Coupled Biophysical Models of Transport and Demography of Plankton and Fish in a Dynamic Coastal Upwelling Environment

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Abstract

Coupled biophysical models that link 1) physical circulation and mixing, 2) lower trophic level ecosystems, and 3) higher trophic levels are being used to explore spatial and temporal distributions of animals in wind-driven upwelling systems. While the specific applications described are focused on macrozooplankton (copepods), the techniques used apply equally well to fish larvae. Results of both two- and three-dimensional simulations using idealized and realistic coastal geometry and bathymetry, simple physical forcing, and relatively well understood lower trophic (NPZD) ecosystem models will be shown. Individual based models (IBMs) that account for the physiological condition and behavior of individual organisms are modeled in a Lagrangian particle tracking model (PTM). Advection, diffusion and food fields from separate Eulerian simulations of the physics-NPZD model are used to force the IBM-PTM model. Some of the simulations incorporate a full bioenergetics-based model of individual's vital rates (growth, birth, death) and behavior, while other applications ignore vital rates and consider only behavioral effects interacting with the physics. Approaches that use both forward time and backwards-in-time trajectory (BITT) approaches for linking the Eulerian and Lagrangian models are described. The specific question of interest determines the more appropriate approach to use. When the source locations and times of particle release are known, forward time PTMs are the obvious and simplest choice. Conversely, in applications in which the destinations of particles are known and information on the source is desired, BITT PTMs may be useful, despite some of their limitations. Examples of both approaches will be shown.

IBM Modeling Philosophy

i-State Distribution and i-State Configuration Models

- fundamental tool of demographic theory
- produce differential or difference equations
- examples:
  NPZ+ models
  Lotka-Volterra models
  McKendrick-von Foerster equation models
Assumes: global mixing, and few dimensions (e.g., age, size) control dynamics

- aka Individual Based Models
- Each individual has a vector of characteristics associated with it
Examples:
  * Body Size (wt, length)
  * Age
  * Reproductive Condition
  * Nutritional Status
  * Behavior

= f (history)

System State =
     History + Present Environment

"The past of the system affects its response to the present."
Caswell and John (1992)

i-State Configuration Advantages
- Biology is mechanistically explicit (not hidden in differential eqns)
- Biol-Chem-Physical interactions are clearly detailed
- Individual is the fundamental biological unit; natural and intuitive to model at that level, rather than at the population level
- Permits explicit inclusion of an individual's history and behavior
- Spatial heterogeneity interactions 'easily' handled

i-State Configuration Disadvantages
- Difficult to implement feedback (e.g., across multiple trophic levels, prey depletion)
- Difficult to simulate realistic abundances (large numbers of individuals)
- Difficult (impossible?) to simulate density dependence
- Many and complex biological/biochemical processes for individuals impose an extensive computation penalty

A Simple i-state Distribution Model
Nutrient - Phytoplankton - Zooplankton Model
(after Franks et al. 1986)

Uptake (U) = f(N,light)
Grazing (G) = Ivlev w/o threshold
Egestion(E) = fraction not assim.
Mz = Mortality of Z; immediate remineralization
Mp = Mortality of P; immediate remineralization

