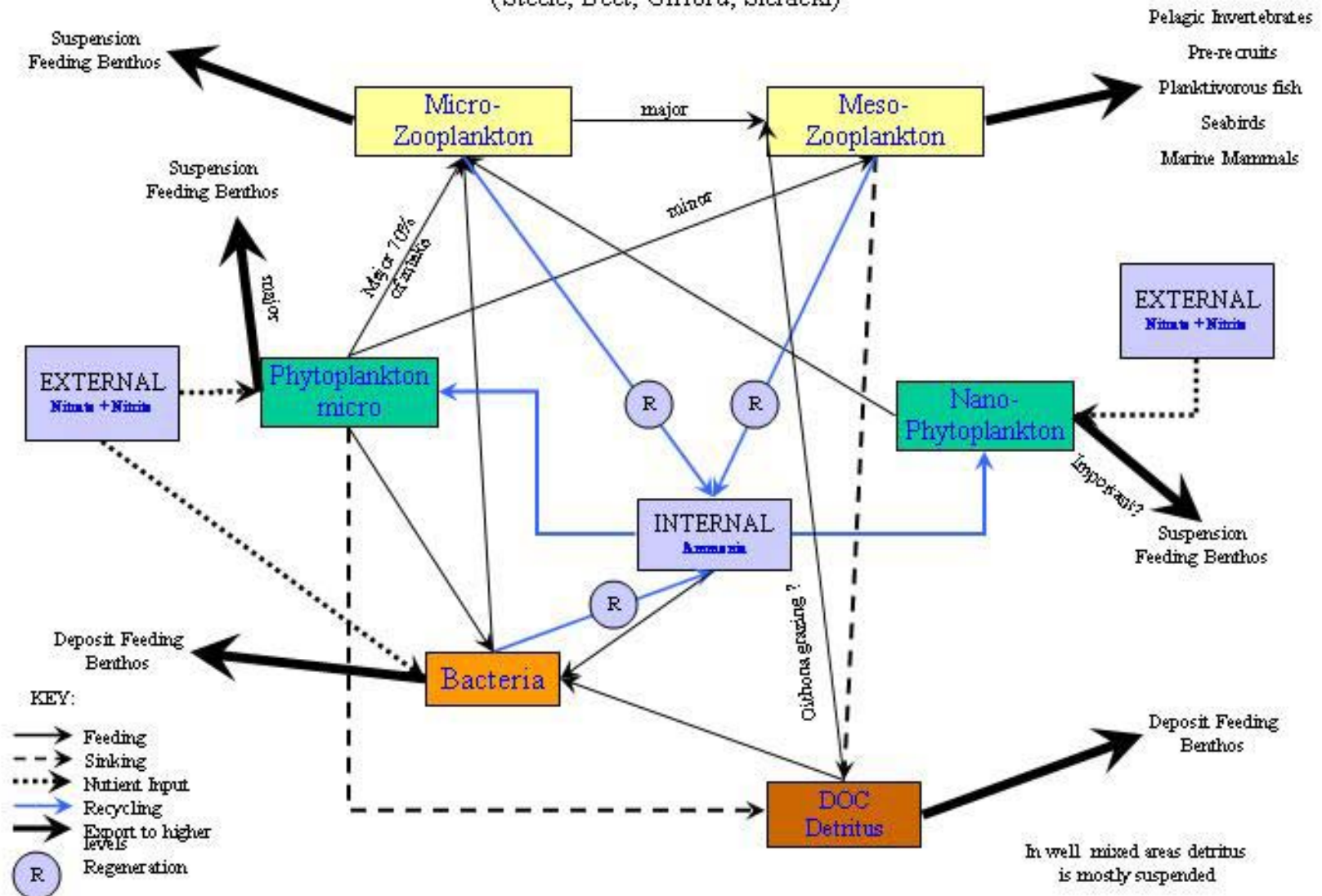is an asymptotic approximation of the decay rate of perturbations to (1) where λ_1 is the dominant eigenvalue of the community matrix, $\mathbf{A}$ and $\operatorname{Re}(\cdot)$ is the real part of the