Biological-physical interactions and modeling
MOMSEI 2015

Rubao Ji, Benjamin Jones

October 2015
An example of biological-physical interaction

- Phytoplankton bloom
What is a phytoplankton bloom?
What is a phytoplankton bloom?

What are phytoplankton?
What is a phytoplankton bloom?

What are phytoplankton?

- *phyto*: plant.
- *plankton*: marine or aquatic organisms that cannot swim against a current.
What is a phytoplankton bloom?

What are phytoplankton?

Phytoplankton are marine or aquatic organisms that are autotrophic and drift with currents.
What is a phytoplankton bloom?

What are phytoplankton?

Phytoplankton are marine or aquatic organisms that are autotrophic and drift with currents.

Phytoplankton blooms are periods of increased phytoplankton abundance.
What size are phytoplankton and phytoplankton blooms?
What size are phytoplankton?

<table>
<thead>
<tr>
<th>Class</th>
<th>Size</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femptoplankton</td>
<td>≤0.2µm</td>
</tr>
<tr>
<td>Picoplankton</td>
<td>0.2-2µm</td>
</tr>
<tr>
<td>Nanoplankton</td>
<td>2-2µm</td>
</tr>
<tr>
<td>Microplankton</td>
<td>20-200µm</td>
</tr>
<tr>
<td>Mesoplankton</td>
<td>0.2-20mm</td>
</tr>
<tr>
<td>Macroplankton</td>
<td>2-20cm</td>
</tr>
</tbody>
</table>
What size are phytoplankton blooms?

[Image Credit: NASA–Earth Observatory]

[Image Credit: http://investigationsoanisetoceanographiee.wordpress.com/2012/04/page/2]

[Image Credit: NASA–Earth Observatory]
Why should we care?

- Marine phytoplankton fix 50% of the planet's oxygen.
- Marine phytoplankton first oxidized our atmosphere.
- Marine phytoplankton are major contributors to the global carbon cycle.
- Marine phytoplankton form the base of the pelagic food web.
How do we detect phytoplankton blooms?

- Ship-based sampling
How do we detect phytoplankton blooms?

- Flow cytometry

Flow Cytometry

Sheath fluid → Sample (stained cells in suspension) → Nozzle

Hydrodynamic Focusing: Cells pass through in 'single file'

Laser light source

Fluorescence emitted from stained cells detected

Forward and side scattered light from all cells detected

How do we detect phytoplankton blooms?

- Flow cytometry

[Image Credit: http://ifcb-data.whoi.edu/mvco]
How do we detect phytoplankton blooms?

- Aerial photography (satellites)
How do we detect phytoplankton blooms?

- Aerial photography (satellites)

[Image Credit: NASA]
How do we detect phytoplankton blooms?

- Ship-based sampling
- Flow cytometry
- Aerial photography (satellites)
How would you describe a phytoplankton bloom?
How would you describe a phytoplankton bloom?

- Where?
- When?
- How intense?
Describing where a bloom occurs—Latitude and Longitude
Describing where a bloom occurs—Region
Describing where a bloom occurs

- Latitude and Longitude
- Region
- Oceanography?
Describing when a bloom occurs—Start date

<table>
<thead>
<tr>
<th>Start Date</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar 15</td>
<td>0.0</td>
</tr>
<tr>
<td>Apr 01</td>
<td>0.5</td>
</tr>
<tr>
<td>Apr 15</td>
<td>1.0</td>
</tr>
<tr>
<td>May 01</td>
<td>1.5</td>
</tr>
</tbody>
</table>

**Time**

**Phytoplankton**
Describing when a bloom occurs—Maximum growth rate

![Graph showing phytoplankton abundance over time from March 15 to May 15. The graph peaks around April 15 with a maximum abundance value, with time on the x-axis and abundance on the y-axis.]}
Describing when a bloom occurs—Maximum abundance

![Graph showing the abundance of phytoplankton over time from March 15 to May 15.](graph)
Describing when a bloom occurs – Season/Climatology

[SCHL graph with various lines and markers representing different months and years.]