Assumes: all Z at a given locale are identical

Conclusions

1) It is rare that individual members of populations can be justifiably aggregated into a single state variable representing abundance.
2) To accurately describe population dynamics we need to consider the specific processes and histories of individuals. For coupled physical-biological processes in the ocean, this means particle tracking models (PTMs) forced by Eulerian fields (from models or observations).
3) Feedback to Eulerian fields is difficult and simulating realistic densities and density-dependence is awkward and expensive.
4) Need to consider diffusive processes in PTMs. Advective transport alone gives only a part of the story, and often gets it wrong.
5) The interaction of individual behavior with physical transports can be as important in determining distributions as advection and diffusion alone.
6) IBMs require a number of external inputs (forcing functions). Some of these (e.g., temperature) are relatively easily provided through observations or models, while others data types (food concentrations, prey types) are more difficult. Models used to generate these input fields should provide patterns that 'mimic' nature.
7) Too early (not enough simulations completed) to evaluate the consistency of the BITT approach. (Stay Tuned)
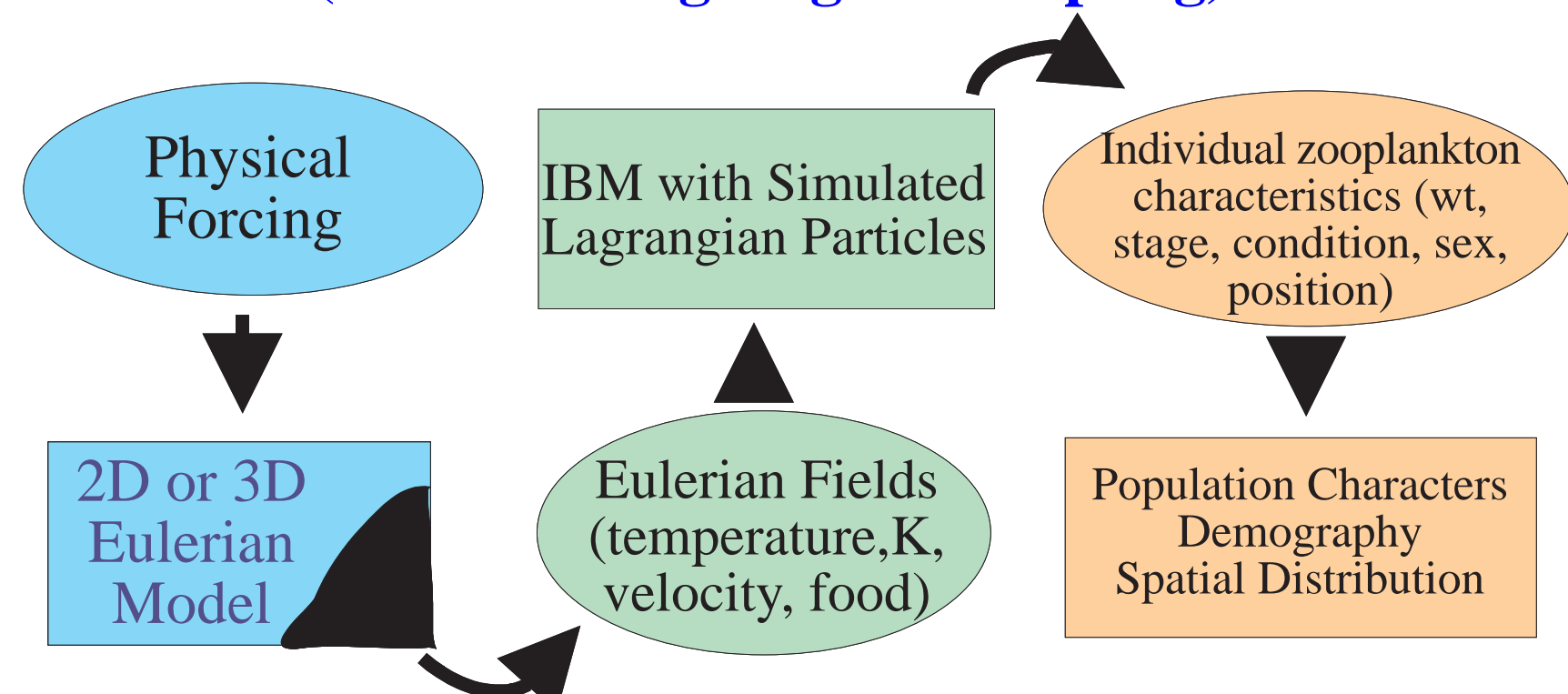
Design Considerations for Particle Tracking

1) advection, advection-diffusion, or advection-diffusion-reaction
   - 'reaction' here refers to any processes that convert a passive tracer into an active or non-conservative tracer (e.g., reproduction, mortality, swimming behavior)
   - Note that sinking and/or buoyancy adjustments can be handled within an Eulerian framework (unless the sinking rate is a function of particle size, age, etc.)
2) Selection of appropriate time-step (biologically or physically determined?)
3) Dimension of the problem (1D, 2D, 3D, depth integrated)
4) Forward-Time (FITT) vs. Backward-Time (BITT) Simulations
   - Depends on the nature of the question (known sources vs. known destinations)
   - Source, sink, single vs. continuous emission
   - 'Reactions' may be difficult (impossible) to simulate in BITT simulations
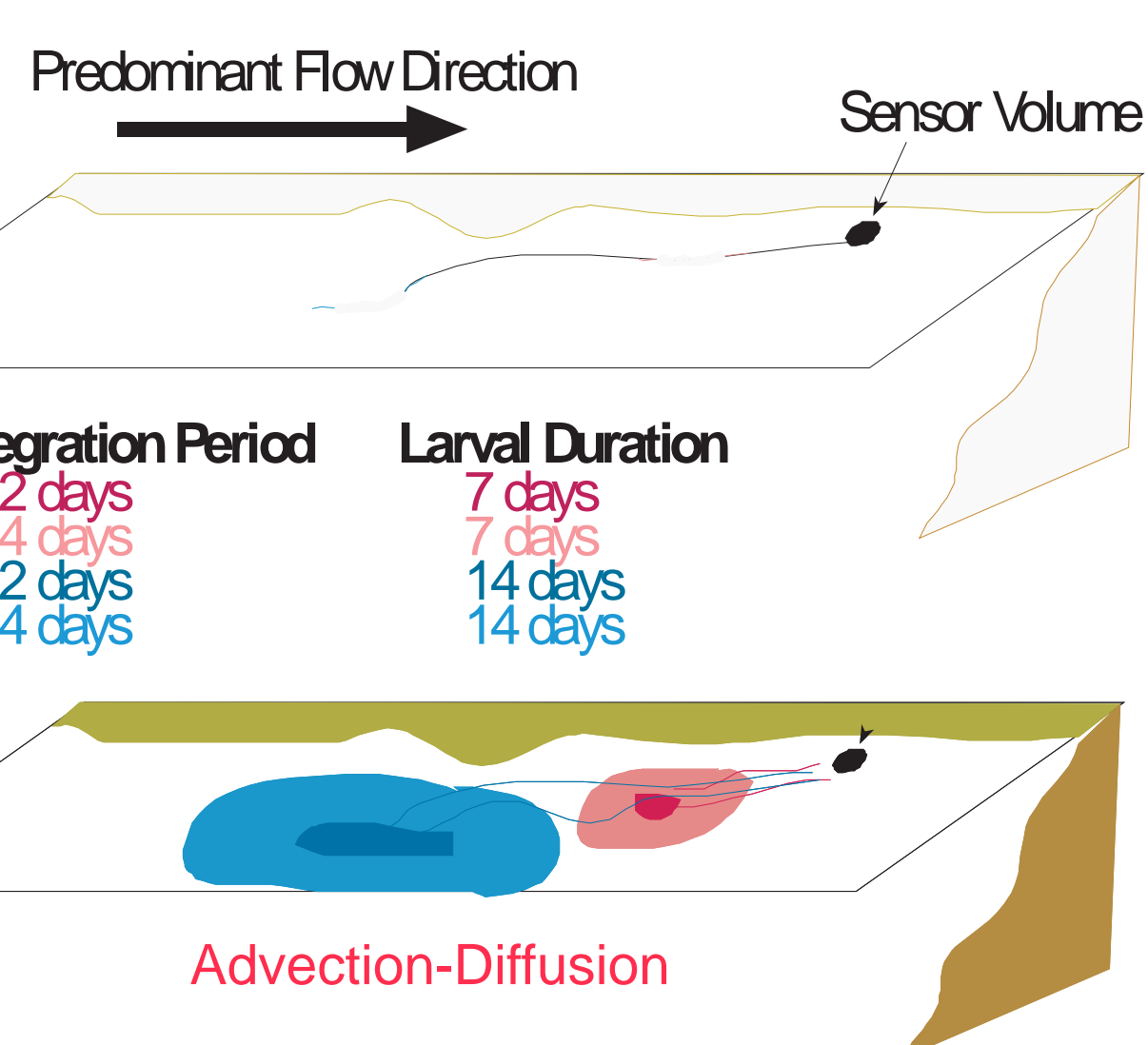
2D Simulations of Coastal Upwelling Systems

