

The Princeton Ocean Ecosystem Model (POEM)

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The Model

The Princeton Ocean Ecosystem Model (POEM) has two main components: (1) the Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT) marine ecosystem model and (2) a size-structured model of high-trophic level dynamics.

COBALT

COBALT is used to provide the biogeochemical and planktonic food web dynamics for the size-structured food web model herein. COBALT uses 33 state variables to resolve global-scale cycles of nitrogen, carbon, phosphate, silicate, iron, calcium carbonate, oxygen, and lithogenic material. COBALT is run as part of the Modular Ocean Model (MOM) version 4.1, with 60 year simulations (1948-2008) forced by the Common Ocean-Ice Reference Experiment (CORE-II) data set as well as a future scenario running from 2006 to 2100 using relative concentration pathways (rcp) 8.5 as the carbon emissions scenario. The horizontal resolution of the simulation is 1° Latitude/Longitude, except along the equator where the resolution is refined to $1/3^\circ$. The model uses 50 vertical layers, with a resolution of 10m over the top 200m. The representation of planktonic food web dynamics within COBALT includes small and large phytoplankton with the latter group comprised of diatoms and dinoflagellates, and three zooplankton groups that feed on phytoplankton, bacteria and each other according to mean predator prey size ratios. The “small” zooplankton group represents microzooplankton that are $< 200\mu m$ in equivalent spherical diameter (ESD). The medium zooplankton are parameterized as small to medium bodied copepods ($0.2 - 2mm$ ESD), and the large zooplankton are parameterized as large copepods/krill ($2 - 20mm$ ESD). The parameterization of trophic interactions relies primarily on the allometric and bioenergetics relationships described in, and the model was calibrated to ensure quantitative consistency with large-scale planktonic food web dynamics, including patterns in primary and meso-zooplankton production. COBALT estimates zooplankton mortality rates using a density dependent closure term. This mortality term accounts for all zooplankton production that is not consumed by other zooplankton, and hence represents feeding by higher predators and other sources of mortality that are not

resolved explicitly. This density dependence has empirical support and reflects an assumption that the biomass of predators responds to the biomass of prey.

COBALT is linked to the size-structured food web model described herein in an “off-line” fashion. That is the biomass abundance and mortality rates of zooplankton (to fish) from COBALT are used to drive the dynamics of the size-structured food web model. Furthermore, the rate of detrital flux to the sea-floor is used to drive a benthic size-structured food-web model. The size-structured food-web model is comprised of three major animal groups: planktivorous fish, piscivorous fish and benthic invertebrates. The dynamics of these groups are all modeled using the size-structured formulation of Van Leeuwen et al. 2008 (How Cod Shapes its World). Each group (planktivore, piscivore, detrivore) is modeled as a collection of size-classes, with smaller classes growing (somatically) into larger size classes. The size-structured model is the same across groups, but with difference in dynamics governed by the choice of parameters.

Size-Structured Ecosystem Model

The general form of the size-structure model, which is applied to each the planktivore, piscivore and detrivore groups, is as follows. The rate of change of biomass density ($g\ m^{-2}$) for the smallest size classes indexed 1:

$$B_1^* = B_1^t + \sum_{j \neq 1}^{N-1} (1 - \kappa_j) \nu_j B_j^t - \kappa_1 \gamma_1 B_1^t - d_1 B_1^t, \quad (1)$$

where first term on the right-hand-side is the total amount of newborn biomass (i.e. summed over all larger size classes: $j \neq i$) recruiting to the smallest size-class. ν_i is the total energy available for growth and κ is a unit-less parameter that controls the fraction of ν used for somatic growth, hence $1 - \kappa_j$ is the energy invested in the production of larvae/eggs for each size-class j . The total amount of newborn biomass recruiting to the first size-class is hence the summation of larvae/egg production over all larger size-classes ($j \neq i$). The second term is the loss of biomass (of size-class 1) due to somatic growth or maturation, where γ is a function of ν that accounts for the loss of biomass within a size-class. The last term is the loss of

44 biomass due to natural mortality.

For any larger size class of any group, the rate of change of biomass is:

$$B_i^* = B_i^n + \kappa_{i-1}\gamma_{i-1}B_{i-1} - \kappa_i\gamma_iB_i - (1 - \kappa_i)\nu_iB_i - d_iB_i, \quad (2)$$

45 for $i = 2, \dots, N$. Here, the first term on the right-hand-side is maturing biomass from the previous size-class,
 46 the second term is the loss of biomass due to somatic growth, the third term is the loss of biomass to
 47 egg/larvae production and the last term is the loss of biomass due to natural mortality. Note, there is no
 48 recruitment term, for we assume all newborn biomass recruits to the smallest size-class.