[Image Credit: Levy et al. 2007]
Describing when a bloom occurs

- Start Date
- Maximum Growth Rate
- Maximum Abundance
- Season or Climatology
Describing bloom intensity—Maximum abundance
Describing bloom intensity—Maximum growth rate

Time
Abundance
Phytoplankton
Describing Phytoplankton Blooms

Bloom Location
- Lat. and Lon.
- Region
- Oceanography

Bloom Timing
- Start date
- Max growth rate
- Max abundance

Bloom Intensity
- Max abundance
- Max growth rate
- Cum. abundance
<table>
<thead>
<tr>
<th>Bloom Location</th>
<th>Bloom Timing</th>
<th>Bloom Intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lat. and Lon.</td>
<td>Start date</td>
<td>Max abundance</td>
</tr>
<tr>
<td>Region</td>
<td>Max growth rate</td>
<td>Max growth rate</td>
</tr>
<tr>
<td>Oceanography</td>
<td>Max abundance</td>
<td>Cum. abundance</td>
</tr>
</tbody>
</table>
Phytoplankton Blooms in the Indian Ocean

[Image Credit: Levy et al. 2007]
The northern Indian Ocean has 2 seasonal blooms per year

[Image Credit: Levy et al. 2007]
Bloom timing varies geographically

[Image Credit: Levy et al. 2007]
What causes a bloom?

- If growth > mortality, then the bloom grows.
- If growth < mortality, then the bloom decays.
What causes a bloom?

- If growth > mortality, then the bloom grows.
- If growth < mortality, then the bloom decays.

What causes the growth rate to exceed the mortality rate?
What causes a bloom?

- If growth > mortality, then the bloom grows.

What causes the growth rate to exceed the mortality rate?
- The growth rate can increase.
- The mortality rate can decrease.
What causes a bloom?

- If growth > mortality, then the bloom grows.

What causes the growth rate to exceed the mortality rate?
- The growth rate can increase.
- The mortality rate can decrease.

What causes the growth rate to increase?
What is limiting the growth rate?
What limits phytoplankton growth in the oceans?
What limits phytoplankton growth in the oceans?

- **Light**

[Image Credit: http://oceanworld.tamu.edu/resources/ocng_textbook/chapter06/Images/Fig6-18.htm]
What limits phytoplankton growth in the oceans?

- Light

[Image Credit: Miller 2012]
What limits phytoplankton growth in the oceans?

- Nutrients

[Image Credit: Moore et al. 2013]
What limits phytoplankton growth in the oceans?

- **Light**
  Photosynthesis is limited to the euphotic zone (first 100m depth).

- **Nutrients**
  Nutrient limitation varies by region. Most commonly, nitrogen or iron is the primary limiting nutrient.
What limits phytoplankton growth in the oceans?

- **Light**
  Photosynthesis is limited to the euphotic zone (first 100m depth).

- **Nutrients**
  Nutrient limitation varies by region. Most commonly, nitrogen or iron is the primary limiting nutrient.

What are some conditions that may lead to a phytoplankton bloom in the ocean? What about near a river delta or an estuary?
Conditions leading to phytoplankton blooms

- Influx of nutrients from anthropogenic sources.
- Influx of nutrients from upwelling.
- Influx of nutrients from deepening of the mixed layer.
Sverdrup critical depth hypothesis

[Image Credit: http://www.jochemnet.de/fiu/OCB3043_22.html]
What causes a bloom?

- If growth > mortality, then a bloom grows.

What causes the growth rate to exceed the mortality rate?
- The growth rate can increase.

What causes the growth rate to increase?
- Influx of nutrients from anthropogenic sources
- Influx of nutrients from upwelling
- Influx of nutrients from mixed layer deepening.
- Shoaling of the mixed layer.
What causes a bloom?

- If growth > mortality, then a bloom grows.

What causes the growth rate to exceed the mortality rate?
- The growth rate can increase.

What causes the growth rate to increase?
- Influx of nutrients from anthropogenic sources
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- Influx of nutrients from mixed layer deepening.
- Shoaling of the mixed layer.
What causes a bloom?

- If growth > mortality, then a bloom grows.

What causes the growth rate to exceed the mortality rate?

- The growth rate can increase.
- The mortality rate can decrease.
What causes the mortality rate to decrease?

- There are fewer predators.
What causes a bloom to grow?

- If growth > mortality, then a bloom grows.
  - The growth rate can increase.
    - Influx of nutrients from anthropogenic sources
    - Influx of nutrients from upwelling
    - Influx of nutrients from mixed layer deepening.
  - The mortality rate can decrease.
    - There are fewer predators.
What causes a bloom to grow and decay?

- If growth > mortality, then a bloom grows.
  - The growth rate can increase.
    - Influx of nutrients from anthropogenic sources
    - Influx of nutrients from upwelling
    - Influx of nutrients from mixed layer deepening.
  - The mortality rate can decrease.
    - There are fewer predators.