Question: How important are diel vertical migration and other individual properties, interacting with spatially dependent transports and food resources, in determining individual and population success, and nearshore retention?

- Model Domain is 100 km offshore, 200 m in depth
- Physical Model includes KPP surface mixing, bottom mixing; forcing by temporally varying idealized upwelling favorable winds.
- Franks et al. NPZ model; 120 day simulation
- Stored snapshots of physics and ecosystem used as input to a PTM-IBM simulation of passive and ontogenetically dependent DVM copepods
- IBM IC's: 5000 randomly located individuals, all identical in weight (usually 10 ug C)

Modeling Approach (Eulerian-Lagrangian Coupling)

Physical Forcing → IBM with Simulated Lagrangian Particles → Individual zooplankton characteristics (wt, stage, condition, sex, position)

2D or 3D Eulerian Model → Eulerian Fields (temperature,K, velocity, food) → Population Characters Demography Spatial Distribution

Phytoplankton Biomass (umole N/l)

Zooplankton Biomass (umole N/l)

Passive Individuals

DVM Individuals

Shown at left are phytoplankton and zooplankton fields for day 30 from the Eulerian model, and IBM particle locations and weights for day 40 from a run with passive particles and a run with DVM particles. Z in the Eulerian model are "passive" and have similar spatial pattern (low nearshore, higher offshore) to the zooplankton in the IBM simulation with passive particles. Ontogenetically dependent DVM in the IBM results in a completely opposite spatial pattern (high nearshore, rare offshore) than the simulation without migration.

The 2D results are submitted for publication in Progress in Oceanography,

Batchelder, H. P., C. A. Edwards, and T. M. Powell. Individual-based models of copepod populations in coastal upwelling regions: Implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Prog. Oceanogr.

Schematic of Source Region Identification Assuming Fixed Sensor Location with Advection Only

Predominant Flow Direction — Sensor Volume

Integration Period
2 days
4 days
2 days
4 days

Larval Duration
7 days
7 days
14 days
14 days

Advection-Diffusion

3D Simulations with Idealized Geometry and Forcing

Question: Where are the trajectories and sources of meroplanktonic recruits to larval collectors at fixed, known locations in the nearshore?

- 3D Spectral Element Ocean Model (SEOM); 30 day simulation
- Idealized shelf-bank geometry; Domain of 600 km offshore, 900 km alongshore, 900 m depth
- Sinusoidal wind stress between strongly and weakly upwelling favorable
- No ecosystem model, passive transport or simple behavior only
- Stored snapshots of physical fields used to explore particle trajectories
- Advection-only; Advection-Diffusion; Advection-Diffusion-Reaction Cases
- Backward-Time model to predict source of particles arriving at fixed destination; assumed 7 day pelagic larval phase

% Nearshore 7 Days Prior to Settlement

Wt	A	AD	AR	ADR
1.3	9	53	7.5	54
5.0			20	56
10			67	80
25			100	100

Wt in ug C/ind
A=Advection
AD = Advection-Diffusion
AR = Advection-Reaction
ADR = Adv.-Diff.-Rxn

