# Evaluating the Role of Top-down vs. Bottom-up Ecosystem Regulation from a Modeling Perspective

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# Background

- Relative roles of top down vs. bottom up regulation of marine ecosystems is a common topic of scientific discussion but the resolution of the question remains elusive.
- Field-based studies to establish the importance of these two processes are a difficult undertaking given the complexity of even the smallest marine ecosystem.
- More difficult in continental shelf and open ocean domains where the ecosystems are not generally isolated.
- Idea of this presentation is to examine the available modeling tools that describe these types of controls.

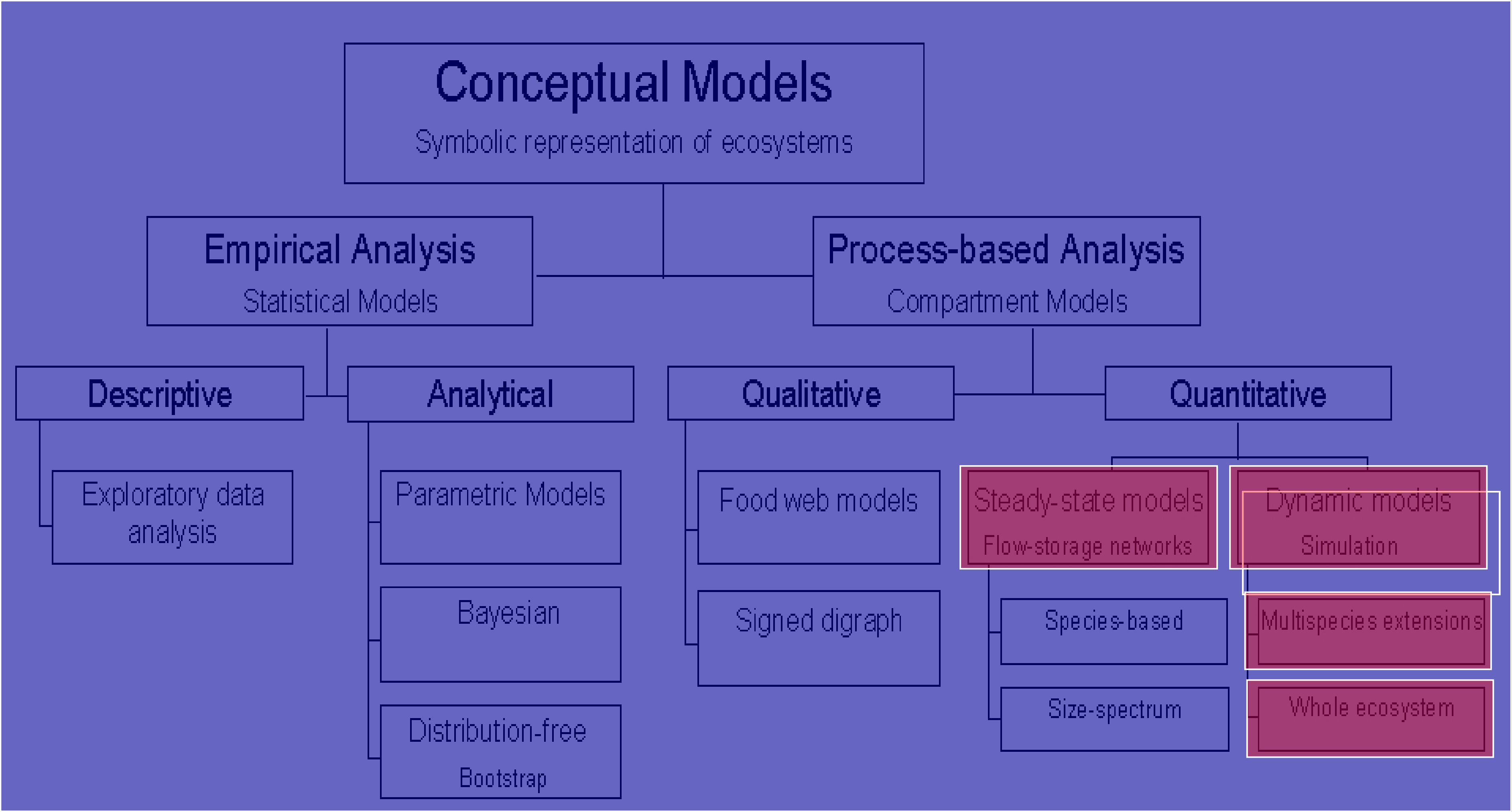
# Objective

- Evaluate present-day modeling capabilities which could help identify or describe if a marine ecosystem is controlled top-down or bottom-up.
- Consider modeling approaches based on the detail in which they describe the dynamics of marine ecosystems.

# Overview

- Model taxonomy
- Definitions
- Modeling Approaches
  - Advantages/disadvantages
  - Ways to parameterize TD-BU control
- Conclusions/Summary

# Model Taxonomy



Conceptual Models

Symbolic representation of ecosystems

Empirical Analysis

Statistical Models

Process-based Analysis

Compartment Models

Descriptive

Exploratory data analysis

Analytical

Parametric Models

Bayesian

Distribution-free

Bootstrap

Qualitative

Food web models

Signed digraph

Quantitative

Steady-state models

Flow-storage networks

Species-based

Size-spectrum

Dynamic models

Simulation

Multispecies extensions

Whole ecosystem

*Whipple et al. 2000. Fish and Fisheries*

# Operational Definitions

## Bottom Up

- if the change in the biomass of a group or functional group is dominated by production, then the group likely to be bottom-up controlled.
  - Agent: resource availability/limitation (i.e. physical and chemical factors such as temperature and nutrients)

## Top Down

- if the change in the biomass of a group or functional group is dominated by removals, then the group is likely to be top-down controlled.
  - Agent: Competition and predation by higher trophic levels on lower levels.

# Ecopath

$$B_i \left( \frac{P}{B} \right)_i EE_i = BA_i + E_i + Y_i + \sum_{j=1}^{n} B_j \left( \frac{Q}{B} \right)_j DC_{ji}$$

Static, balanced mass balance equation

B – biomass

P/B$^*$ – production to biomass ratio

Q/B* – consumption to biomass ratio

DC* – fraction of prey in diet

EE* – ecotrophic efficiency

Know any three and estimate the unknown

BA – biomass accumulation rate

Y – fisheries catch

E – net migration rate (emigration-immigration)

# Ecopath Pros/Cons

**Advantages**

- has to balance – provides information on data gaps
- conceptually simple
- easy-to-use software facilitates use and exploration

**Disadvantages**

- assumes ecosystem networks are static
- assumes steady state
- very limited ability to accommodate detailed mechanisms
- difficult or impossible to estimate many parameters from field or lab data

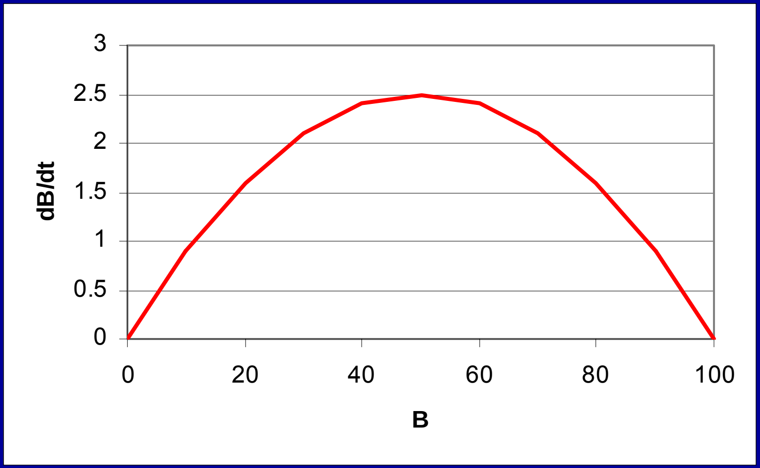
# Production Models

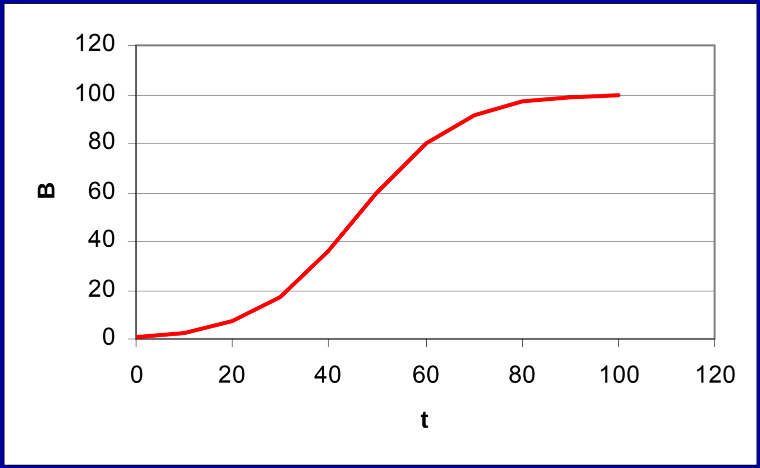
$$\frac{dB}{dt} = rB\left(1 - \frac{B}{K}\right)$$