eigenvalue, λ_1. Maximizing resilience is equivalent to minimizing the real part of the dominant eigenvalue of the matrix, $\mathbf{A}$. The larger the resilience, the faster the perturbations decay.
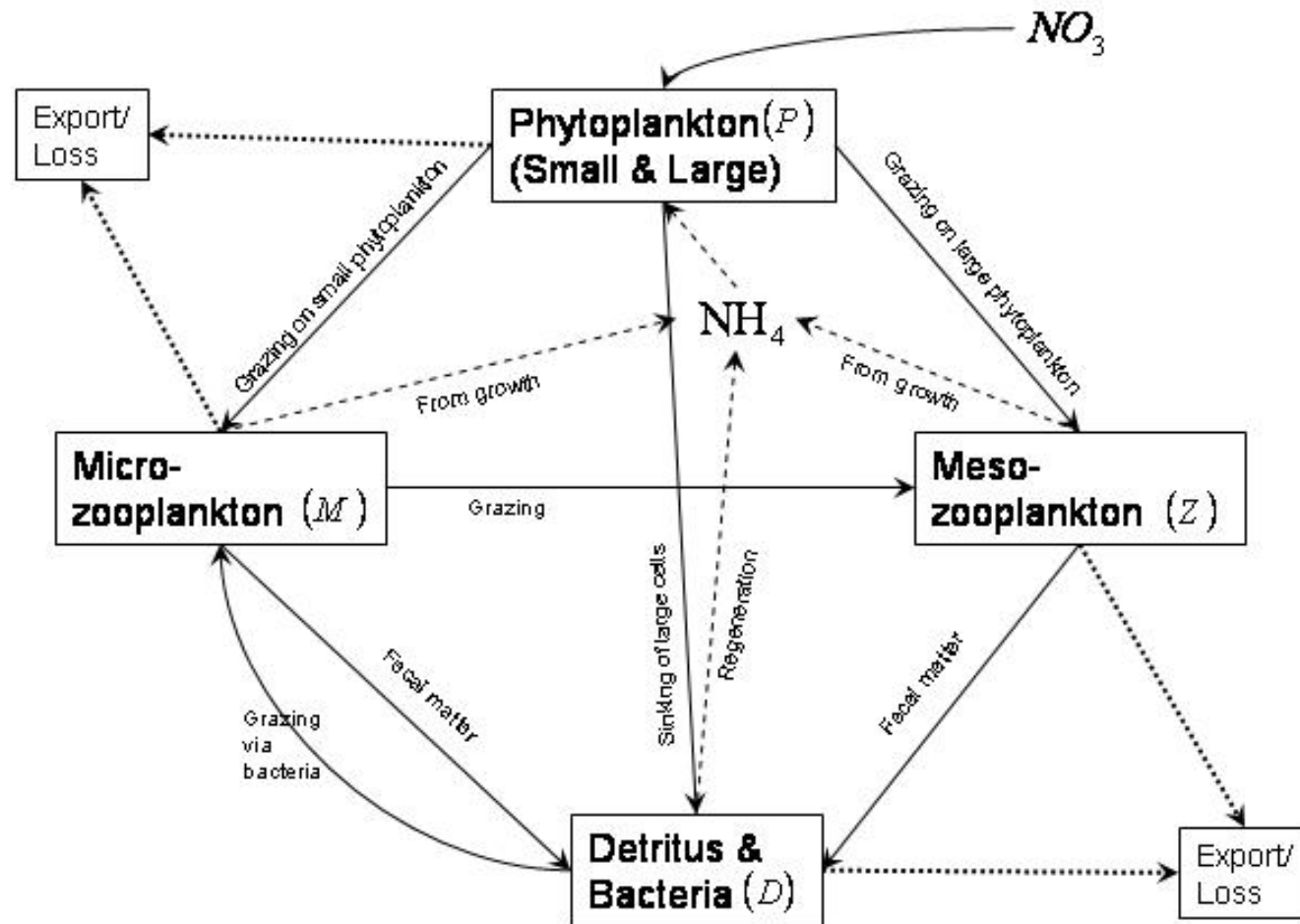
Georges Bank food web