- If growth < mortality, then a bloom decays.
  - There are insufficient nutrients
  - There are more predators
Location of the summer bloom

[Image Credit: Levy et al. 2007]
Timing of the onset of the physical bloom

[Image Credit: Levy et al. 2007]
Regionalization of the summer bloom

[Image Credit: Levy et al. 2007]
Wind circulation during the summer monsoon

[Image Credit: Talley et al. 2011]
Ocean circulation during the summer monsoon

[Image Credit: Talley et al. 2011]
Ekman transport drives upwelling

Upwelling induces a bloom in coastal regions

[Image Credit: Levy et al. 2007]
Deepening of the mixed layer drives a bloom in the Central Arabian Sea

[Image Credit: Levy et al. 2007]
Physical drivers of the summer bloom

Cumulative Chl

Max MLD

W-velocity

[Image Credit: Levy et al. 2007]
Physical Drivers of the Summer Bloom

- Ekman transport drives nutrient rich upwelling in nearshore regions.
- Horizontal advection and deepening of the mixed layer drive a bloom in the Central Arabian Sea.
- Rossby waves result in different initiation times for blooms throughout the northern Indian Ocean.
The winter bloom is less widespread than the summer bloom.

[Image Credit: Levy et al. 2007]
Upwelling does not drive the winter bloom

[Image Credit: Levy et al. 2007]
Mixed layer deepening may drive the winter bloom

[Image Credit: Levy et al. 2007]
Wind circulation during the winter bloom

[Image Credit: Talley et al. 2011]
Physical drivers of the winter bloom

Cumulative Chl

Max MLD

W-velocity

[Image Credit: Levy et al. 2007]
Physical drivers of the winter bloom

- The winter bloom is not driven by upwelling in most regions.
- Convective mixing and mixed layer mixing may drive the winter bloom.
- The relationship between primary production and MLD changes is not well understood.
Many parts of the northern experience 2 seasonal phytoplankton blooms each year. The onset timing of phytoplankton blooms in the northern Indian Ocean varies by region. Upwelling drives the summer bloom in many regions. Convective mixing may drive the winter bloom in the northern Arabian Sea. Processes regulating the summer blooms are better understood than those regulating the winter blooms.
Model equation

to compute

\[ B_i(x,y,z,t) \]

\[ \frac{\partial B_i}{\partial t} = R_{B_i} - \vec{v} \cdot \nabla B_i + \nabla (K \nabla B_i) \]

- Biological source and sink term
- Advection term
- Diffusion term
Model equations

\[
\frac{\partial B_1}{\partial t} = R_{B_1} - \left( u \frac{\partial B_1}{\partial x} + v \frac{\partial B_1}{\partial y} + w \frac{\partial B_1}{\partial z} \right) + \frac{\partial}{\partial x} \left( K_x \frac{\partial B_1}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial B_1}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial B_1}{\partial z} \right)
\]

\[
\frac{\partial B_2}{\partial t} = R_{B_2} - \left( u \frac{\partial B_2}{\partial x} + v \frac{\partial B_2}{\partial y} + w \frac{\partial B_2}{\partial z} \right) + \frac{\partial}{\partial x} \left( K_x \frac{\partial B_2}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial B_2}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial B_2}{\partial z} \right)
\]
Biological source/sink terms

\[
\frac{dP}{dt} = \frac{V_m NP}{K_s + N} - mP - ZR_m (1 - e^{-\Lambda_P})
\]

\[
\frac{dZ}{dt} = \gamma ZR_m (1 - e^{-\Lambda_P}) - gZ
\]

\[
\frac{dN}{dt} = \frac{V_m NP}{K_s + N} + mP + gZ - (1 - \gamma) ZR_m (1 - e^{-\Lambda_P}).
\]


Highlighted in Miller’s book ‘Biological Oceanography’
P-I relationship

Michaelis-Menten: \[ F(I) = \frac{I}{K_I + I} \]

Steele function: \[ f(I) = \frac{I}{I_S} \exp(1 - \frac{I}{I_S}) \]

Exponential saturation: \[ f(I) = (1 - \exp(-\frac{I}{I_S})) \exp(-b \frac{I}{I_S}) \]

Hyperbolic saturation: \[ f(I) = \frac{I/I_H}{(1 + (I/I_H)^2)^{1/2}} \frac{1}{(1 + b(I/I_H)^2)^{n/2}} \]

Tanh function: \[ f(I) = \tanh \frac{I}{I_C} \]
Grazing function

**Holling Type I**

Mechaelis-Menten

Rate of grazing = \( G_{max} \left( \frac{P}{K_s + P} \right) \)