Schaefer Production Model

Logistic Model

● Bottom Up Parameters





# Production Model with Yield

$$\frac{dB}{dt} = rB\left(1-\frac{B}{K}\right) - C$$

🔵 Bottom Up Parameters

🔴 Top Down Parameters

# Production Model with Mutispecies Interactions and Yield

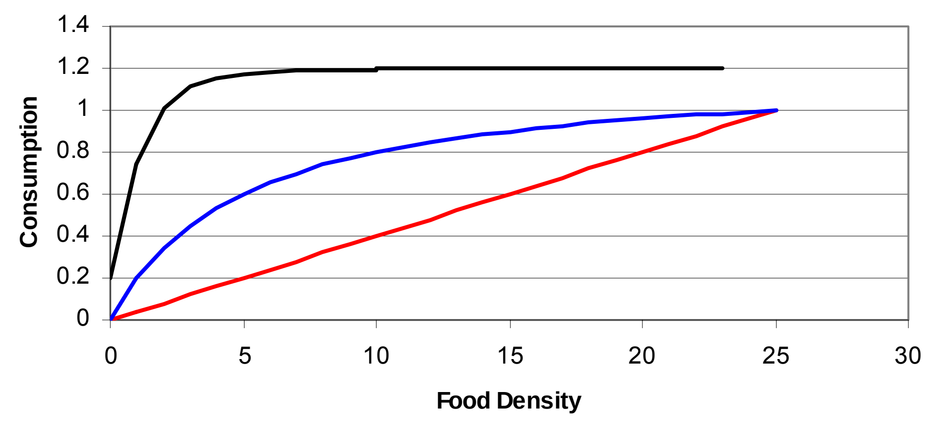
$$\frac{dB_1}{dt} = rB_1\left(1-\frac{B_1}{K}\right) \pm cB_2 \pm dB_3 - C_1$$

- If $B_1$ is a prey and $B_2$ is a predator then c will be negative
- $B_1$ is a predator and $B_2$ is the prey then c will be positive
- If $B_3$ is a competitor of $B_1$ then d will be negative

🔵 Bottom Up Parameters

🔴 Top Down Parameters

# Predator Functional Response



Holling I $f(B) = \alpha B$

Holling II $f(B) = \dfrac{\alpha B}{\beta + B}$

Holling III $f(B) = \dfrac{\alpha B^{\gamma}}{\beta + B^{\gamma}}$

Ecological Features

- Search time
- Probability of capture
- Suitability of each prey item to predator
- Time lags to constrain predation to specific life stages

# Multispecies Interactions

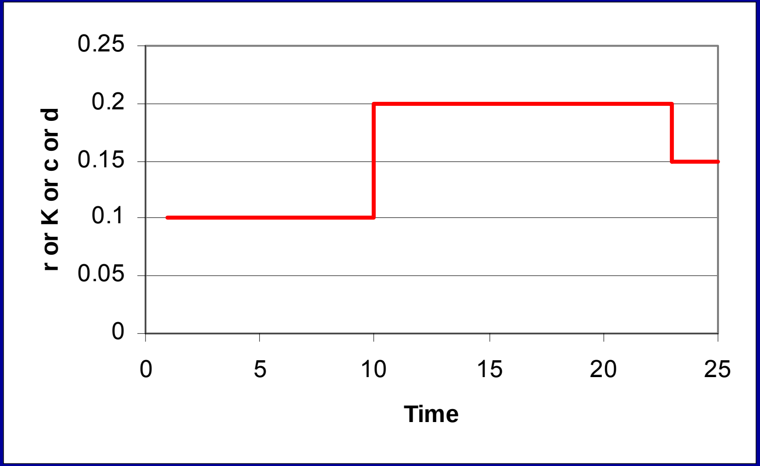
| **Interaction** | ***Species i*** | ***Species j*** |
|---|---|---|
| Competition | - | - |
| Predator-Prey | + | - |
| Mutualism | + | + |
| Commensalism | + | 0 |

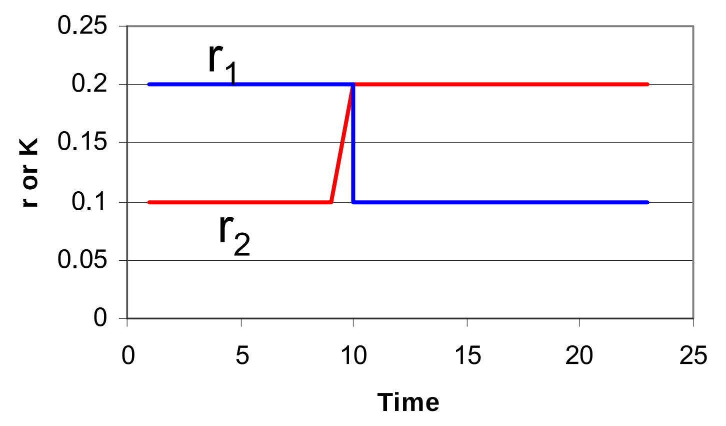
-: Negative effect, +: positive effect, 0: no effect

# Production Model with Mutispecies Interactions, Yield, and Environmental Effects

$$\frac{dB_1}{dt} = rB_1\left(1 - \frac{B_1}{K}\right) \pm cB_2 \pm dB_3 - C_1$$

Time-dependent parameter values





# Control of a Marine Food Web: An Example

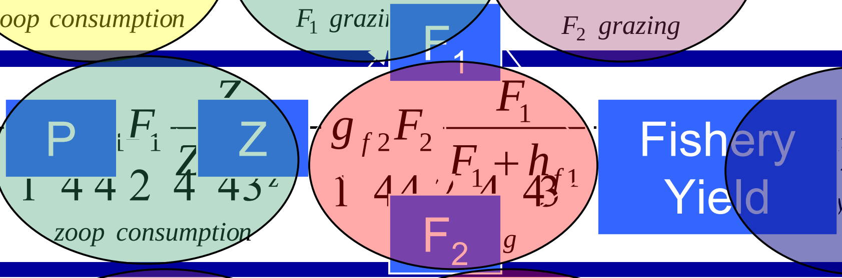
$$\frac{dP}{dt} = \underbrace{r_p P(1-\frac{P}{K_p})}_{\text{DD production}} - \underbrace{g_z Z \frac{P}{P+h_a}}_{\text{zoop grazing}}$$

$$\frac{dZ}{dt} = \underbrace{r_z Z(1-\frac{Z}{K_z})}_{\text{DD production}} + \underbrace{e_z g_z Z \frac{P}{P+h_a}}_{\text{zoop consumption}} - \underbrace{g_{f1} F_1 \frac{Z}{Z+h_z}}_{F_1 \text{ grazi}} - \underbrace{g_{f2} F_2 \frac{Z}{Z+h_z}}_{F_2 \text{ grazing}} - \underbrace{m_z Z}_{\text{mortality}}$$

$$\frac{dF_1}{dt} = \underbrace{r_{f1} F_1(1-\frac{F_1}{K_{f1}})}_{\text{DD production}} + \underbrace{e_{f1} g_{f1} F_1 \frac{Z}{Z+h_z}}_{\text{zoop consumption}} - \underbrace{g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{\text{g}} - \underbrace{E_{f1} F_1}_{\text{y removals}}$$

$$\frac{dF_2}{dt} = \underbrace{r_{f2} F_2(1-\frac{F_2}{K_{f2}})}_{\text{DD production}} + \underbrace{e_{f2} g_{f2} F_2 \frac{Z}{Z+h_z}}_{\text{zoop consumption}} + \underbrace{e_{f2} g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{F_1 \text{ consumption}} - \underbrace{m_{f2} F_2}_{\text{mortality}} - \underbrace{q_{f2} E_{f2} F_2}_{\text{fushery removals}}$$

$$\frac{dY}{dt} = q_{f1} E_{f1} F_1 + q_{f2} E_{f2} F_2$$



P

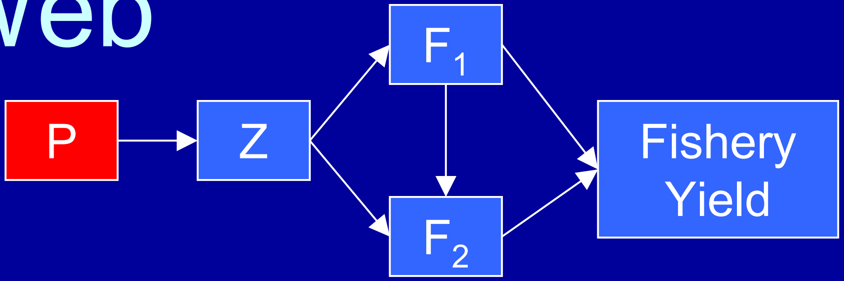
Z

$F_1$

$F_2$

Fishery Yield

# Bottom-Up Control of a Marine Food Web



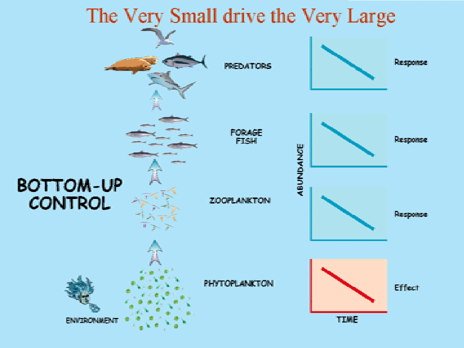
$$\frac{dP}{dt} = \underbrace{r_p P(1-\frac{P}{K_p})}_{\text{DD production}} - \underbrace{g_z Z \frac{P}{P+h_a}}_{\text{zoop grazing}}$$