Fishing
Lobsters: 0.9
Shellfish: 0.9
Fish: 0.24+0.48+0.24

↓ spawning
↑ recruitment

Benthivorous Fish B: 0.88

Piscivorous Fish B: 2.76 — 6.2

Planktivorous Fish B: 9.85

Seabirds 0.08

Marine Mammals 6.0 from fish & Squid 1.8 from Zoo — 7.8 total

Pre-recruits

Pre-recruits

Pre-recruits

30.19 Suspension-feeding Benthos

285 Micro-Zooplankton

202 Meso-Zooplankton

Pelagic Invertebrate Predators (squids) Sullivan & Meise 1996

55.54 Deposit-feeding Benthos

1197 Phytoplankton

2793 Nano-Phytoplankton

900 Bacteria

Phyto 501 R Zoo ?

4.8x10^5 mg at N s^-1 Nitrate+Nitrite

DOC 638 Detritus

2.2x10^6 mg at N s^-1 Ammonia

Microbial Part of Food web

(Steele, Beet, Gifford, Sieracki)

Suspension Feeding Benthos

Pelagic Invertebrates
Pre-recruits
Planktivorous fish
Seabirds
Marine Mammals

Micro-Zooplankton

major

Meso-Zooplankton

Suspension Feeding Benthos

minor

Major 70% estimate

EXTERNAL
Nitrate + Nitrite

Phytoplankton micro

R   R

Nano-Phytoplankton

EXTERNAL
Nitrate + Nitrite

major

INTERNAL
Ammonia

Important?