Larval Collector

Advection Only

Advection-Diffusion

Advection-Diffusion-Reaction

Wt(ug)	%Near
1.3	53.7
5.0	56.1
10.0	80.0
25.0	100.0

Results

1) in this idealized upwelling system, most larvae arriving at the collector came from offshore
2) including diffusion (via a random walk) in the calculation of trajectories, results in a higher probability that an individual originated in the nearshore (within 10 km of shore [green box]) than when transport is calculated from advection alone.
3) Even limited DVM (ca. 7 m day-to-night) can further increase the probability that the larvae had a source nearshore.
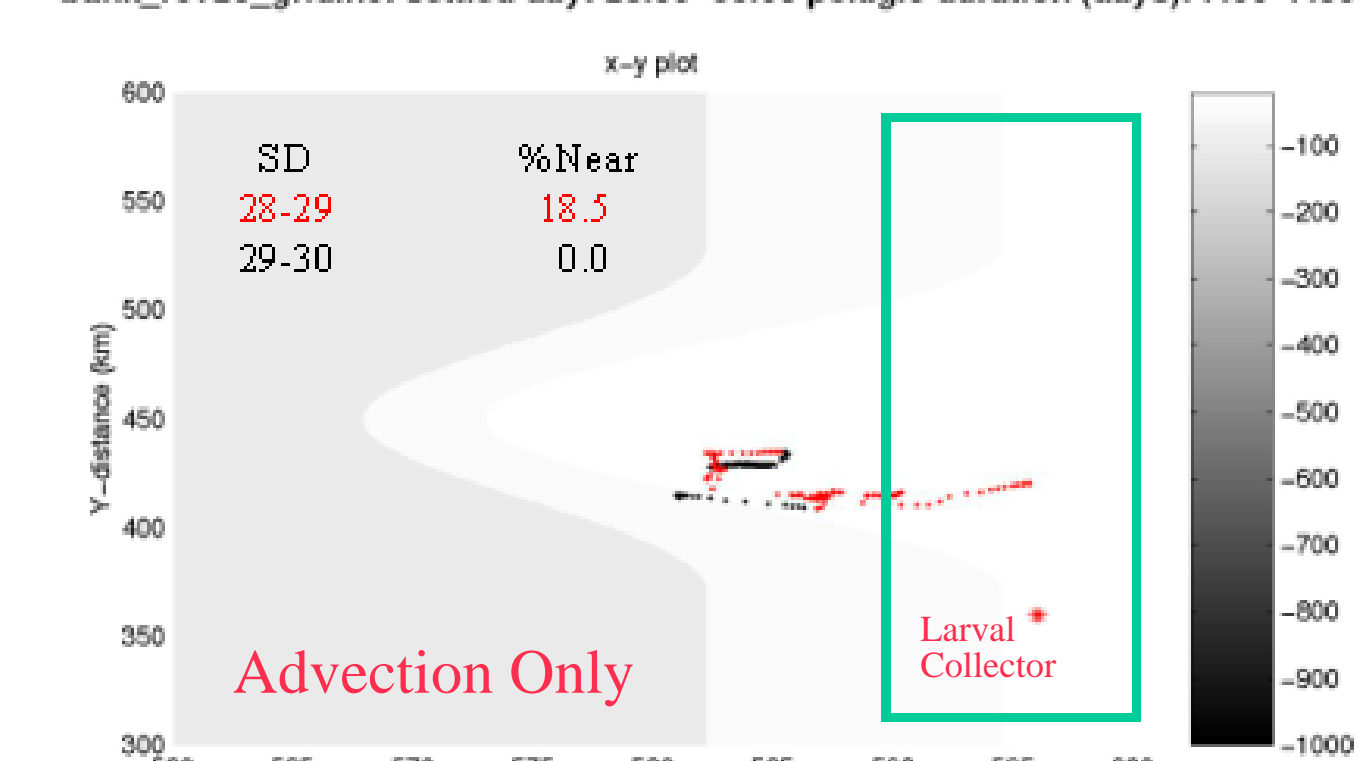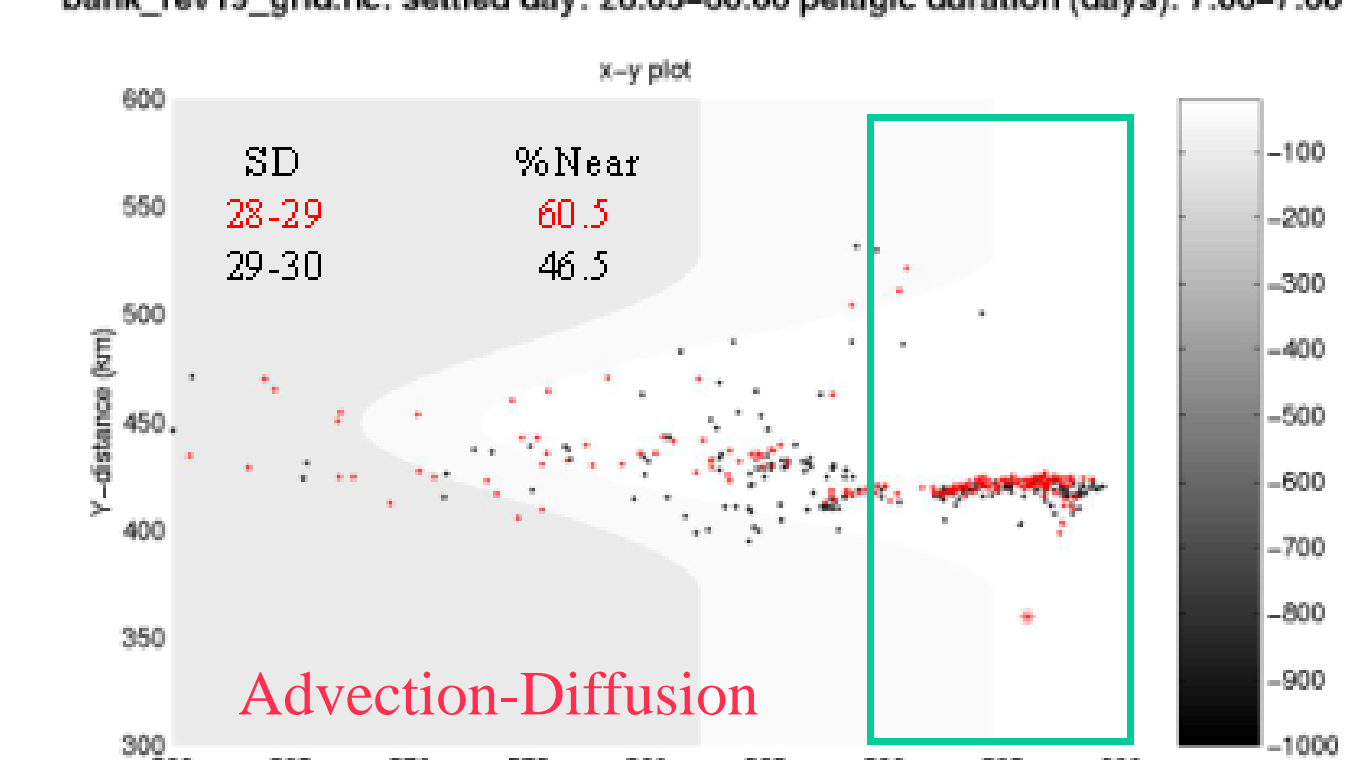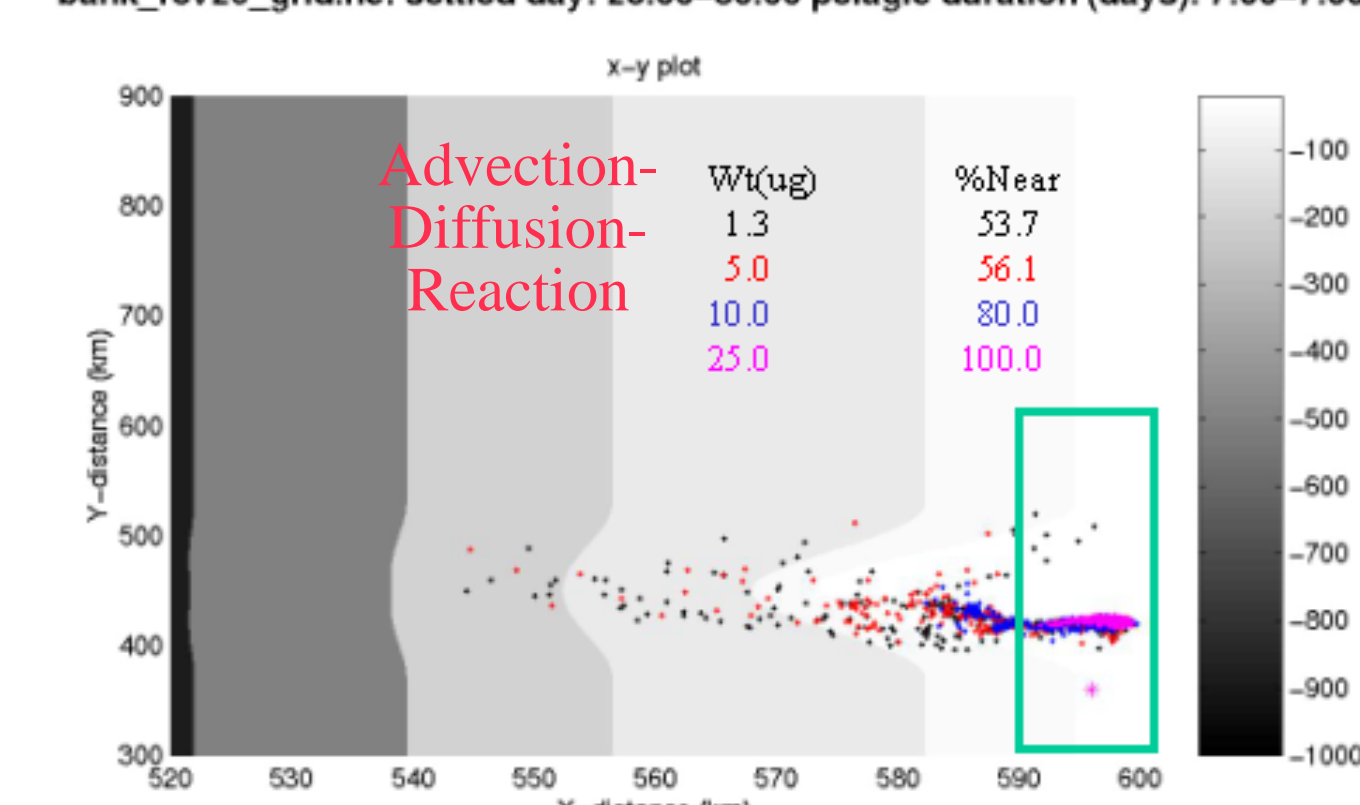