$$\frac{dZ}{dt} = \underbrace{r_z Z(1-\frac{Z}{K_z})}_{\text{DD production}} + \underbrace{e_z g_z Z \frac{P}{P+h_a}}_{\text{zoop consumption}} - \underbrace{g_{f1} F_1 \frac{Z}{Z+h_z}}_{F_1 \text{ grazing}} - \underbrace{g_{f2} F_2 \frac{Z}{Z+h_z}}_{F_2 \text{ grazing}} - \underbrace{m_z Z}_{\text{mortality}}$$

$$\frac{dF_1}{dt} = \underbrace{r_{f1} F_1(1-\frac{F_1}{K_{f1}})}_{\text{DD production}} + \underbrace{e_{f1} g_{f1} F_1 \frac{Z}{Z+h_z}}_{\text{zoop consumption}} - \underbrace{g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{F_2 \text{ grazing}} - \underbrace{m_{f1} F_1}_{\text{mortality}} - \underbrace{q_{f1} E_{f1} F_1}_{\text{fishery removals}}$$

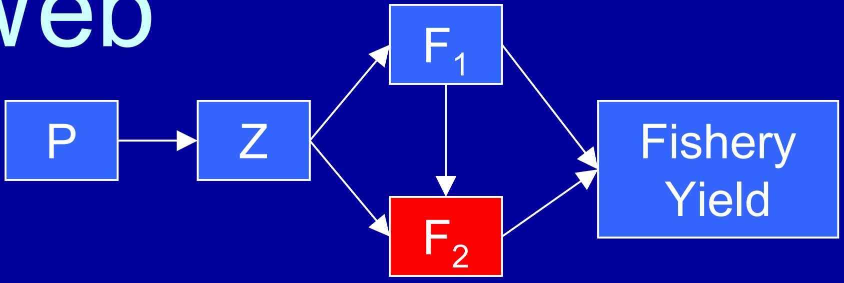
$$\frac{dF_2}{dt} = \underbrace{r_{f2} F_2(1-\frac{F_2}{K_{f2}})}_{\text{DD production}} + \underbrace{e_{f2} g_{f2} F_2 \frac{Z}{Z+h_z}}_{\text{zoop consumption}} + \underbrace{e_{f2} g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{F_1 \text{ consumption}} - \underbrace{m_{f2} F_2}_{\text{mortality}_2} - \underbrace{q_{f2} E_{f2} F_2}_{\text{fushery removals}}$$

$$\frac{dY}{dt} = q_{f1} E_{f1} F_1 + q_{f2} E_{f2} F_2$$



*Cury et al. 2001*

# Top-Down Control of a Marine Food Web


P

Z

$F_1$

$F_2$

Fishery Yield

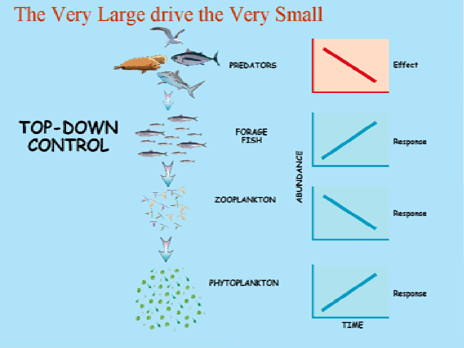
$$\frac{dP}{dt} = \underbrace{r_p P\left(1-\frac{P}{K_p}\right)}_{DD\ production} - \underbrace{g_z Z \frac{P}{P+h_a}}_{zoop\ grazing}$$

$$\frac{dZ}{dt} = \underbrace{r_z Z\left(1-\frac{Z}{K_z}\right)}_{DD\ production} + \underbrace{e_z g_z Z \frac{P}{P+h_a}}_{zoop\ consumption} - \underbrace{g_{f1} F_1 \frac{Z}{Z+h_z}}_{F_1\ grazing} - \underbrace{g_{f2} F_2 \frac{Z}{Z+h_z}}_{F_2\ grazing} - \underbrace{m_z Z}_{mortality}$$

$$\frac{dF_1}{dt} = \underbrace{r_{f1} F_1\left(1-\frac{F_1}{K_{f1}}\right)}_{DD\ production} + \underbrace{e_{f1} g_{f1} F_1 \frac{Z}{Z+h_z}}_{zoop\ consumption} - \underbrace{g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{F_2\ grazing} - \underbrace{m_{f1} F_1}_{mortality} - \underbrace{q_{f1} E_{f1} F_1}_{fishery\ removals}$$

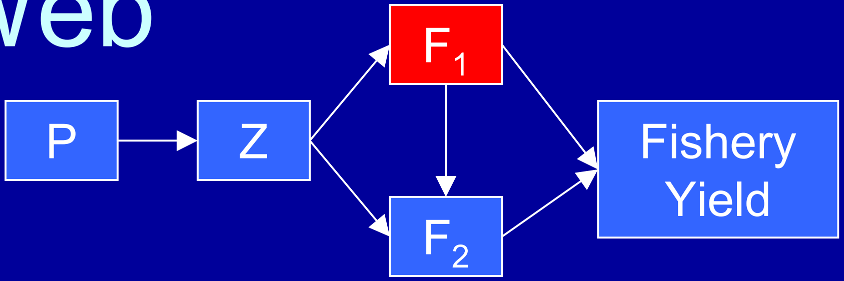
$$\frac{dF_2}{dt} = \underbrace{r_{f2} F_2\left(1-\frac{F_2}{K_{f2}}\right)}_{DD\ production} + \underbrace{e_{f2} g_{f2} F_2 \frac{Z}{Z+h_z}}_{zoop\ consumption} + \underbrace{e_{f2} g_{f2} F_2 \frac{F_1}{F_1+h_{f1}}}_{F_1\ consumption} - \underbrace{m_{f2} F_2}_{mortality\ _2} - \underbrace{q_{f2} E_{f2} F_2}_{fushery\ removals}$$

$$\frac{dY}{dt} = q_{f1} E_{f1} F_1 + q_{f2} E_{f2} F_2$$



*Cury et al. 2001*

# Wasp-Waist Control of a Marine Food Web



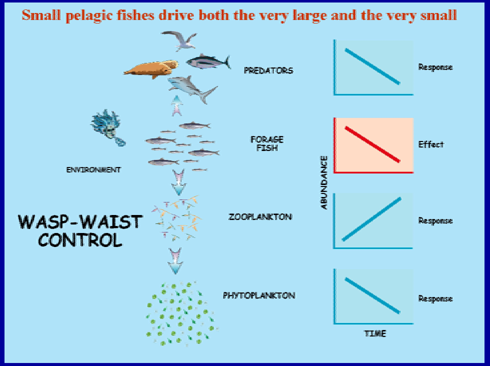
$$\frac{dP}{dt} = \underbrace{r_p P(1-\frac{P}{K_p})}_{DD\ production} - \underbrace{g_z Z\frac{P}{P+h_a}}_{zoop\ grazing}$$

$$\frac{dZ}{dt} = \underbrace{r_z Z(1-\frac{Z}{K_z})}_{DD\ production} + \underbrace{e_z g_z Z\frac{P}{P+h_a}}_{zoop\ consumption} - \underbrace{g_{f1}F_1\frac{Z}{Z+h_z}}_{F_1\ grazing} - \underbrace{g_{f2}F_2\frac{Z}{Z+h_z}}_{F_2\ grazing} - \underbrace{m_z Z}_{mortality}$$

$$\frac{dF_1}{dt} = \underbrace{r_{f1}F_1(1-\frac{F_1}{K_{f1}})}_{DD\ production} + \underbrace{e_{f1}g_{f1}F_1\frac{Z}{Z+h_z}}_{zoop\ consumption} - \underbrace{g_{f2}F_2\frac{F_1}{F_1+h_{f1}}}_{F_2\ grazing} - \underbrace{m_{f1}F_1}_{mortality} - \underbrace{q_{f1}E_{f1}F_1}_{fishery\ removals}$$