Suspension Feeding Benthos

Oithona grazing ?

R

Deposit Feeding Benthos

Bacteria

KEY:

Deposit Feeding Benthos

→ Feeding
⇢ Sinking
····▸ Nutrient Input
→ Recycling
➤ Export to higher levels
Ⓡ Regeneration

DOC Detritus

In well mixed areas detritus is mostly suspended

Simplified Microbial Loop
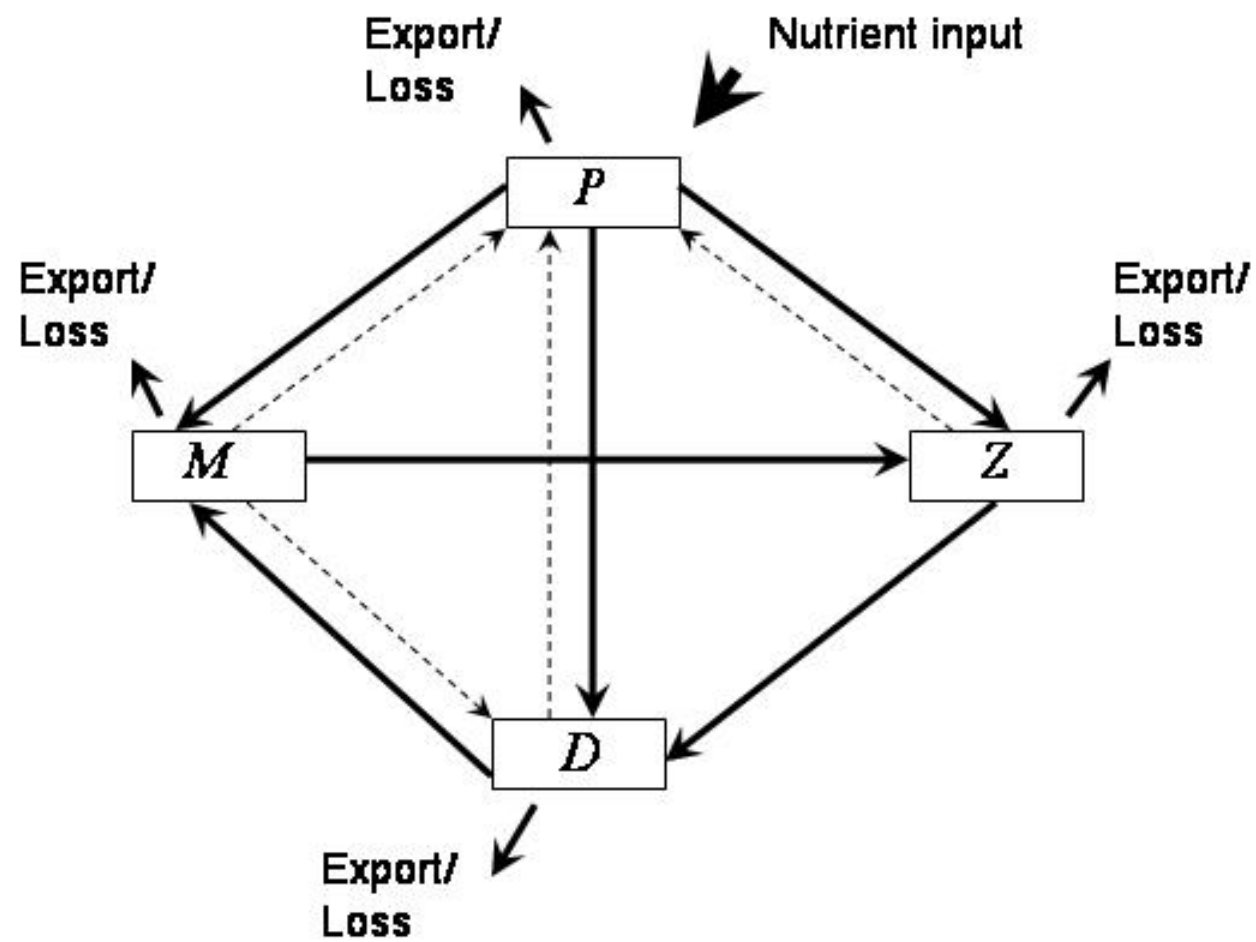
The food web we present consists of $m = 4$ trophic groups and is described at equilibrium by the m mass balance equations,
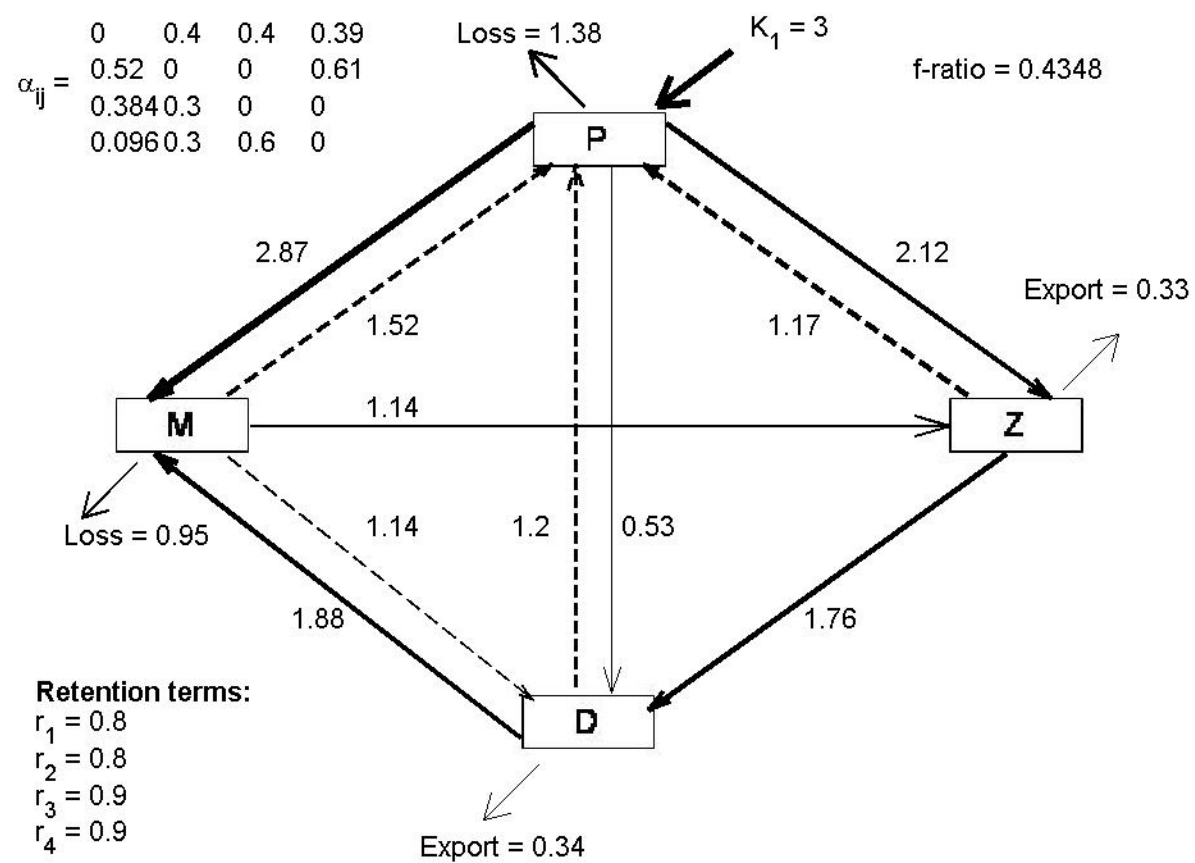
$$\frac{dP}{dt} = r_1\left(\alpha_{12}M + \alpha_{13}Z + \alpha_{14}D + k_1\right) - P\sum_{k=1}^{m}\alpha_{k1} = 0$$