1D Simulations with NPZD+ Models

Questions: What is the minimum NPZD+ model that "mimics" nature adequately? How do we define "adequately"?

- Phytoplankton in nearshore high-N locations (e.g., upwelling) are often different (diatoms) than in offshore, low-N locations (flagellates, picoplankton), and distributed differently with depth.
- Regeneration of nutrients through a rapidly cycling microbial loop is important in low-N regions.
- Different cells and/or detritus particles have different sinking rates; export of N to depth.

A minimum model should reproduce the high-to-low-N gradient of phytoplankton composition, include a microbial loop, and perhaps different detrital pools.
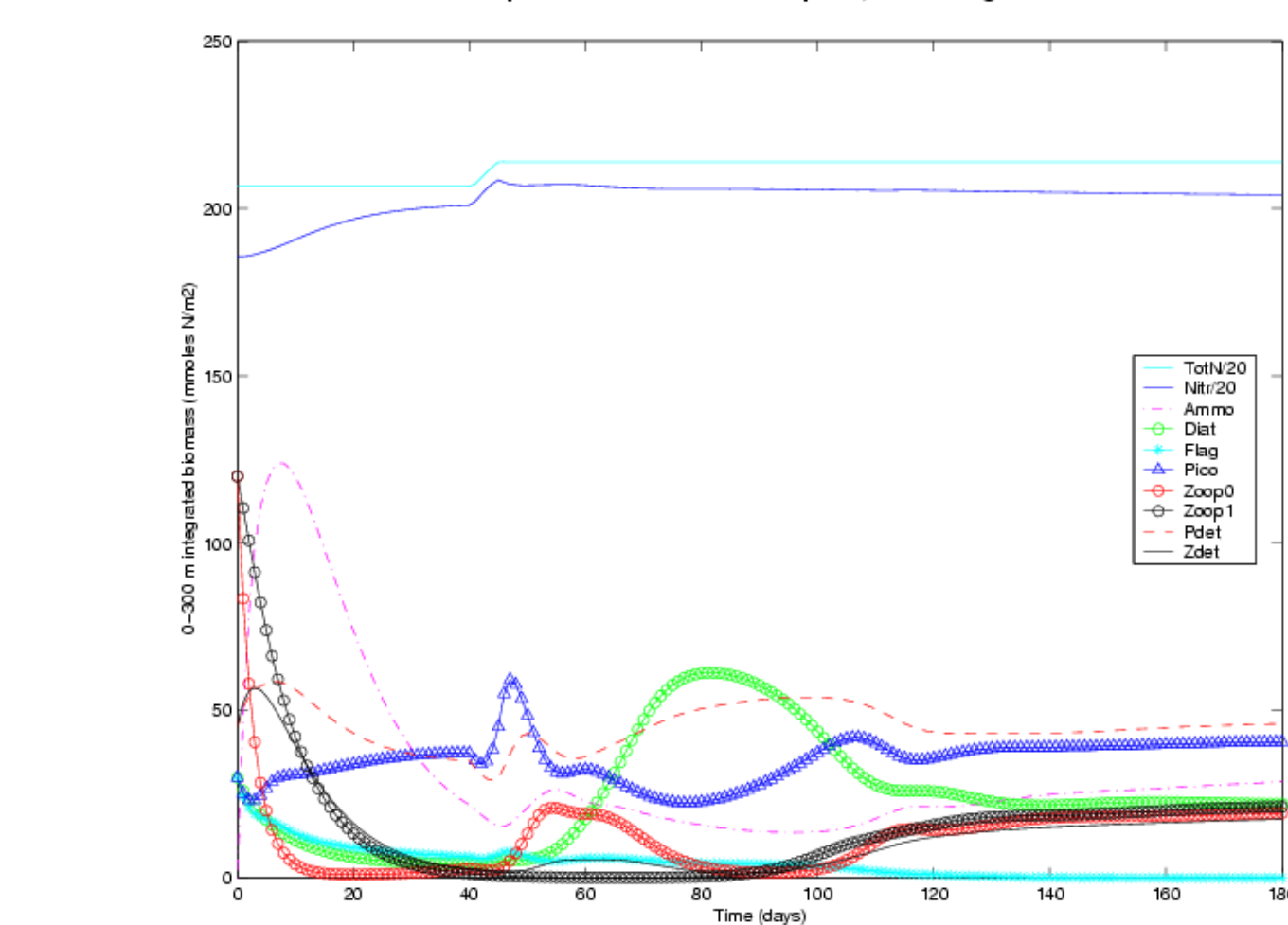
n2p3z2d2 Model
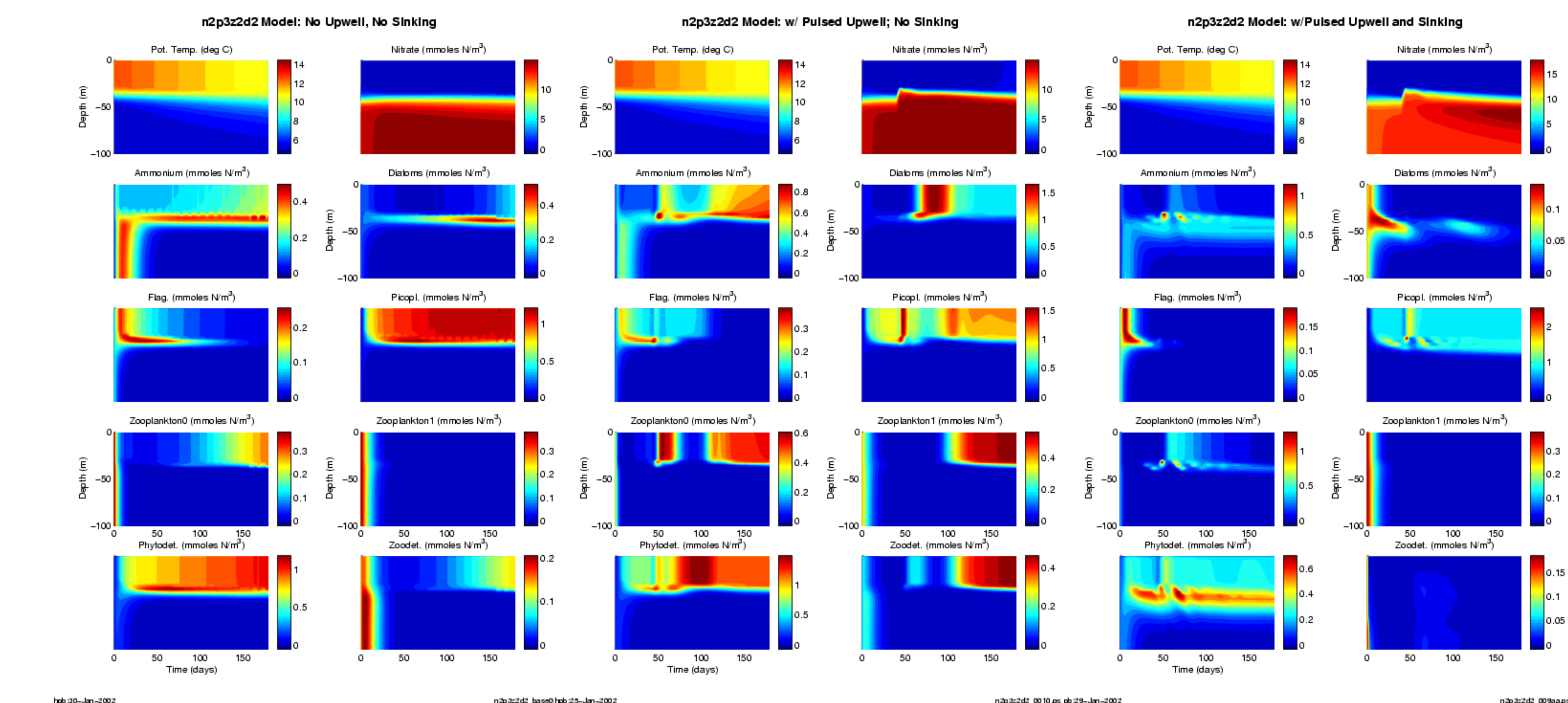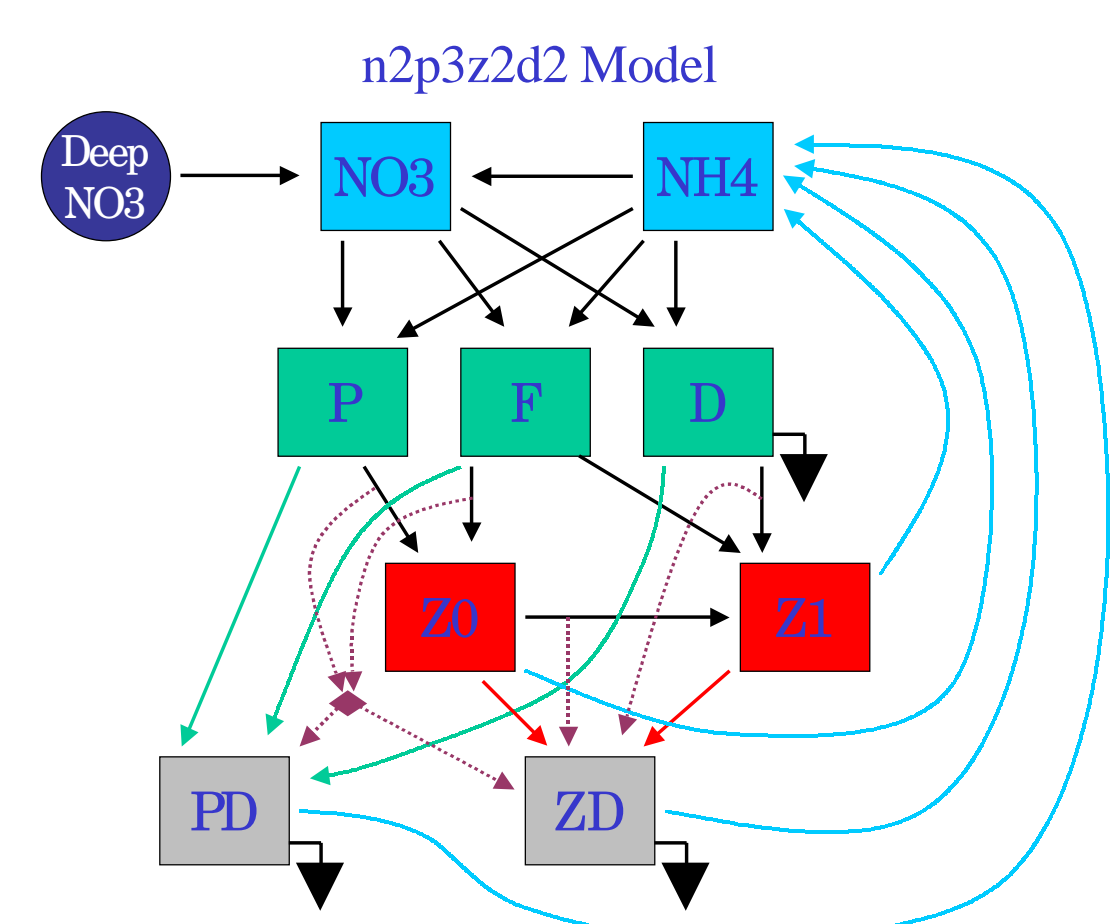
Preliminary Results—Just Beginning
1) Photic zone with low-N dominated by Pico and small zooplankton (Zoop0)—GOOD!
2) In absence of sinking, a pulse of upwelled NO3 leads to production of Diat and Zoop1—GOOD! But, the response is very slow, order 20-30 days, rather than 2-4 days—NOT GOOD
3) With sinking, same upwelling pulse of N shows no production of Diat and Zoop1—NOT GOOD.
4) Lots more work to do!