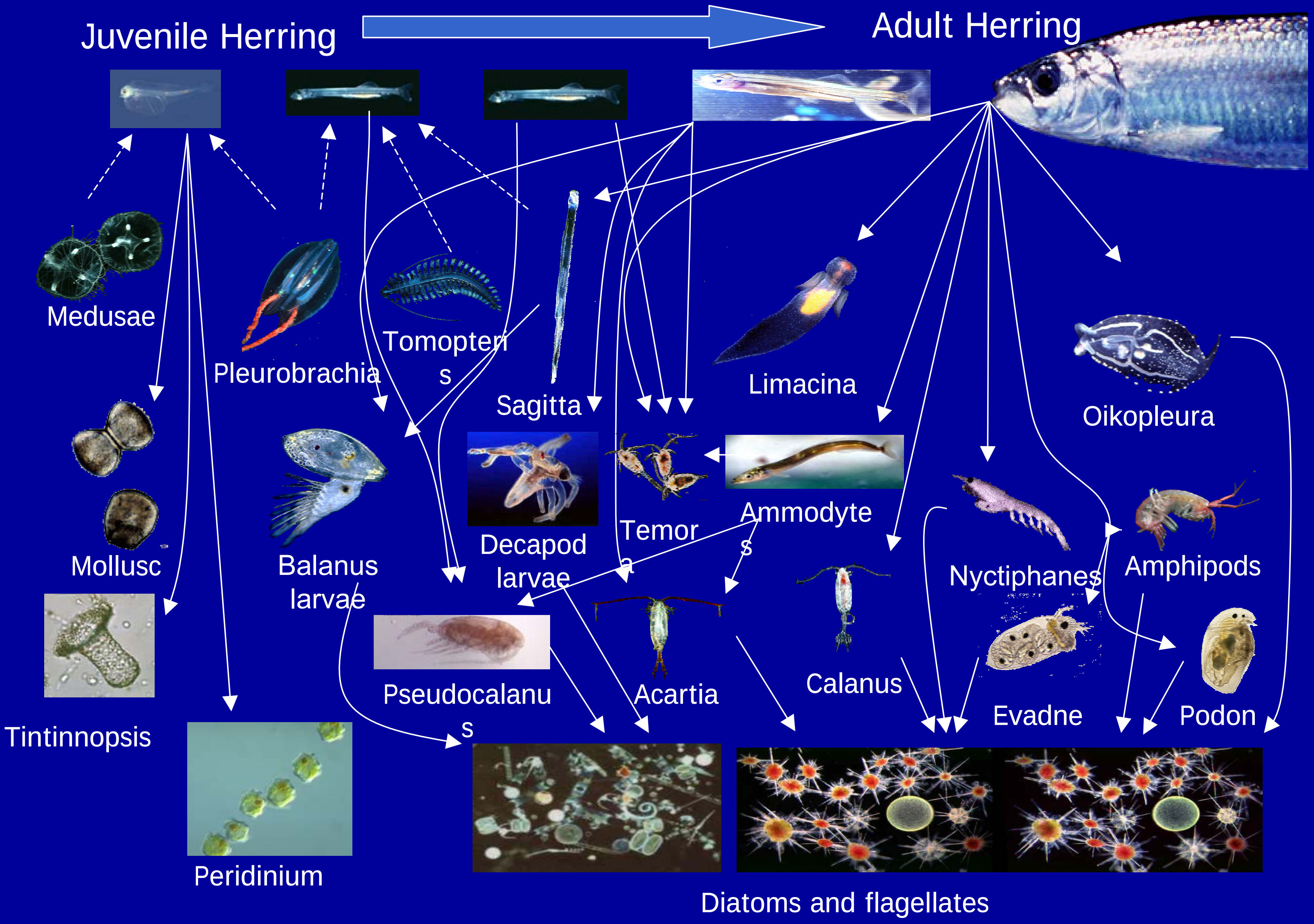
$$\frac{dF_2}{dt} = \underbrace{r_{f2}F_2(1-\frac{F_2}{K_{f2}})}_{DD\ production} + \underbrace{e_{f2}g_{f2}F_2\frac{Z}{Z+h_z}}_{zoop\ consumption} + \underbrace{e_{f2}g_{f2}F_2\frac{F_1}{F_1+h_{f1}}}_{F_1\ consumption} - \underbrace{m_{f2}F_2}_{mortality\ 2} - \underbrace{q_{f2}E_{f2}F_2}_{fushery\ removals}$$

$$\frac{dY}{dt} = q_{f1}E_{f1}F_1 + q_{f2}E_{f2}F_2$$



*Cury et al. 2001*

# Hardy’s (1924) web untangled into functional groups



Juvenile Herring

Adult Herring

Medusae

Pleurobrachia

Tomopteris

Sagitta

Limacina

Oikopleura

Mollusc

Balanus larvae

Decapod larvae

Temora

Ammodytes

Nyctiphanes

Amphipods

Tintinnopsis

Pseudocalanus

Acartia

Calanus

Evadne

Podon

Peridinium

Diatoms and flagellates

# MSP Pros/Cons

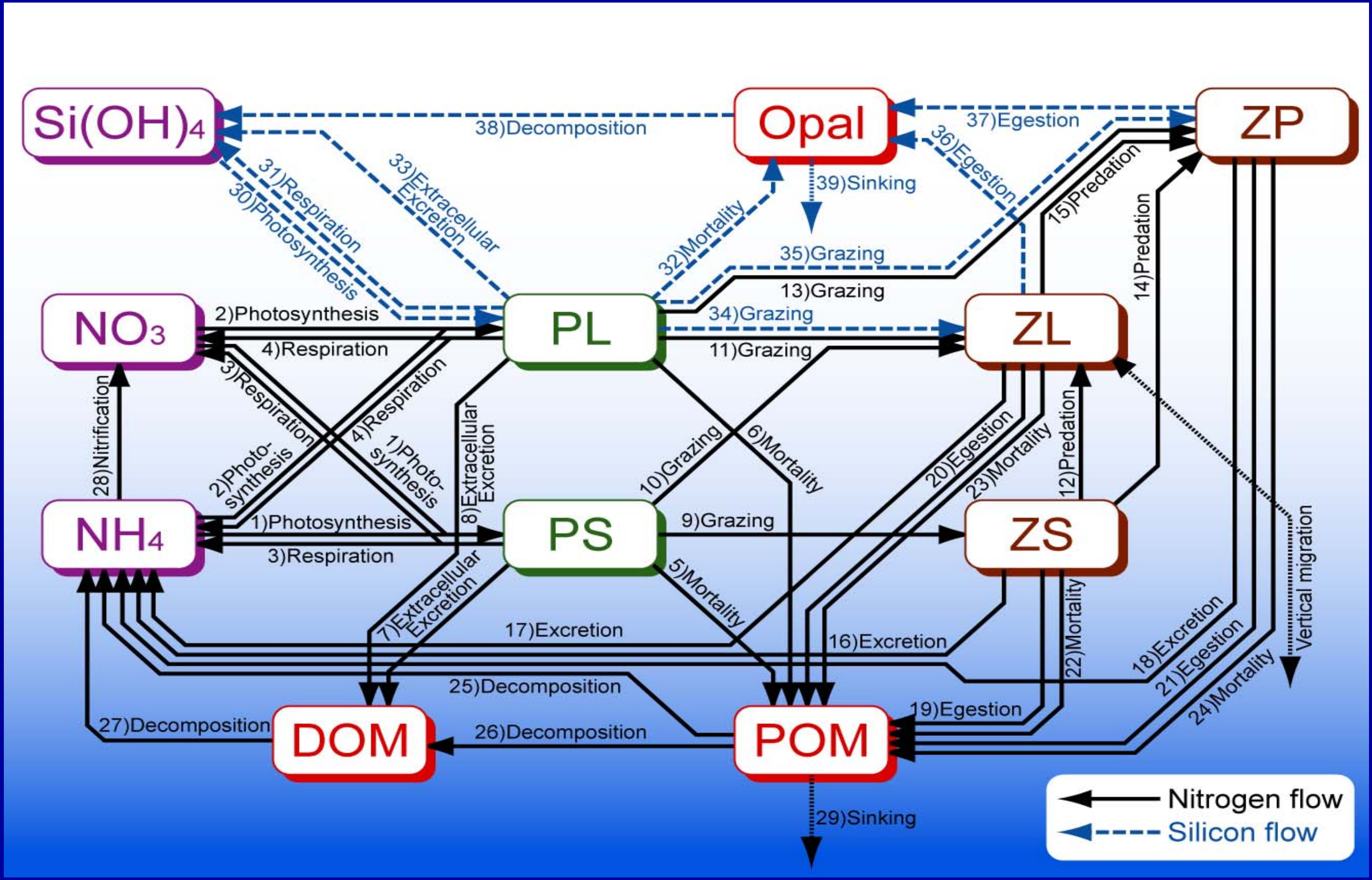
**Advantages**

- ability to address top-down and bottom-up control
- ecological realism - includes important species interactions