$$\frac{dM}{dt} = r_2\left(\alpha_{21}P + \alpha_{24}D\right) - M\sum_{k=1}^{m}\alpha_{k2} = 0$$

$$\frac{dZ}{dt} = r_3\left(\alpha_{31}P + \alpha_{32}M\right) - Z\sum_{k=1}^{m}\alpha_{k3} = 0$$

$$\frac{dD}{dt} = r_4\left(\alpha_{41}P + \alpha_{42}M + \alpha_{43}Z\right) - D\sum_{k=1}^{m}\alpha_{k4} = 0$$

subject to the constraints $\quad l_{\alpha_{ij}} < \alpha_{ij} < u_{\alpha_{ij}}, \quad \sum_{i=1}^{m}\alpha_{ij} = 1, \text{ and } l_{r_{ij}} < r_i < u_{r_{ij}}$
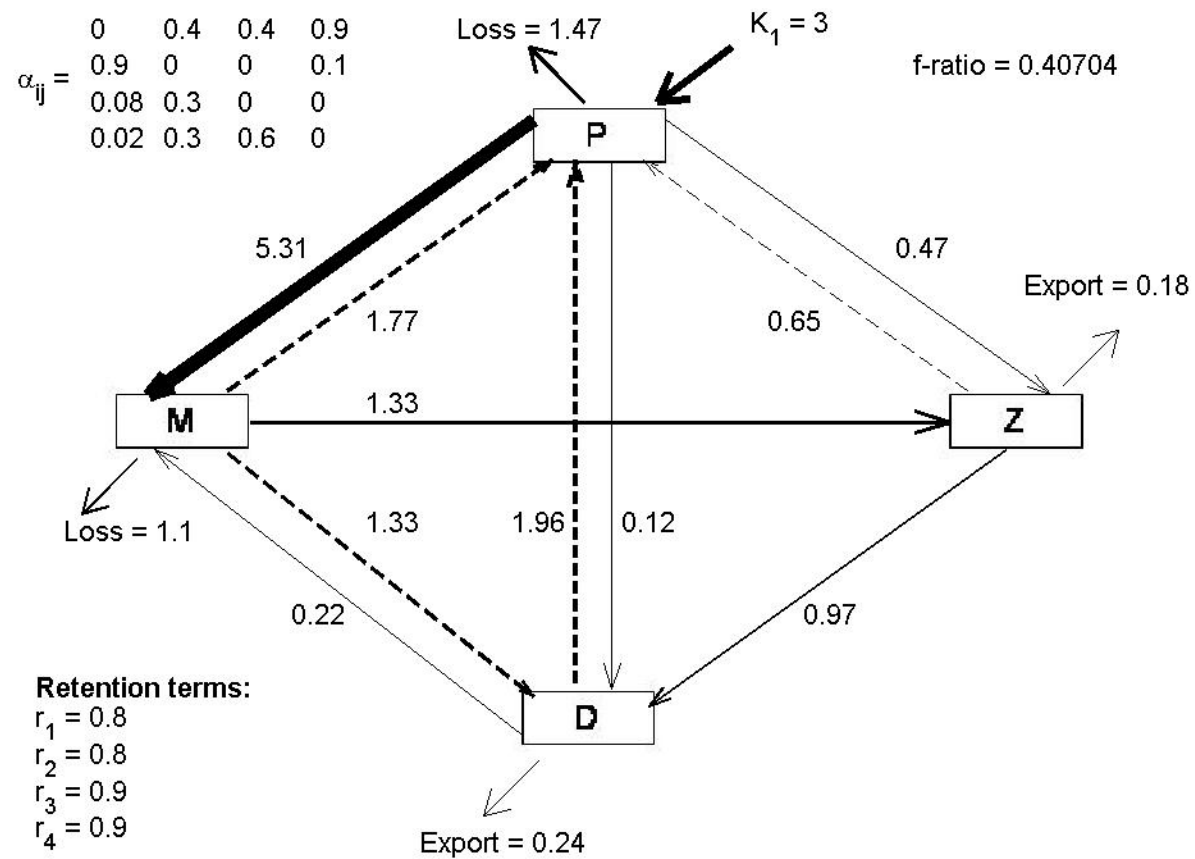
where α_{ij} represents the proportion of nitrogen that flows from trophic group j to trophic group i and r_i represents the proportion of nitrogen retained in the system by group i and is equivalent to ecological efficiency in higher trophic systems.