The energy available for growth for a given size-class i is:

$$\nu_i = \lambda I_i - T_i, \quad (3)$$

where λ is the food assimilation efficiency ($g_i g_j^{-1}$), I is the biomass consumed ($g_j g_i d^{-1}$) and T is biomass-specific metabolic costs ($g_i g_i^{-1} d^{-1}$). The energy available for somatic growth is:

$$\gamma_i = \frac{\nu_i - \frac{1}{\kappa_i}d_i}{1 - z_i^{(1-d_i)/(\kappa_i\nu_i)}}, \quad (4)$$

49 where d_i is the natural mortality rate of size-class i ($g_i g_i^{-1} d^{-1}$) and z_i is the ratio of the initial and the
 50 final body size that a particular life stage encompasses and hence reflects the size range that an individual
 51 has to grow through before maturing to the next stage.

52 Consumption

Consumption of prey biomass, for each group, is calculated using a multi-prey Type II feeding function:

$$I_i = \sum_{j \in J} \frac{a_i B_j^t \phi_{ij}}{1 + a_i \tau_i \sum_{j \in J} B_j^t \phi_{ij}}, \quad (5)$$

53 where we for the sake of generality, we use the index i to identify any size-class from any group, and j its
 54 prey which is in the set J , which depends on the predator (and group that that predator belongs too). a_i is
 55 the size-class specific per unit body-mass search rate ($m^2 d^{-1} g_i^{-1}$), τ_i is the time it takes for one individual
 56 of size-class i , in terms of body-weight, to digest a unit of biomass of prey j ($d g_j g_i^{-1}$). Here, j indexes all
 57 size-classes in all groups, and it is a diet-preference factor ϕ_{ij} that determines how much of any given prey,
 58 piscivore i eats.

The diet set J varies greatly amongst the groups. For the piscivore the set J encompasses all groups: piscivore (hence it is carnivorous), planktivore, detritivore and zooplankton. The planktivore size-classes only eat zooplankton. The detritivore size-classes are carnivorous and also eats benthic detrital matter, which is modeled explicitly:

$$W^{t+1} = W^t + Det - Sed - \sum_i^{\tilde{N}} I_i, \quad (6)$$

59 where W is the biomass pool of detrital matter on the sea-floor ($g m^{-2}$), D is the flux of detrital matter
 60 from the water column ($g m^{-2} d^{-1}$; this is given by COBALT as an offline component), S is the rate of
 61 sedimentation of this biomass ($g m^{-2} d^{-1}$; again a rate given by COBALT) and I_i is the consumption by
 62 the detritivore of size-class i of which there are \tilde{N} .

63 Demographic Parameters

64 The parameters of the size-structured model are: the minimum and maximum size-classes for each group,
 65 the fraction of biomass that is used for somatic growth κ_i , the natural mortality rate d , the rate at which

66 biomass is lost due to metabolic costs T , the diet preference of each size class in each group ϕ_{ij} , the areal
 67 search rate a_i (which is also the diffusivity used in modeling movement, and the per unit biomass handling
 68 time τ_i .

69 We assume that medium and large zooplankton are each defined by a unique and discrete body-size: $2mm$
 70 and $20mm$ equivalent spherical diameter (ESD) respectively. Using the following empirical relationship for
 71 dry weight (DW): $\ln(DW) = 2.96 + 2.73\ln(ESD)$ (McCauley et al. 1984), we estimate the body mass (g)
 72 for medium and large zooplankton. These values are then used in the construction of ϕ_{ij} to identify which
 73 fish size classes eat zooplankton.

74 The areal search rate a_i ($m^2 \text{ day}^{-1} g^{-1}$) was determined using a mechanistic relationship between body size
 75 and visual search radius: $a_i = \omega_i L_i \nu_i / s_i$, where ω is the fraction of time spent hunting for food, L_i and ν_i
 76 are the length (m) and swimming speed ($m \text{ day}^{-1}$) of size class i respectively. Body lengths are calculated
 77 from the empirical relationship: $L_i = (s_i/0.025)^{(1/3)}/100$. Swimming speeds are taken from Megrey et al.
 78 2007...

79 Handling times ($days$) between all pairs of size classes are calculated using a relationship between predator
 80 and prey body size developed by (Rall et al. 2012): $\tau_{ij} = t_0 s_i^{83} s_j^{0.5}$, where t_0 is a constant determined
 81 from empirical data (93.69 days). The assimilation efficiency $\lambda = 0.7$ accounts for many individual level
 82 processes, for example egestion.

83 Diet preferences are defined using empirical predator-prey mass ratios (PPMRs). Specifically, $PPMR$ values
 84 are taken from the empirical gut-content analysis of Barnes et al. 2010, who defined a mean $PPMR$ $\psi = 3$,
 85 with a $PPMR$ standard deviation $\sigma = 1.3$. Similar to Blanchard et al. 2009, ϕ_{ij} values were then assumed
 86 to be a Gaussian function of the logarithm of predator and prey body masses, \hat{s}_i and \hat{s}_j respectively, with a
 87 maximum value when the $PPMR$ is ψ and a standard deviation σ : $\phi_{ij} = 1/(\sigma\sqrt{2\pi}) \cdot \exp(-(\hat{s}_i - \hat{s}_j - \psi)/2\sigma^2)$
 88 when $\hat{s}_i - \hat{s}_j > 0$, otherwise $\phi_{ij} = 0$.