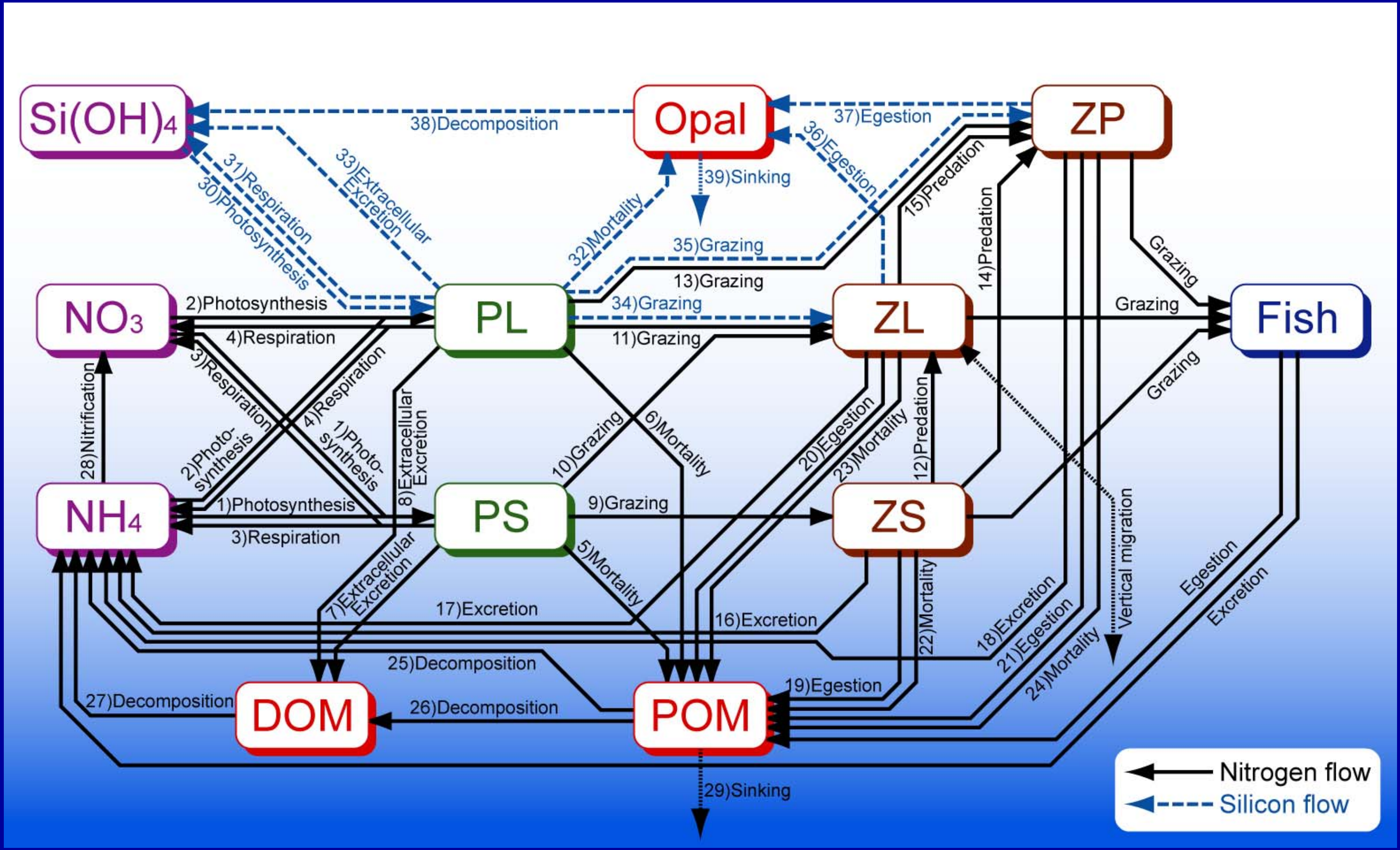
**Disadvantages**

- estimation of interaction parameters difficult
- number of species that can be modeled is low due to parameter needs
- uncertainty about functional relationships between species
- other competing hypotheses can explain population response
- direct lower trophic level effects missing

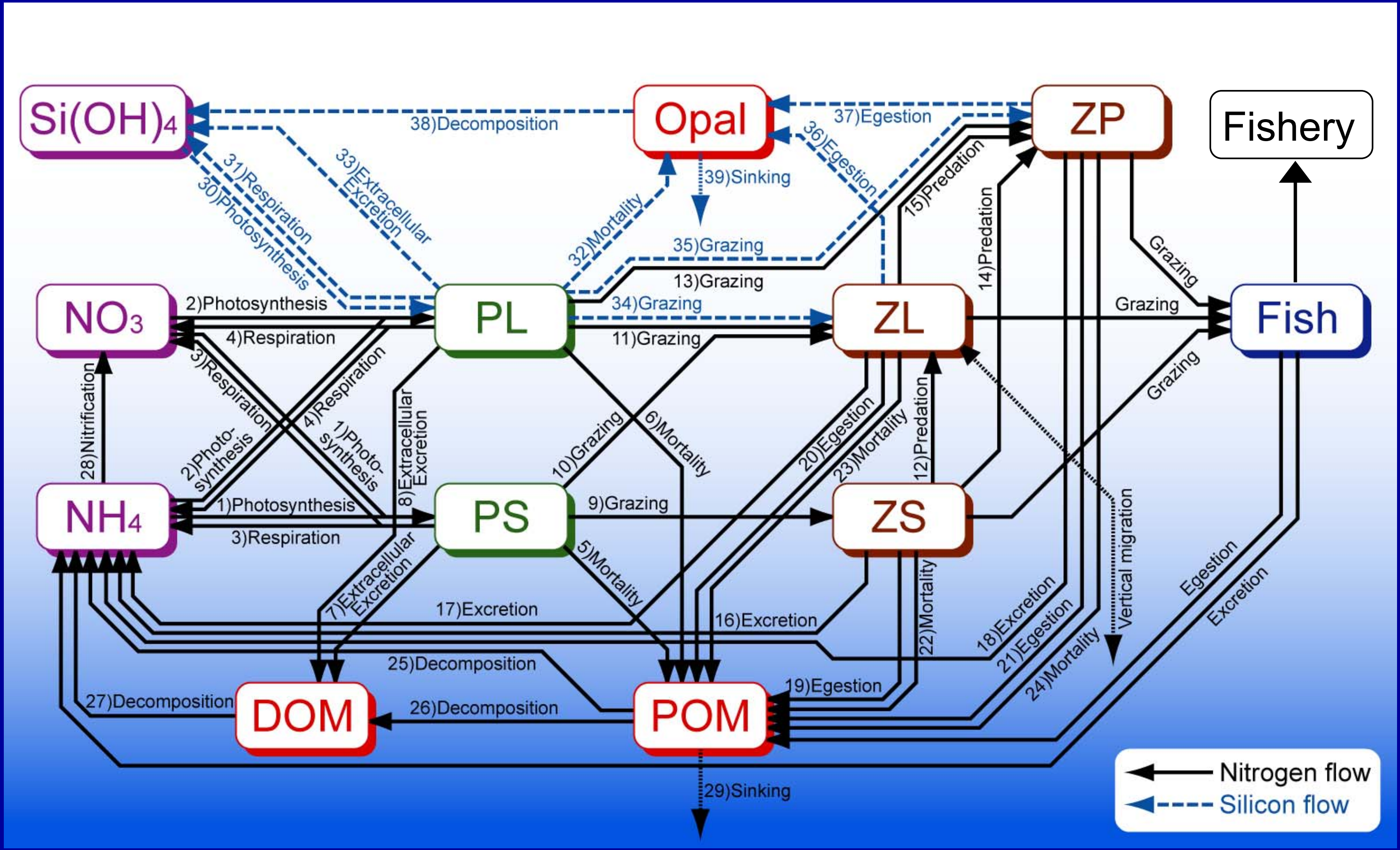
# Whole Ecosystem Models- NEMURO



# NEMURO.FISH


Si(OH)4
Opal
ZP
NO3
PL
ZL
Fish
NH4
PS
ZS
DOM
POM
38)Decomposition
37)Egestion
36)Egestion
31)Respiration
30)Photosynthesis
33)Extracellular Excretion
32)Mortality
39)Sinking
35)Grazing
15)Predation
13)Grazing
14)Predation
Grazing
2)Photosynthesis
34)Grazing
Grazing
4)Respiration
11)Grazing
3)Respiration
4)Respiration
1)Photo-synthesis
8)Extracellular Excretion
Grazing
28)Nitrification
2)Photo-synthesis
10)Grazing
6)Mortality
20)Egestion
23)Mortality
12)Predation
1)Photosynthesis
9)Grazing
3)Respiration
5)Mortality
7)Extracellular Excretion
22)Mortality
Vertical migration
17)Excretion
16)Excretion
18)Excretion
21)Egestion
24)Mortality
Egestion
Excretion
25)Decomposition
19)Egestion
27)Decomposition
26)Decomposition
29)Sinking
Nitrogen flow
Silicon flow

# NEMURO.FISH


Si(OH)4
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Vertical migration
Egestion
Excretion
25)Decomposition
19)Egestion
27)Decomposition
DOM
26)Decomposition
POM
29)Sinking
Nitrogen flow
Silicon flow