n2p3z2d2 Model: No Upwell, No Sinking
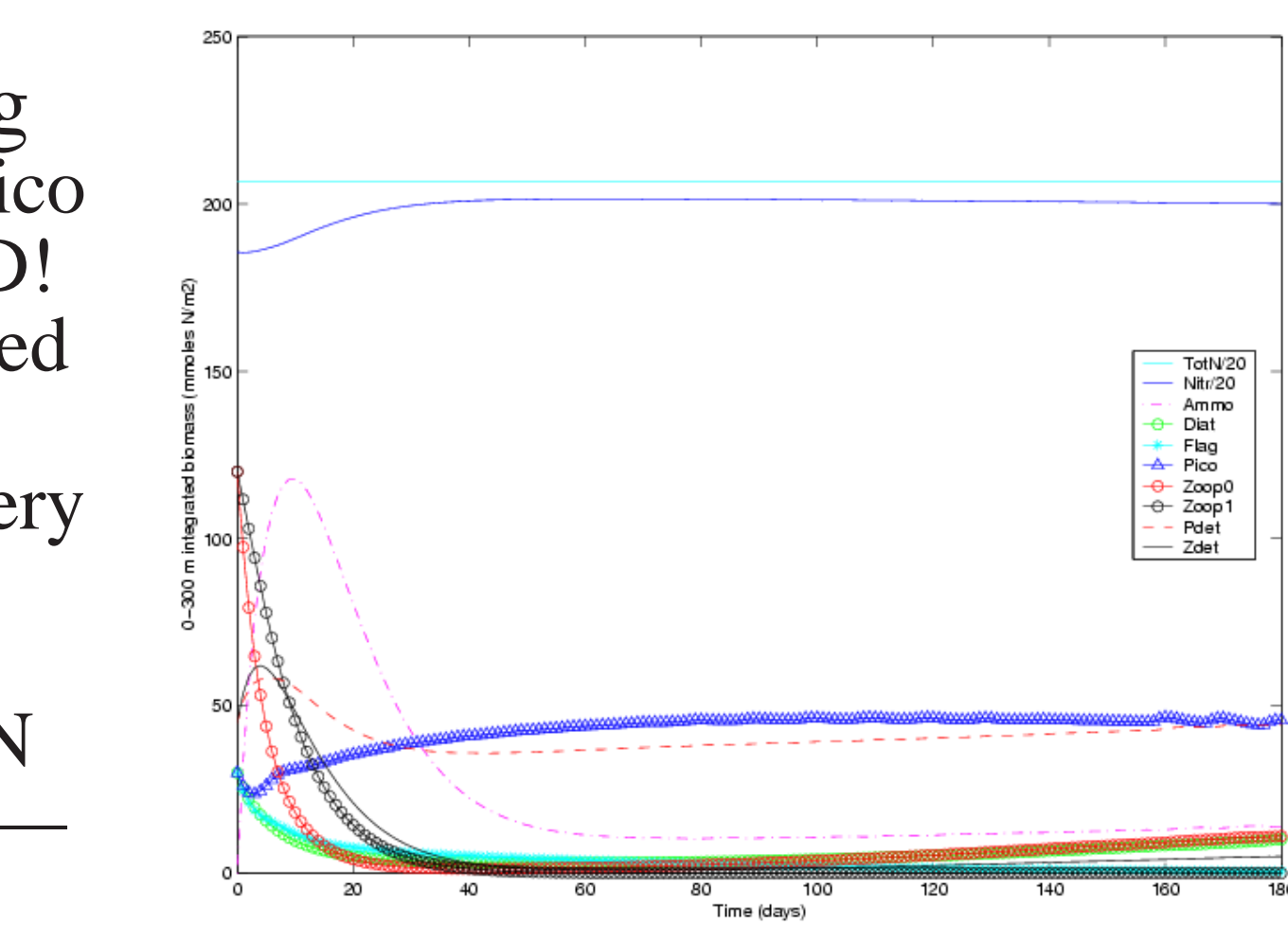
n2p3z2d2 Model: w/ Pulsed Upwell; No Sinking

n2p3z2d2 Model: w/Pulsed Upwell and Sinking