Modified Mechaelis-Menten

Rate of grazing = \( G_{max} \left[ \frac{(P-P_0)}{(K_s + P-P_0)} \right] \)

**Holling Type II**

Modified Mechaelis-Menten

Rate of grazing = \( G_{max} \left( \frac{P^2}{K_s^2 + P^2} \right) \)

**Ivlev function**

Rate of grazing = \( G_{max} \left( 1 - \exp(-kP) \right) \)
Biological source/sink term

$N^3P^2Z^2D^2$

Multiple N,P,Z and D
Model equation

to compute

\[ B_i(x,y,z,t) \]

\[ \frac{\partial B_i}{\partial t} = R_{B_i} - \vec{v} \cdot \nabla B_i + \nabla (K \nabla B_i) \]
Advection/diffusion terms

\[
\begin{align*}
\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + v \frac{\partial u}{\partial y} + w \frac{\partial u}{\partial z} - f_v = & \frac{1}{\rho_o} \frac{\partial (p_H + p_a)}{\partial x} - \frac{1}{\rho_o} \frac{\partial q}{\partial x} + \frac{\partial}{\partial z} \left( K_m \frac{\partial u}{\partial z} \right) + F_u \\
\frac{\partial v}{\partial t} + u \frac{\partial v}{\partial x} + v \frac{\partial v}{\partial y} + w \frac{\partial v}{\partial z} + f_u = & \frac{1}{\rho_o} \frac{\partial (p_H + p_a)}{\partial y} - \frac{1}{\rho_o} \frac{\partial q}{\partial y} + \frac{\partial}{\partial z} \left( K_m \frac{\partial v}{\partial z} \right) + F_v \\
\frac{\partial w}{\partial t} + u \frac{\partial w}{\partial x} + v \frac{\partial w}{\partial y} + w \frac{\partial w}{\partial z} = & -\frac{1}{\rho_o} \frac{\partial q}{\partial z} + \frac{\partial}{\partial z} \left( K_m \frac{\partial w}{\partial z} \right) + F_w \\
\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = & 0 \\
\frac{\partial T}{\partial t} + u \frac{\partial T}{\partial x} + v \frac{\partial T}{\partial y} + w \frac{\partial T}{\partial z} = & \frac{\partial}{\partial z} \left( K_h \frac{\partial T}{\partial z} \right) + F_T \\
\frac{\partial S}{\partial t} + u \frac{\partial S}{\partial x} + v \frac{\partial S}{\partial y} + w \frac{\partial S}{\partial z} = & \frac{\partial}{\partial z} \left( K_h \frac{\partial S}{\partial z} \right) + F_S \\
\rho = & \rho(T, S, p)
\end{align*}
\]
# Model types

<table>
<thead>
<tr>
<th>Index</th>
<th>Example</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trophic level</td>
<td>Low, high, combined</td>
</tr>
<tr>
<td>Spatial dimension</td>
<td>0D, 1D, 2D, 3D</td>
</tr>
<tr>
<td>Biological structure</td>
<td>Functional group model, size-structured model, population dynamics model ...</td>
</tr>
<tr>
<td>Purposes</td>
<td>Theoretical, heuristic, predictive</td>
</tr>
<tr>
<td>Simulation mode</td>
<td>Hindcast, nowcast, forecast</td>
</tr>
<tr>
<td>Sequence</td>
<td>Forward, inverse</td>
</tr>
<tr>
<td>Mesh configuration</td>
<td>Structured, unstructured</td>
</tr>
<tr>
<td>Numerical approach</td>
<td>Eulerian, Lagrangian</td>
</tr>
</tbody>
</table>
Model by trophic level

- Lower trophic level (LTL): Nutrient-Phytoplankton-Zooplankton

- Higher trophic level (HTL): Fish, whale etc.

- Combined (LTL+HTL): usually a one way coupling from LTL to HTL.
Model by trophic level

*Rhomboid approach, de Young et al., 2004*
Model by spatial domain

\[ \frac{\partial B_1}{\partial t} = R_{B_1} - \left( u \frac{\partial B_1}{\partial x} + v \frac{\partial B_1}{\partial y} + w \frac{\partial B_1}{\partial z} \right) + \frac{\partial}{\partial x} \left( K_x \frac{\partial B_1}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial B_1}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial B_1}{\partial z} \right) \]

\[ \frac{\partial B_2}{\partial t} = R_{B_2} - \left( u \frac{\partial B_2}{\partial x} + v \frac{\partial B_2}{\partial y} + w \frac{\partial B_2}{\partial z} \right) + \frac{\partial}{\partial x} \left( K_x \frac{\partial B_2}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial B_2}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial B_2}{\partial z} \right) \]

\[ \vdots \]

\[ \vdots \]
Model by biological structure

- Functional group model: model compartment has similar type of ecosystem function.
  - NPZD can be viewed as a simple functional group model
  - More complex models have more functional groups