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$production = V_{\max S} \cdot \underbrace{\left( \frac{NO_3}{NO_3 + K_{NO3S}} \cdot \exp(-\varphi_S * NH_4) + \frac{NH_4}{NH_4 + K_{NH4S}} \right)}_{nitrogen\ dependence}$$

$$\cdot \underbrace{\exp(k_{GppS} \cdot T)}_{temperature\ dependence} \cdot \underbrace{\int_{-H}^{0} \frac{I}{I_{optS}} \cdot \exp\left(1 - \frac{I}{I_{optS}}\right)}_{light\ dependence} dz \cdot PS$$

$$I = I_0 \cdot \exp(-\kappa |Z|)$$

$$\kappa = \alpha_1 + \alpha_2 (PS + PL)$$

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$respiration = \underbrace{\mathrm{Re}s_{PS0}}_{mortality} \cdot \underbrace{\exp(k_{RPS} \cdot T)}_{temperature\ dependence} \cdot PS$$

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$mortality = \underbrace{M_{PS0}}_{mortality} \cdot \underbrace{\exp(k_{MPS} T)}_{temperature\ dependence} \cdot [PS]^2$$

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$excretion = \gamma_{PS} \cdot production$$

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$grazing\ \ by\ \ ZS = \mathrm{Max}\left[0, GR\max\ ps \cdot \underbrace{\exp(k_{GraS} \cdot T)}_{temperature\ dependence} \cdot \underbrace{\left\{1 - \exp(\lambda_S \cdot (PS2ZS^* - PS))\right\}}_{Ivlev\ \ prey\ \ preference} \cdot ZS\right]$$

$$grazing\ \ by\ \ ZL = \mathrm{Max}\left[0, GR\max\ ps \cdot \underbrace{\exp(k_{GraL} \cdot T)}_{temperature\ \ dependence} \cdot \underbrace{\left\{1 - \exp(\lambda_L \cdot (PS2ZL^* - PS))\right\}}_{Ivlev\ \ prey\ \ preference} \cdot ZL\right]$$

# Mechanistic Differential Equation

$$\frac{dPS}{dt} = production - respiration - mortality - excretion - grazing\ by\ ZS - grazing\ by\ ZL$$

$$production = V_{\max S} \cdot \underbrace{\left( \frac{NO_3}{NO_3 + K_{NO3S}} \exp(-\varphi_S * NH_4) + \frac{NH_4}{NH_4 + K_{NH4S}} \right)}_{nitrogen\ dependence}$$

$$\cdot \underbrace{\exp(k_{GppS} \cdot T)}_{temperature\ dependence} \cdot \underbrace{\int_{-H}^{0} \frac{I}{I_{optS}} \exp\left(1 - \frac{I}{I_{optS}}\right) dz}_{light\ dependence} \cdot PhySn$$

$$I = I_0 \exp(-\kappa |Z|)$$

$$\kappa = \alpha_1 + \alpha_2 (PhySn + PhyLn)$$

$$respiration = \underbrace{\mathrm{Res}_{PS0}}_{mortality} \cdot \underbrace{\exp(k_{RPS} \cdot T)}_{temperature\ dependence} \cdot PS$$

$$excretion = \gamma_{PS} \cdot production$$

$$mortality = \underbrace{M_{PS0}}_{mortality} \cdot \underbrace{\exp(k_{MPS} \cdot T)}_{temperature\ dependence} \cdot [PS]^2$$

$$grazing\ by\ ZS = \mathrm{Max}\left[ 0, GR\max ps \cdot \underbrace{\exp(k_{GraS} \cdot T)}_{temperature\ dependence} \cdot \left\{ \underbrace{1 - \exp(\lambda_S \cdot (PS2ZS^* - PS))}_{Ivlev\ prey\ preference} \right\} \cdot ZS \right]$$

$$grazing\ by\ ZL = \mathrm{Max}\left[ 0, GR\max ps \cdot \underbrace{\exp(k_{GraL} \cdot T)}_{temperature\ dependence} \cdot \left\{ \underbrace{1 - \exp(\lambda_L \cdot (PS2ZL^* - PS))}_{Ivlev\ prey\ preference} \right\} \cdot ZL \right]$$

6 detailed process submodels and 20 parameters

# Whole Ecosystem Pros/Cons

**Advantages**

- ability to address top-down and bottom-up control through detailed process description
- ecological realism - includes important species interactions and biological processes
- parameters can be estimated with laboratory experiments

**Disadvantages**

- large amounts of data are required for parameterization (NEMURO.FISH – 191 parameters)
- somewhat restricted to well studies species and functional groups
- number of species that can be modeled is low due to parameter needs
- uncertainty about functional relationships between species
- other competing hypotheses can explain population response

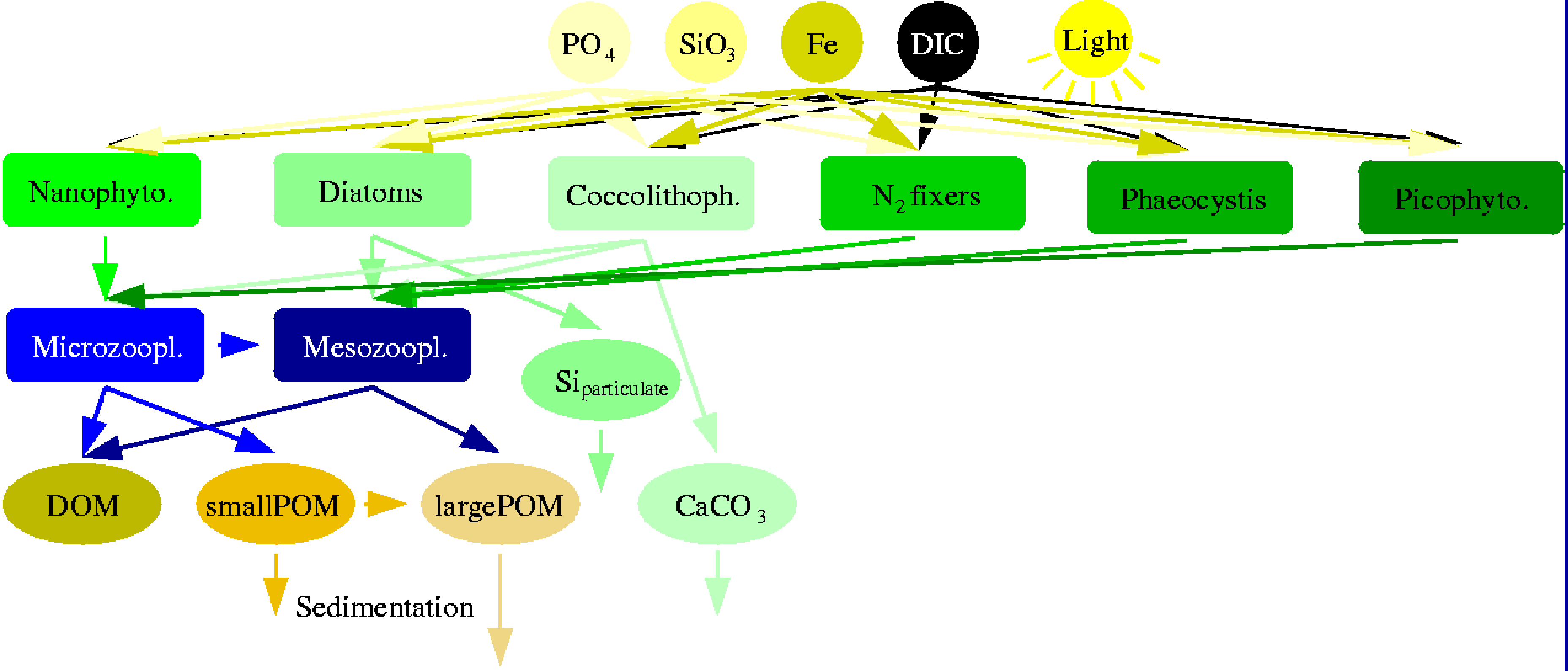
# Qualitative Characteristics

| | **Ecopath** | **Multispecies Production** | **Whole Ecosystem Model** |
|---|---|---|---|
| Age/Size Structure | Yes | No | Yes |
| Biomass Predictions | Yes | Yes | Yes |
| Data Requirements | High | Intermediate | High |
| Mass/Energy Balance | Yes | No | Yes |
| Number of Species | High | Low | Intermediate |
| Spatial Resolution | Possible | No | Possible |
| Taxonomic Resolution | Species or groups | Species or groups | Species |
| Temporal Resolution | Annual | Annual | Daily |
| Ecological Realism | Low | Intermediate | High |
| Estimate Parameters? | No | Intermediate | Yes |
| TD-BU Control Emergent Behavior? | No | Possible | Possible |