The following figures show the reconstructed food web fluxes using both objective functions (sum of squared flows and resilience) for representations of well mixed, stratified, and sporadically stratified systems.
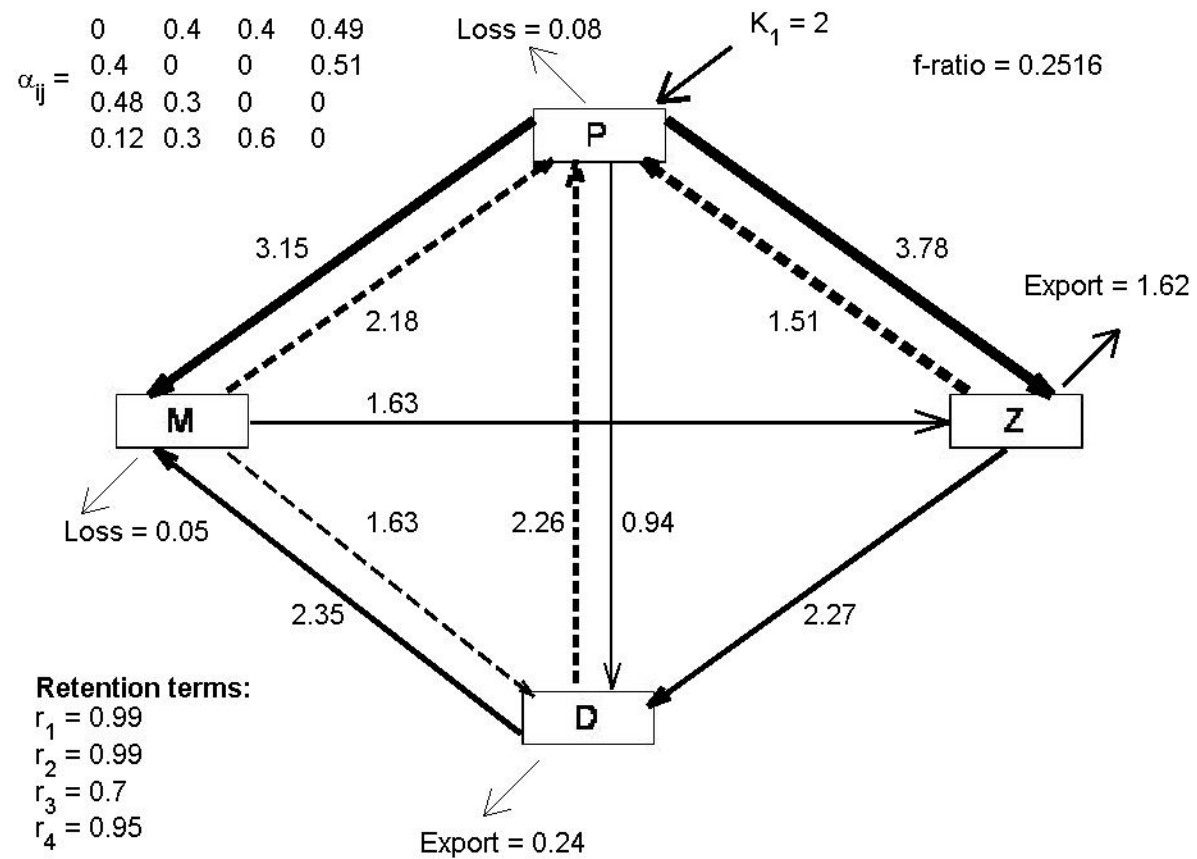
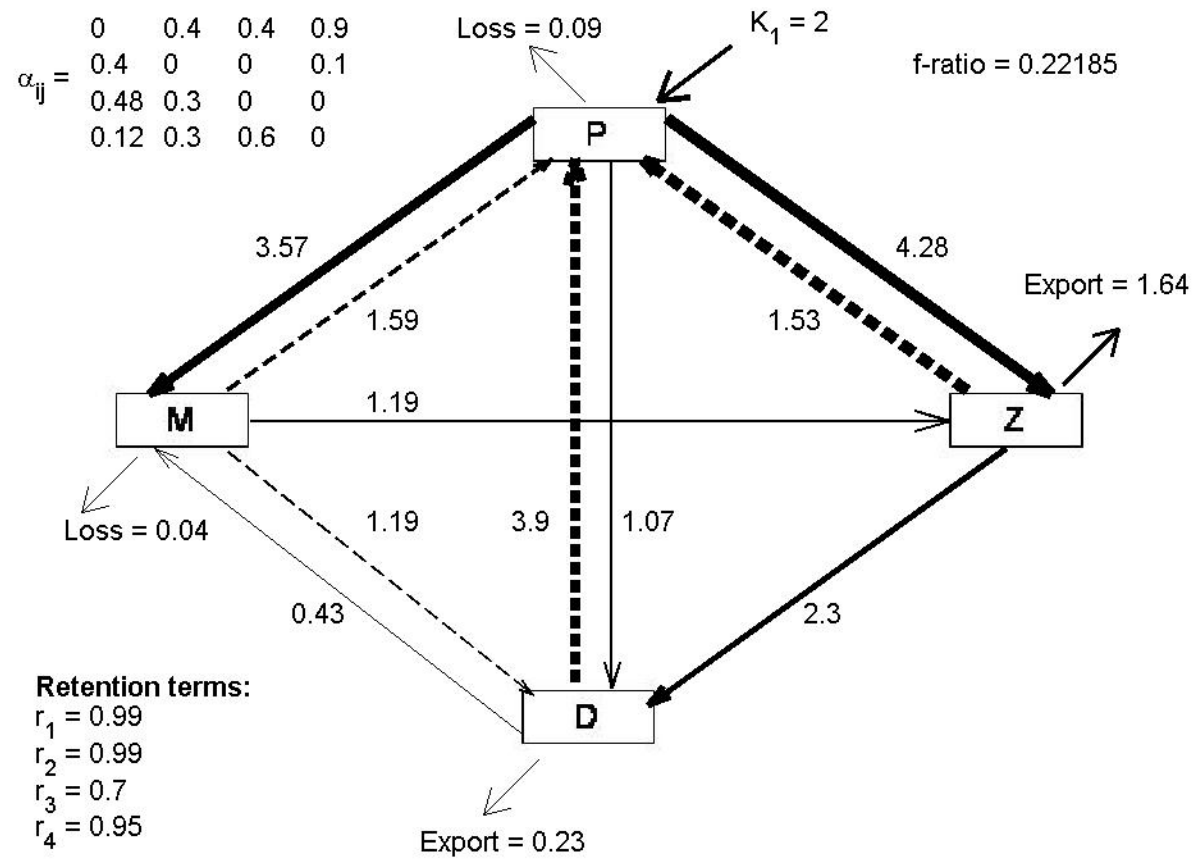# Well mixed system optimizing for the sum of squared fluxes

$$\alpha_{ij} = \begin{matrix} 0 & 0.4 & 0.4 & 0.39 \\ 0.52 & 0 & 0 & 0.61 \\ 0.384 & 0.3 & 0 & 0 \\ 0.096 & 0.3 & 0.6 & 0 \end{matrix}$$