- Size-structured model: model groups based on the size of organisms. (different from size-spectrum model)

- Population-dynamics model: focusing on individual populations, stage or age resolved
Example of functional-group model

$N^3P^2Z^2D^2$

Multiple $N,P,Z$ and $D$

Ji et al., 2006
Example of functional group model

Doney et al., 1996; 2009. Moore et al., 2004
Example of functional group model

Walsh et al., 2001
Example of size-structured model

Baird and Suthers, 2007
# Allometric relationship

## Table 1 – Allometric relationships for phytoplankton

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Allometric relationship</th>
<th>Units</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon content$^a$</td>
<td>$m_{PC} = 2.12(x/ \div 2.46)V_P^{0.761(\pm0.0272)}$</td>
<td>mol C cell$^{-1}$</td>
<td>37</td>
</tr>
<tr>
<td>Chlorophyll concentration$^b$</td>
<td>$C = 2.06 \times 10^7(x/ \div 1.36)(10^{18}V_P)^{-0.320(\pm0.035)}$</td>
<td>mg Chl a m$^{-3}$</td>
<td>16</td>
</tr>
<tr>
<td>Maximum growth rate$^c$</td>
<td>$\mu_p^{\text{max}} = 3.46(x/ \div 1.16)(10^{18}V_P)^{-0.15(\pm0.019)}$</td>
<td>day$^{-1}$</td>
<td>126</td>
</tr>
<tr>
<td>Sinking velocity$^d$</td>
<td>$w_P = 5.60(x/ \div 2.29)\rho_P^{1.17(\pm0.071)}$</td>
<td>m s$^{-1}$</td>
<td>22</td>
</tr>
<tr>
<td>Swimming velocity$^e$</td>
<td>$U_p = 0.00272(x/ \div 6.43)\rho_P^{0.229(\pm0.155)}$</td>
<td>m s$^{-1}$</td>
<td>19</td>
</tr>
</tbody>
</table>

## Table 2 – Allometric relationships for protozoa

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Allometric relationship</th>
<th>Units</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon content$^a$</td>
<td>$m_{z,c} = 1.29(\pm0.168) \times 10^5 V_Z$</td>
<td>g C cell$^{-1}$</td>
<td>9</td>
</tr>
<tr>
<td>Swimming speed$^b$</td>
<td>$U_Z = 0.0885(x/ \div 9.91)\rho_Z^{0.553(\pm0.196)}$</td>
<td>m s$^{-1}$</td>
<td>21</td>
</tr>
<tr>
<td>Sinking speed$^c$</td>
<td>$w_Z = 5.60(x/ \div 2.29)\rho_Z^{1.17(\pm0.071)}$</td>
<td>m s$^{-1}$</td>
<td>22</td>
</tr>
<tr>
<td>Maximum growth rate$^d$</td>
<td>$\mu_Z^{\text{max}} = 0.00271(x/ \div 3.31)\rho_Z^{-0.529(\pm0.101)}$</td>
<td>day$^{-1}$</td>
<td>41</td>
</tr>
<tr>
<td>Yield$^e$</td>
<td>$\gamma_Z = 0.308(\pm0.0266)$</td>
<td>mol mol$^{-1}$</td>
<td>14</td>
</tr>
<tr>
<td>Minimum predator-prey size ratio$^f$</td>
<td>$\eta_{Z,\text{min}} = 3.00(\pm0.930)$</td>
<td>–</td>
<td>4</td>
</tr>
<tr>
<td>Maximum predator-prey size ratio$^g$</td>
<td>$\eta_{Z,\text{max}} = 22.6(\pm8.01)$</td>
<td>–</td>
<td>3</td>
</tr>
</tbody>
</table>
Example of population dynamics model

Krill model, Carlotti and Sciandra, 1989
food web + population model

Physical models

Ocean GCM
Global Tidal Model
Freshwater Input

Atmospheric Model MM5/WRF

Ocean Model (FVCOM)

Satellite SST, U,V Buoys T,S,U,V

Food web model

Nitrogen → Phytoplankton
Phytoplankton → Detritus → Zooplankton

Copepod model

Egg → Nauplii → Copepodite → Adult

Ji et al., 2009
Model by purpose

(Franks 1996)