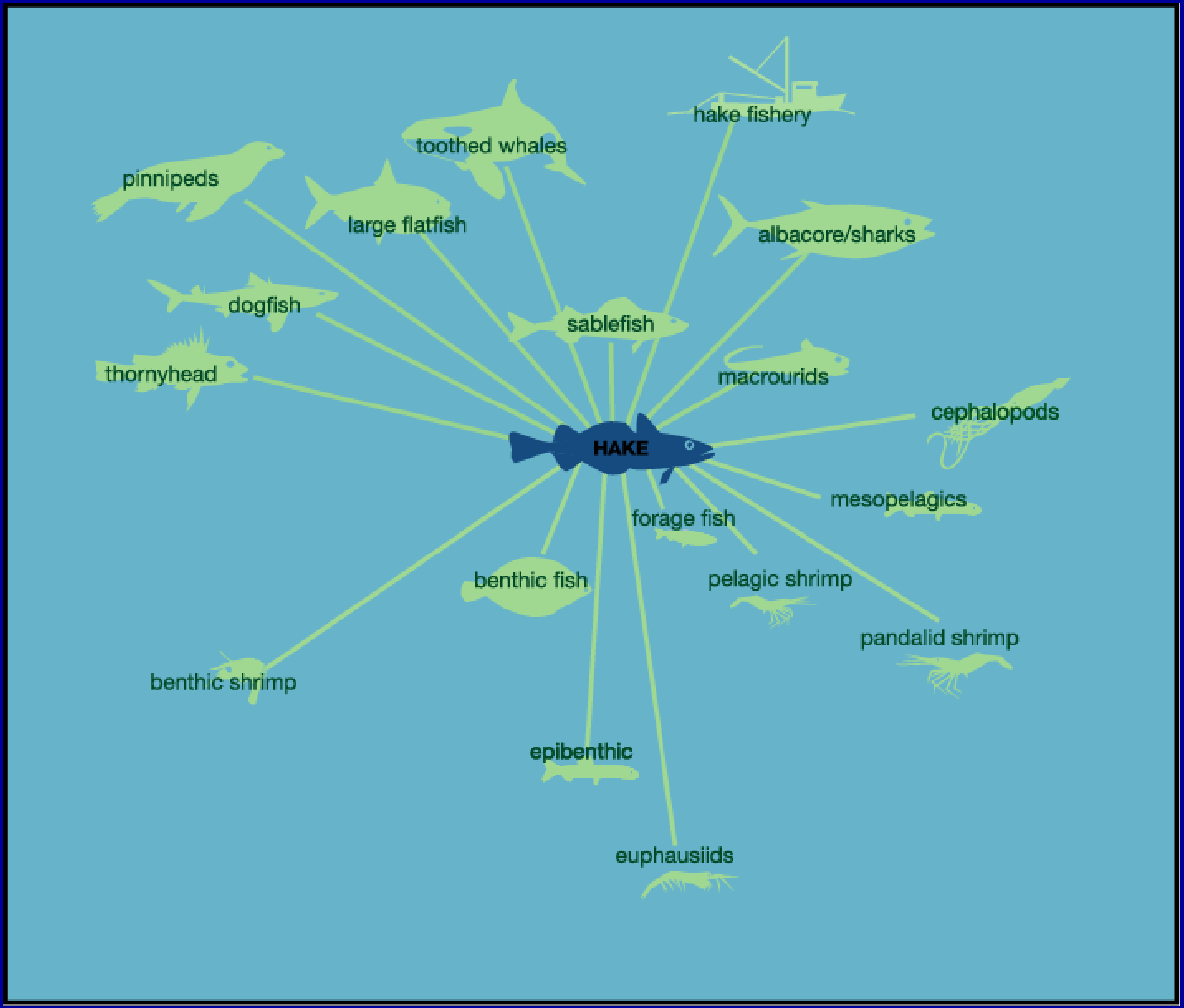
# How does TD-BU Control Manifest Itself Through Modeling?