Loss = 1.38

$K_1 = 3$

f-ratio = 0.4348

P

2.87

1.52

2.12

Export = 0.33

1.17

M

1.14

Z

Loss = 0.95

1.14

1.2

0.53

1.88

1.76

Retention terms:
$r_1 = 0.8$
$r_2 = 0.8$
$r_3 = 0.9$
$r_4 = 0.9$

D

Export = 0.34

Well mixed system optimizing for resilience

Stratified system optimizing for the sum of squared fluxes

$$\alpha_{ij} = \begin{matrix} 0 & 0.4 & 0.4 & 0.49 \\ 0.4 & 0 & 0 & 0.51 \\ 0.48 & 0.3 & 0 & 0 \\ 0.12 & 0.3 & 0.6 & 0 \end{matrix}$$

Loss = 0.08

$K_1 = 2$

f-ratio = 0.2516

P

3.15

3.78

Export = 1.62

2.18

1.51

M

1.63

Z

Loss = 0.05

1.63

2.26

0.94

2.35

2.27

Retention terms:
$r_1 = 0.99$
$r_2 = 0.99$
$r_3 = 0.7$
$r_4 = 0.95$
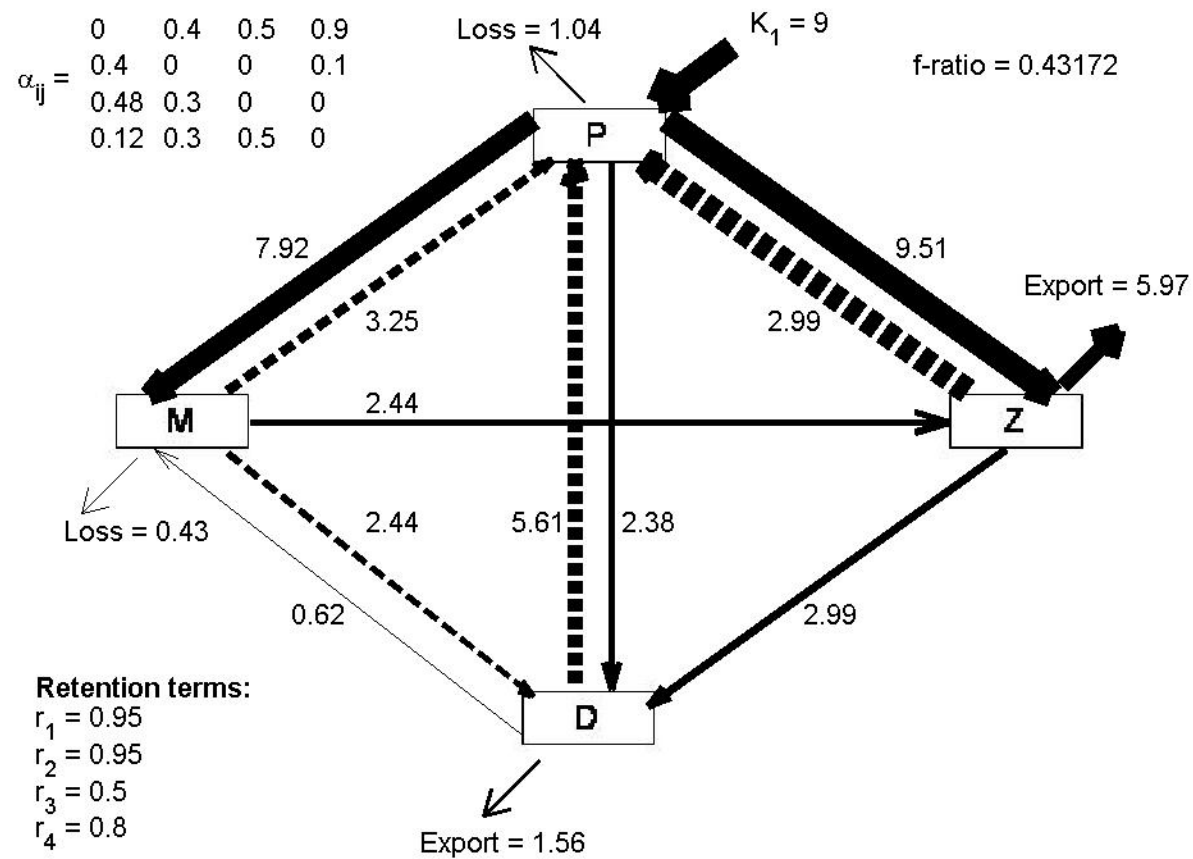
D

Export = 0.24

Stratified system optimizing for resilience

Sporadically stratified system optimizing for the sum of squared fluxes

$$\alpha_{ij} = \begin{matrix} 0 & 0.4 & 0.5 & 0.38 \\ 0.4 & 0 & 0 & 0.62 \\ 0.48 & 0.3 & 0 & 0 \\ 0.12 & 0.3 & 0.5 & 0 \end{matrix}$$