- Theoretical models: (or process-oriented models)
  - “what will happen if ...?”
  - Theoretical models are usually used to explore general principles of biological-physical processes and to predict potential outcomes based on idealized scenarios.
  - models are not intended to simulate any specific system, but are often used to predict the general pattern of system responses to the modeled processes.
Model by purpose

(Franks 1996)

- Heuristic models (Dynamic interpolation models)
  - “How did this happen ... ?”
  - Models are formulated and parameterized based on evidences from field measurements or laboratory experiments.
  - mainly used to interpret the retrospective data sets and to explore how a particular scenario occurs.
Predictive models

- “what will happen ...?”
- Models that are well-tested or calibrated by long-term measurement data, to render them capable of predicting the behavior of the ecosystem beyond the constraints of available data.
- Our current understanding of marine ecosystem remain inadequate due to particularly complex interactions between physical and biological processes.
Model by simulation mode

- **Hindcast**: Simulation of the past states
  - Most models are in hindcast mode

- **Nowcast**: Simulation of the present (or immediate future) states

- **Forecast**: Simulation of the future states
  - Still a challenge
Model by sequence

- Forward model: run forward in time from specified initial conditions and parameters. The simulation is compared to observations to assess its realism or predictive power.

- Inverse model: Use observation to reconstruct the initial conditions and/or the parameters.

- Both (data assimilation): run model in forward and inverse modes iteratively.
Model by grid configuration

Structured e.g. POM, ROMS, HyCOM

Unstructured e.g. FVCOM, QUODDY

Vertical co-ordinate also varies Sigma, z, isopycnal, hybrid etc.
Model by grid configuration

Structured grid, but curvilinear
Model by grid configuration
Model by numerical approach

- **Eulerian**: Concentration based model
- **Lagrangian**: Individual based model
Existing models ...

- Physics vs biology
- Climatology vs interannual variability
- Lower vs higher trophic level
- Hindercast vs forecast model
- Process oriented vs real simulation
- Bulk property vs population level
- Rhomboid vs end-to-end
Another example of biological-physical interaction

Marine population connectivity
What is population connectivity

Population connectivity is the exchange of individuals among geographically separated subpopulations that comprise a metapopulation.

Cowen & Sponaugle 2009
Population connectivity is the exchange of individuals among geographically separated subpopulations that comprise a metapopulation.

Cowen & Sponaugle 2009

A metapopulation is a set of local populations, with the dynamics of local populations strongly dependent upon local demographic processes, but also influenced by a nontrivial element of external replenishment.

Kritzer & Sale 2004
What is population connectivity

Population connectivity is the exchange of individuals among geographically separated subpopulations that comprise a metapopulation.

Cowen & Sponaugle 2009
Population connectivity can allow a metapopulation to persist even when each individual patch would not.
Estimating Larval Dispersal

- In situ observations
- Geochemical tracers
- Direct genetic methods
- Indirect genetic methods
- Biophysical models
Estimating Larval Dispersal

- In situ observations
- Geochemical tracers
- **Direct genetic methods**
- Indirect genetic methods
- **Biophysical models**
Estimating Larval Dispersal—Direct Genetic Methods

[Image Credit: Simon Thorrold–WHOI]
Estimating Larval Dispersal–Direct Genetic Methods

A. Satellite image of Kimbe Bay showing the study areas.
B. Detailed map of Kimbe Bay with labeled islands.
C. Underwater image of a coral reef.
D. Photograph of a clownfish in its anemone.

[Image Credit: Planes et al. 2009]
Estimating Larval Dispersal—Direct Genetic Methods

[Image Credit: Planes et al. 2009]
Individual Based Biophysical Modeling

**Physical model**
Numerically simulate high resolution velocity, temperature, salinity, *etc.* fields.

**Biophysical model**
Spawn virtual larvae and track their position and state over time.

**Analysis**
Synthesize the particle-tracking results into ecologically meaningful information.
Individual Based Biophysical Modeling

- Read the configuration
- Create the individuals
- Load forcing data
- Update the individual states:
  - Interpolation
  - Movement
  - Biology
- Record individual states
- Cleanup and exit
Individual Based Biophysical Modeling

- Read the configuration
- Create the individuals
- Load forcing data
- Update the individual states
  - Interpolation
  - Movement
  - Biology
    - Growth
    - Mortality
    - Swimming
- Record individual states
- Cleanup and exit
Study system for the modeling studies