- Prescribed control
- Emergent behavior

# GREEN OCEAN MODEL

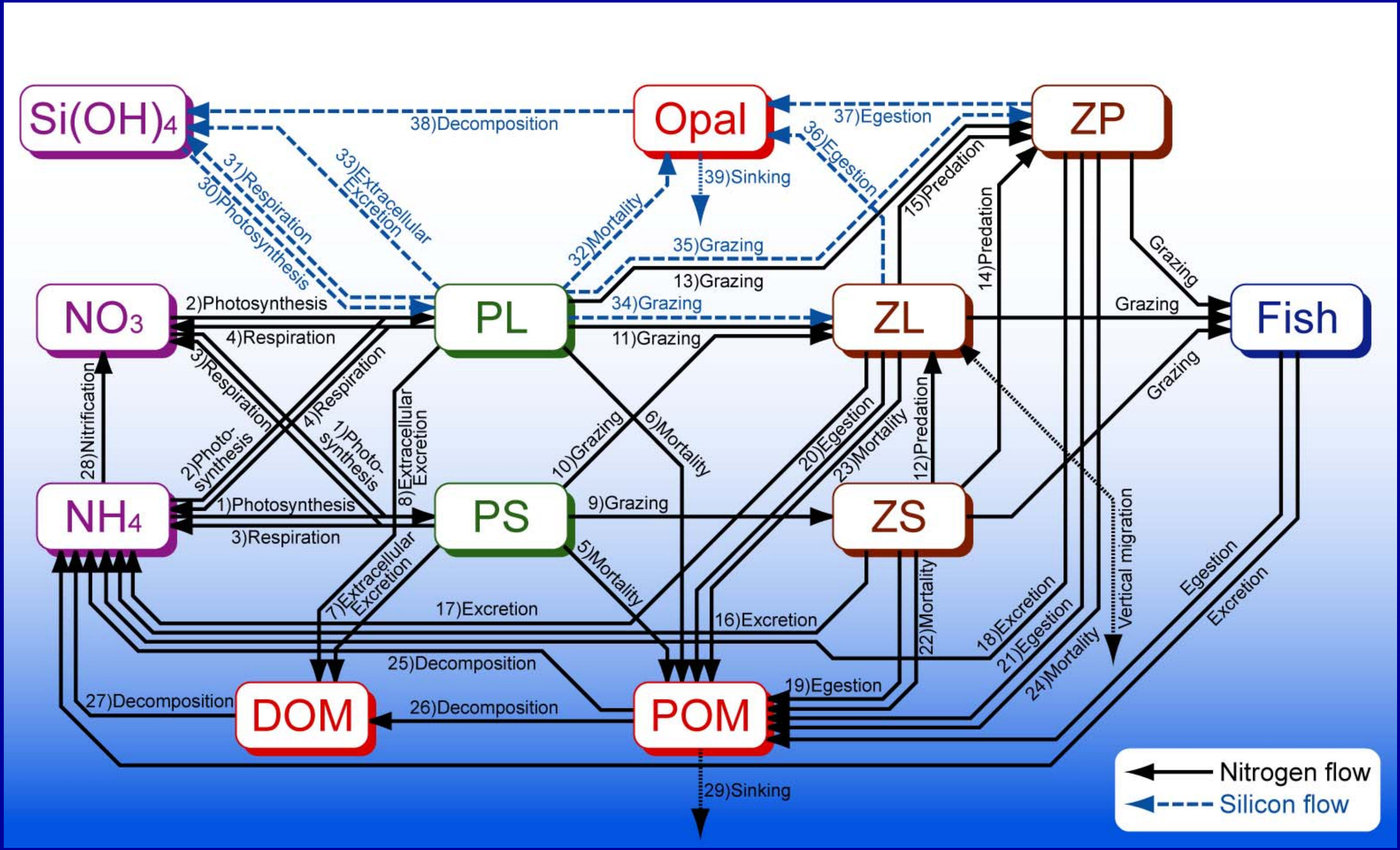


# HAKE FOOD WEB

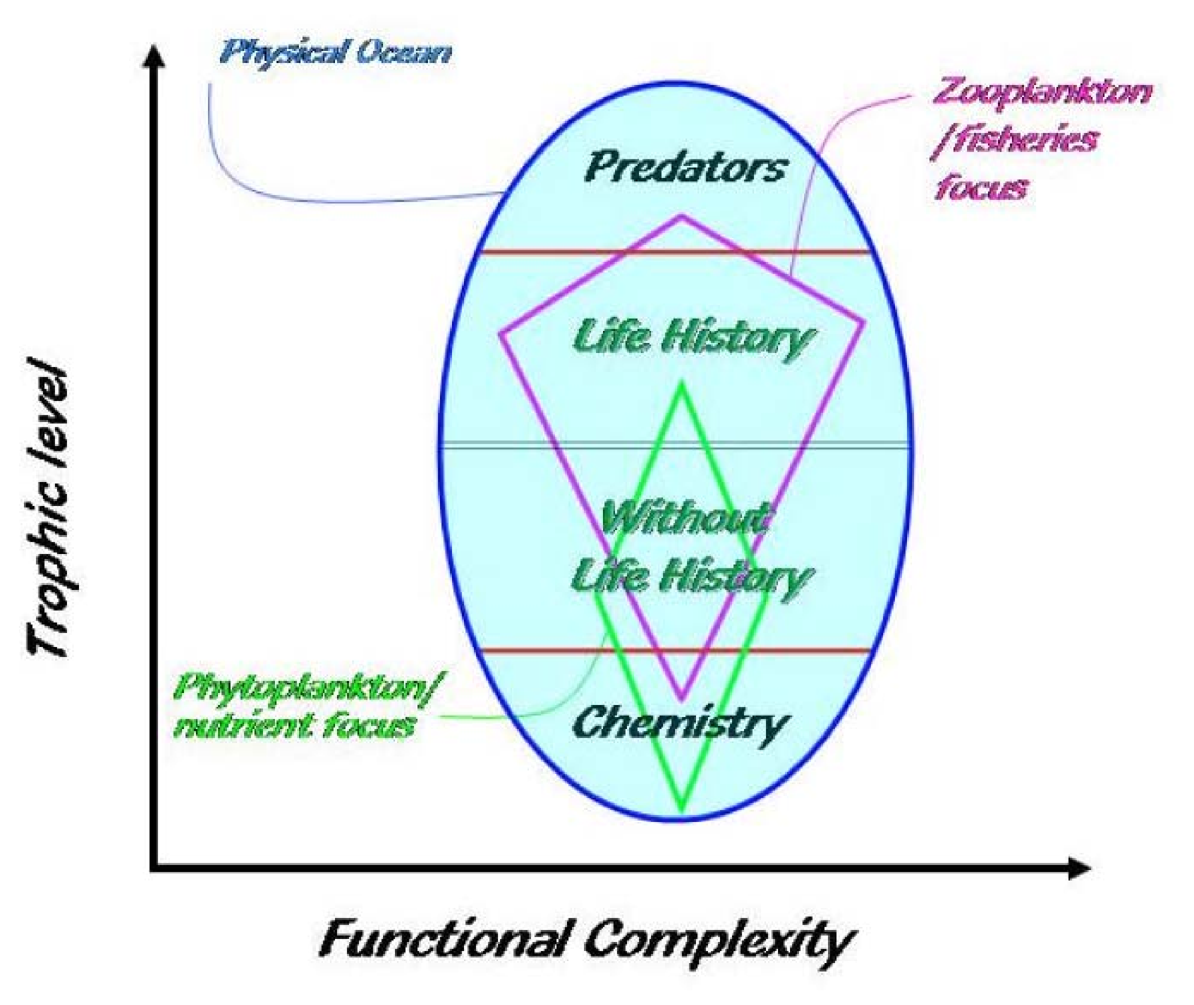


*Agostini, CCCC REX W2 Workshop, PICES 2004*

# NEMURO.FISH


Si(OH)4
38)Decomposition
Opal
37)Egestion
ZP
36)Egestion
31)Respiration
30)Photosynthesis
33)Extracellular Excretion
32)Mortality
39)Sinking
35)Grazing
15)Predation
14)Predation
Grazing
NO3
2)Photosynthesis
13)Grazing
34)Grazing
PL
ZL
Grazing
Fish
4)Respiration
11)Grazing
3)Respiration
4)Respiration
1)Photo-synthesis
8)Extracellular Excretion
Grazing
28)Nitrification
2)Photo-synthesis
10)Grazing
6)Mortality
20)Egestion
23)Mortality
12)Predation
NH4
1)Photosynthesis
PS
9)Grazing
ZS
3)Respiration
7)Extracellular Excretion
5)Mortality
22)Mortality
Vertical migration
Egestion
Excretion
17)Excretion
16)Excretion
18)Excretion
21)Egestion
24)Mortality
25)Decomposition
19)Egestion
27)Decomposition
DOM
26)Decomposition
POM
29)Sinking
Nitrogen flow
Silicon flow

# Harlow Rhomboid



*deYoung et al. 2004 Science*

# Can We Forecasting Future Ecosystem States with Modeling?

*“The ability to predict ecosystem behavior is limited”*

***Cury et al. 2001. Reykavik Conference on Responsible Fisheries in the Marine Ecosystem***

- *No General Theory can be ascribed to the functioning of marine ecosystems*

- *Data on non-commercial ecosystem components are missing or limited or both – opportunity for observations is lacking*

# Limitations to Prediction

- Stochasticity
  - Environment
  - Nonlinear species relationships
  - Ecosystem structure
- Various factors important during different life stages on multiple trophic levels

# Temporal Issues

- Ecosystem structure, species composition and functioning change on several different time scales (i.e. season, annual, decade)

- Changes take can appear as quasi-cyclic, at multiple frequencies, or as sudden shifts between alternative “stable” states

- Temporal fluctuations result in changes in distribution, abundance, and physiology of marine organisms associated with changes in characteristics of the ecosystems in which they live.

# Climate Issues

Climate may affect ecological processes in a variety of ways….

- Climatic fluctuations may affect the relative timing of food requirement and food availability (i.e. the “match-mismatch hypothesis”).

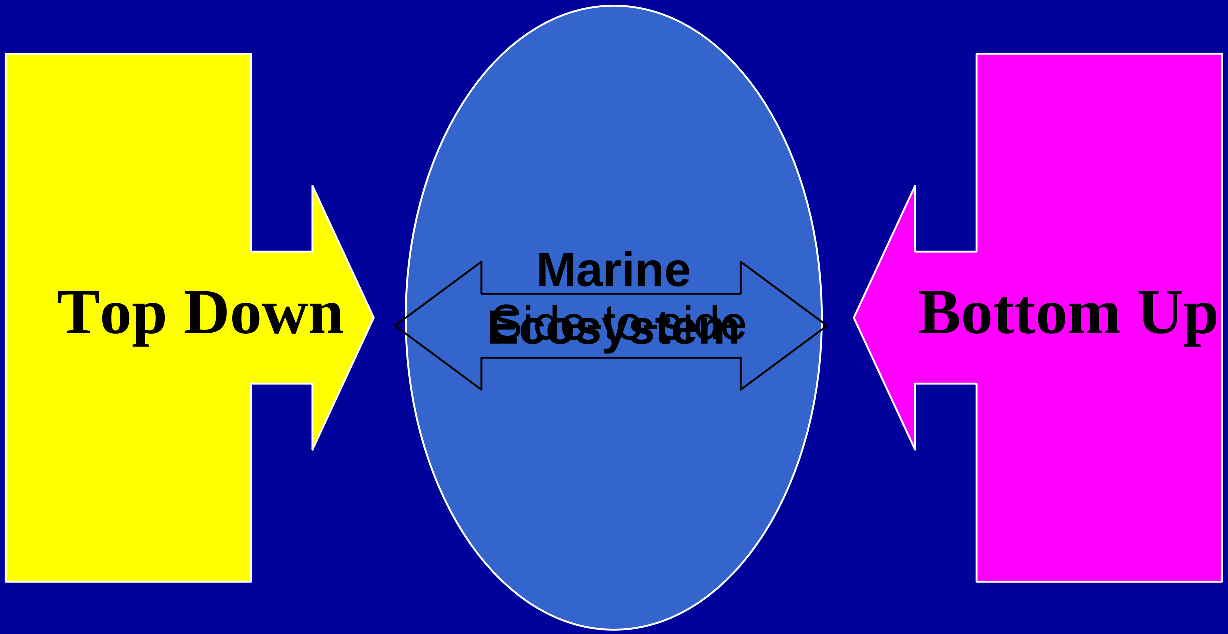
- Climate fluctuations may affect biological processes in linear and nonlinear ways (i.e. size-based predation, prey-switching).

- Between-individual interactions and within species density independent and dependent may vary nonlinearly with climatic factors.

- Climatic fluctuations can differentially affect different life stages.

- Habitat suitability (i.e. thermal stress, exceeding thermal tolerances and preferences, too little sunlight, too much current)

# Which Process Controls Marine Ecosystems?



- Side-to-Side Ecosystem Control (within trophic level competition) *Moon and Stilling 2002. Oikos*

# Mathematics is the Language of Modeling

# Mathematics and The Modeling Challenge

So far as the laws of mathematics refer to reality, they are not certain. And so far as they are certain, they do not refer to reality.

*Albert Einstein*

As complexity rises, precise mathematical statements lose meaning and meaningful mathematical statements lose precision.

*Lotfi Zadeh*

There are tradeoffs

# There is No Silver Bullet!

- TD-BU is not binary - Likely TD and/or BU control is dominant during one time, for one life stage, in one habitat.
- “Correct” model can only be evaluated against the goal of modeling and the hypotheses under study.
- A suite of modeling approaches should maximize information revealed.

# There is No Silver Bullet! (con’t)

- Simplified models cannot replace complex models. Less complicated dynamics may, however, exhibit more clearly the dominating processes and feedback mechnisms at work.
- Robustness of results *can be* tested much better than in simple modles compared to more complex models.
- Complex ecosystem models seem to be the only tool that allowes the possibility of BU-TD behavior as an emergent behavior.

# The End

Go forth and model.

May the $\Phi$ be with you!