89 Space and Movement

Following Watson et al. 2015, we implement a simple gradient ascent approach to model the active movement of fish biomass. First, in each grid-cell and for each size-class in all groups we calculate the gradient of prey biomass. We then assume that all size-classes of all groups swim/move in the direction of the steepest positive gradient, i.e. they essentially follow food. They move with speed $a_{i,m} = \nu_i + U_m$, where U_m is the zonal or meridional ocean current speed depending on which direction fish are swimming. With this swimming speed we employ a XXX numerical advection-diffusion scheme to model active movement: Diffusion is solved for using a 2D Forward in Time Centered Scheme:

$$B_{mn}^- = \alpha(B_{m+1n}^* + B_{m-1n}^*) + \beta(B_{mn+1}^* + B_{mn-1}^*) + (1 - 2\alpha - 2\beta)B_{ij}^*, \quad (7)$$

where $\alpha = D\Delta t/\Delta x^2$ and $\beta = D\Delta t/\Delta y^2$. Advection is solved for using a 2D Lax-Wendroff directional splitting (where the meridional and zonal directions are computed sequentially) scheme, first in the zonal direction:

$$B_{mn}^+ = B_{mn}^- - \frac{U}{2}(B_{m+1n}^- - B_{m-1n}^-) - \frac{U^2}{2}(B_{m+1n}^- - 2B_{mn}^- + B_{m-1n}^-), \quad (8)$$

then in the meridional direction:

$$B_{mn}^{t+1} = B_{mn}^+ - \frac{V}{2}(B_{mn+1}^+ - B_{mn-1}^+) - \frac{V^2}{2}(B_{mn+1}^+ - 2B_{mn}^+ + B_{mn-1}^+) \quad (9)$$

90 where $U = u\Delta t/\Delta x$ and $V = v\Delta t/\Delta y$.

If all resource gradients are negative then that predator size-class is at a local resource maxima and we treat this case slightly differently. Here, we assume that fish will swim against all ocean currents and try to

maintain their position at this maxima. We model this as follows:

$$a_i = \text{sgn}(U_m) \cdot \max(|U_m| - \nu_i, 0), \quad (10)$$

91 where the $\text{sgn}(\cdot)$ operator finds the sign of its input, and $|\cdot|$ is the absolute value operator. Essentially, if
 92 fish want to stay a given location, and can swim faster than the local ocean currents, then they do not move.

93 Numerical Integration and Off-line Coupling

94 We have posed our model as multiple systems of ordinary differential equations; a size-based demographic
 95 system at each spatial grid cell linked by movement, being forced off-line by vertically integrated zooplankton
 96 biomass fields and vertically averaged zooplankton mortality fields. To step the model forward in time we
 97 split the operations; solving the demographics first, then movement. Both processes are calculated using a
 98 simple forward-Euler scheme, integrated forward at a daily resolution. At this temporal scale, and at the
 99 spatial scales of the global model grid, ~ 1 degree latitude/longitude the forward-Euler scheme is stable.

100 The size-based food-web model is initialized by running it forward in time from 1948 to 2008 and looped
 101 repeatedly, until a quasi-equilibrium state is reached. Typically three loops were required. Looping from
 102 2008 back to 1948 does incur a significant shock to the dynamics, and thus our analyses are confined to the
 103 period 1997 – 2007. By this time the transient dynamics produced from the shock have dissipated (?).

104 The size-based food web model and zooplankton fields from COBALT are coupled in a specific manner
 105 to ensure energy constraints are met. The critical consideration is that the rate at which fish consume
 106 zooplankton can differ between the size-structured food-web model and COBALT. Since COBALT has been
 107 calibrated to produce realistic zooplankton consumption rates (?) we tune the size-structured model to
 108 its values. We allow the size-structured model to produce zooplankton consumption rates less than those
 109 produced from COBALT, assuming that unresolved sources of zooplankton mortality, for example predation
 110 of adults on early life stages, account for the difference (?). However, where the size-structured model rates

111 are greater than those of COBALT's, we actively reduce them so that mass is conserved. We do so as follows.
112 Consider medium and large zooplankton as indexed by m and l respectively. At each time step, we calculate
113 how much zooplankton is consumed by each size-class i at a given location in time (i.e. using Eq. 2):
114 $B_i C_{im}$ and $B_i C_{il}$. If $\sum_i B_i C_{im}$ and $\sum_i B_i C_{il}$ are greater than COBALT's medium and large zooplankton
115 mortality rates respectively, we rescale zooplankton consumption rates for each size-class such that the total
116 amount of zooplankton consumed equals the COBALT mortality terms. This rescaling is done in order of
117 zooplankton consumption rates; i.e. size classes that eat more zooplankton have their consumption rates
118 reduced proportionally.