Butler et al.: Behavior of lobster larvae
Dispersal in retentive versus advective environments

The results of the simulation comparing passive and active Panulirus argus larval dispersal from 2 spawning sites in Belize, which differed in coastal oceanography, were similar to the results of the overall simulation runs for all of the 13 release sites. Simulations for the 2 contrasting sites in Belize revealed that total settlement increased by a factor of 4 when larvae vertically migrated, and also resulted in settlement occurring appreciably closer to spawning sites (ca. 570 km closer) than when larvae dispersed passively (Fig. 7). The maximum dispersal of larvae differed little when released in the 2 contrasting environments in Belize. However, the mean dispersal was much lower in the retentive environment near Glovers Atoll (mean dispersal = 210 km) than at Ambergris Cay (mean dispersal = 500 km) where larvae tend to be swept northward (Fig. 7).

The shape of the dispersal kernels also differed between these contrasting hydrodynamic environments depending on larval behavior (Fig. 7). In the advective environment near Ambergris Cay, dispersal was greater and more evenly distributed between 500 and 1500 km when larvae drifted passively. The shape of the bimodal dispersal kernel became strongly asymmetrical when larvae engaged in OVM; most larvae settled ca. 250 km away, although an appreciable number settled >1000 km away. At Glovers Atoll, where a persistent gyre occurs offshore, the dispersal kernel was bimodal for both passive and active larvae, but OVM again accentuated that asymmetry by shifting peak settlement closer (100 km) to their natal origin.

DISCUSSION

We used laboratory experiments to explore ontogenetic changes in larval phototaxis, plankton sampling to verify size-specific larval depth distributions and biophysical modeling to explore the consequences of ontogenetic vertical migration (OVM) and hydrodynamics on the dispersal of spiny lobster larvae. This taxon has a long planktonic larval duration (PLD) and is

[Image credit: Butler et al. 2011]
Ontogenetic vertical migration may influence dispersal trajectories

Figure 4. Panulirus argus. (A) Size-specific depth distribution of phyllosome larvae determined from monthly plankton surveys in 2003 and 2004. The relative abundance of larvae (x-axis) in each of 4 depth bins (y-axis) that were sampled (0–25 m, 25–50 m, 50–75 m and 75–100 m) are plotted for each of the 4 larval size (and estimated age) classes (histograms). (B) Age-specific depth distributions produced by the model algorithm for OVM. Plotted is the relative abundance (% of total) of larvae (x-axis) in each of 5 modeled depth bins (y-axis) for larvae of different ages (histograms)

Figure 5. Panulirus argus. Dispersal kernels (histograms) for spiny lobster phyllosome larvae with and without OVM depicted as the mean probability (× 10⁻⁴ ± 95% CI) that dispersed and arrived at settlement habitat locations at different distances (km) from 11 spawning sites in the Caribbean Sea. (A) Simulation results for passively transported larvae compared with (B) simulations where larvae engaged in OVM. The smoothed lines are the best-fit lines for the dispersal histograms

[Image Credit: Butler et al. 2011]
Ontogenetic vertical migration may influence dispersal trajectories

Fig. 4. *Panulirus argus*. (A) Size-specific depth distribution of phyllosome larvae determined from monthly plankton surveys in 2003 and 2004. The relative abundance of larvae (x-axis) in each of 4 depth bins (y-axis) that were sampled (0–25 m, 25–50 m, 50–75 m and 75–100 m) are plotted for each of the 4 larval size (and estimated age) classes (histograms). (B) Age-specific depth distributions produced by the model algorithm for OVM. Plotted is the relative abundance (% of total) of larvae (x-axis) in each of 5 modeled depth bins (y-axis) for larvae of different ages (histograms)

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[Image Credit: Butler et al. 2011]
Ontogenetic vertical migration may increase dispersal success.
Larvae may orient to chemical, acoustic, or light based cues.
Horizontal swimming increases settlement success.

A  
**Early Orientation**

% of larvae that settle

<table>
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<th>Month</th>
<th>1 km</th>
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<th>10 km</th>
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<td>Aug-Sept</td>
<td>0</td>
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<td>40</td>
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B  
**Late Orientation**

% of larvae that settle

<table>
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<tr>
<th>Month</th>
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<th>10 km</th>
<th>no orientation</th>
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<tr>
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<td>Aug-Sept</td>
<td>20</td>
<td>40</td>
<td>60</td>
<td>80</td>
</tr>
</tbody>
</table>

[Image Credit: Staaterman et al. 2012]
Orientation distance and start time influence success more than cue strength.