Loss = 0.93

$K_1 = 9$

f-ratio = 0.48156

P

7.1

8.52

Export = 5.86

4.25

2.93

M

3.19

Z

Loss = 0.56

3.19

2.51

2.13

4.09

2.93

Retention terms:
$r_1 = 0.95$
$r_2 = 0.95$
$r_3 = 0.5$
$r_4 = 0.8$

D

Export = 1.65
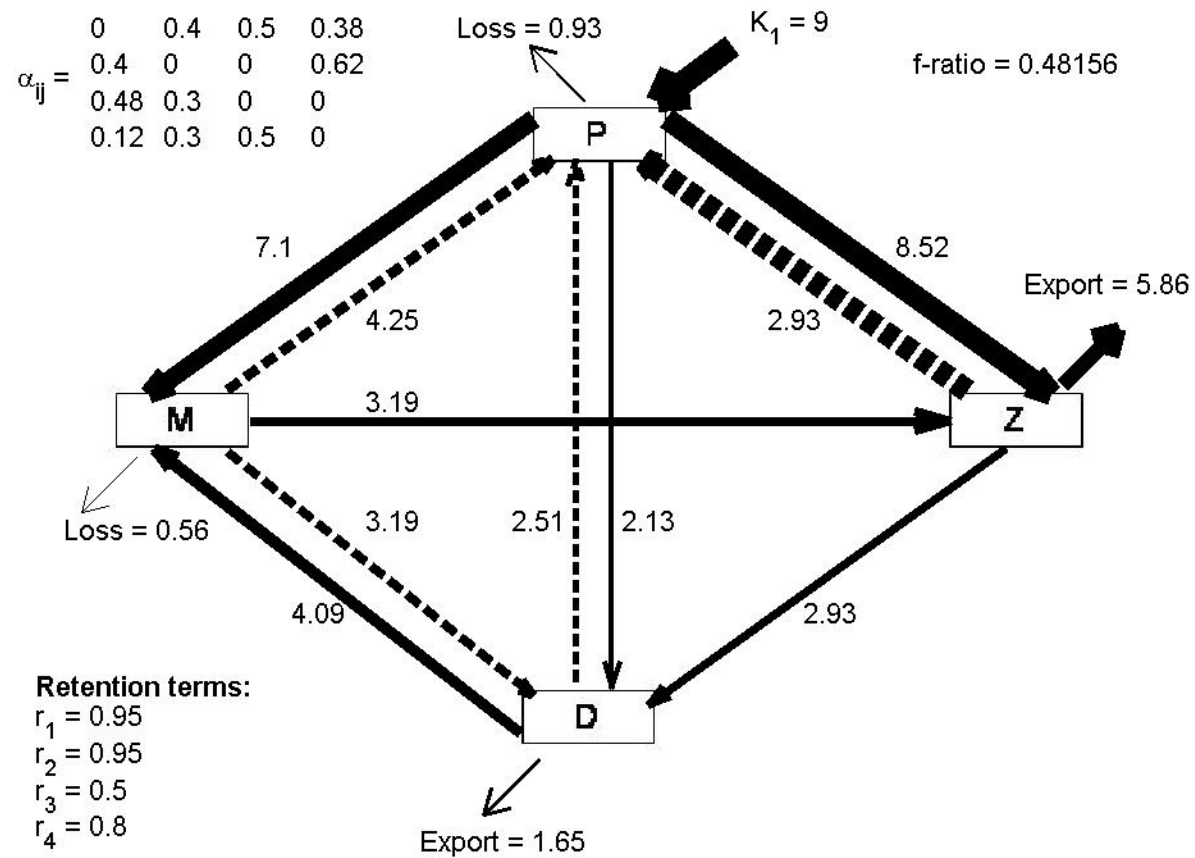
Sporadically stratified system optimizing for resilience

Summary

The immediate conclusion from this study is that the choice of the objective function plays a critical role in the behavior of this simple food web, illustrating that some thought must be given to the selection of an ecologically appropriate objective function. Although optimizing for the sum of squared flows is mathematically and computationally straightforward it has no apparent ecological basis. For the simple model we present, the sum of squared flows objective function does not seem to be able to capture the differences between the stratified and the well mixed systems as would have been expected. Conversely when optimizing for resilience, which is based on the dynamics of the system, the modeled stratified and well mixed systems are reflected in the reconstructed food webs.

Recent interest has been directed toward systems undergoing regime shifts, the concept that an ecosystem may switch from one state to another as a result of external forcing (Collie et al, in press). Systems undergoing regime shifts will therefore occupy alternative stable states. Optimizing for resilience may turn out to be a useful tool in determining the location of these alternate stable states.

References

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