Fig. 4. Sensitivity analysis for the cue strength, $k$. The mean and standard deviation of the percent of larvae that were released from the Dry Tortugas site that settled. Open circle: no orientation scenario, solid line=early orientation, dotted line=late orientation. A larger detection distance and early orientation had a greater effect on settlement than did cue strength, $k$. 

[Image Credit: Staaterman et al. 2012]
Horizontal swimming decreases dispersal distance.
Summary

- Larval swimming may increase settlement success.
- Larval swimming may decrease dispersal distance.
- Evidence exists for larval behaviour in western Pacific fish species.
- Larval sensory biology has vast opportunities for research.
Case Study: Population Connectivity in the Indo-Pacific

Year (1999), and a neutral year (2001). Year selection was based on the Oceanic Niño Index published by the Climate Prediction Center of the National Oceanic and Atmospheric Administration (NOAA). Dispersal simulations were completed in every season for each year.

Table 1

<table>
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<th>Primary graph definitions</th>
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<td>Edge</td>
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<tr>
<td>Neighborhood</td>
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<td>Path</td>
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Fig. 2

Study area showing locations of reefs and land masses across the Tropical Pacific. Bathymetry is in gray with shallow areas in lighter shades.

[Image Credit: Treml et al. 2008]
Treml et al. 2008–Objectives

- How connected is the Indo-Pacific overall?
- How much do species specific parameters influence population connectivity?
- How much does interannual variability influence population connectivity?
Advection-diffusion model

\[
\frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N
\]  

\( \frac{\partial N}{\partial t} \) = change in larval concentration over time at a place.
Advection-diffusion model

\[
\frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N
\]  

- \( \frac{\partial N}{\partial t} \) = change in larval concentration over time at a place.
- \( \frac{\partial N}{\partial x} \) = change in larval concentration along the x-axis.
- \( u \) = velocity along the x-axis.
Advection-diffusion model

\[ \frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N \]  

- \( \frac{\partial N}{\partial t} \) = change in larval concentration over time at a place.
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- \( u \) = velocity along the x-axis.
- \( \frac{\partial N}{\partial y} \) = change in larval concentration along the y-axis.
- \( v \) = velocity along the y-axis.
Advection-diffusion model

\[
\frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N \tag{1}
\]

- \( \frac{\partial N}{\partial t} \) = change in larval concentration over time at a place.
- \( \frac{\partial N}{\partial x} \) = change in larval concentration along the x-axis.
- \( u \) = velocity along the x-axis.
- \( \frac{\partial N}{\partial y} \) = change in larval concentration along the x-axis.
- \( v \) = velocity along the y-axis.
- \( K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) \) = change in larval concentration over space due to diffusion.
Advection-diffusion model

\[
\frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N \tag{1}
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- \( K \left( \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) \) = change in larval concentration over space due to diffusion.
- \( \mu N \) = larval mortality.
Population connectivity as a graph

- $d_{ij}$ = Time taken to move from site $i$ to site $j$.
- $p_{ij}$ = Probability of dispersal = $ae^{-\theta d_{ij}}$
Population connectivity as a graph

- $d_{ij} =$ Time taken to move from site $i$ to site $j$.
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Population connectivity as a graph

- $d_{ij} =$ Time taken to move from site $i$ to site $j$.
- $p_{ij} =$ Probability of dispersal $= ae^{-\theta d_{ij}}$
Calculating the largest component of a graph

[Image Credit: Treml et al. 2008]
El Niño state influences connectedness.
Long PLDs are necessary to connect island groups.
El Niño years connect island groups that are not otherwise connected.
Common dispersal pathways highlight areas that are important to conserve.

[Image Credit: Treml et al. 2008]
Common dispersal pathways highlight areas that are important to conserve.
How connected is the Indo-Pacific overall? Pretty well connected, but there are some isolated island groups.

How much do species specific parameters influence population connectivity?

How much does interannual variability influence population connectivity?
How connected is the Indo-Pacific overall?
Pretty well connected, but there are some isolated island groups.

How much do species specific parameters influence population connectivity?
Not a lot locally, but long PLDs (60 days) can allow for longer distance dispersal.

How much does interannual variability influence population connectivity?
How connected is the Indo-Pacific overall? Pretty well connected, but there are some isolated island groups.

How much do species specific parameters influence population connectivity? Not a lot locally, but long PLDs (60 days) can allow for longer distance dispersal.

How much does interannual variability influence population connectivity? A fair amount. El Niño years tend to be better connected than La Niña years. The average year falls somewhere in between.