Global Marine Tipping Points Under Climate Change

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1 # ABSTRACT

₂ INTRODUCTION

₃ METHODS

₄ The Princeton Ocean Ecosystem Model: POEM

₅ The Princeton Ocean Ecosystem Model (POEM) has two main components: (1) the Carbon, Ocean Biogeo-

₆ chemistry and Lower Trophics or COBALT marine ecosystem model and (2) a size-based model of high-trophic

₇ level dynamics.

₈ COBALT is used to provide the biogeochemical and planktonic food web dynamics for the size-based food web

₉ model herein. COBALT uses 33 state variables to resolve global-scale cycles of nitrogen, carbon, phosphate,

₁₀ silicate, iron, calcium carbonate, oxygen, and lithogenic material (**?**). COBALT is run as part of the Modular

₁₁ Ocean Model (MOM) version 4.1 (**?**), with 60 year simulations (1948-2008) forced by the Common Ocean-Ice

₁₂ Reference Experiment (CORE-II) data set (**?**) as well as a future scenario running from 2006 to 2100 using

₁₃ relative concentration pathways (rcp) 8.5 as the carbon emissions scenario.

₁₄ The horizontal resolution of the simulation is 1° Latitude/Longitude, except along the equator where the

₁₅ resolution is refined to $1/3^o$. The model uses 50 vertical layers, with a resolution of 10m over the top 200m.

₁₆ The representation of planktonic food web dynamics within COBALT includes small and large phytoplankton

₁₇ with the latter group comprised of diatoms and dinoflagellates, and three zooplankton groups that feed on

₁₈ phytoplankton, bacteria and each other according to mean predator prey size ratios (e.g. **?**). The "small"

₁₉ zooplankton group represents microzooplankton that are $< 200 \mu m$ in equivalent spherical diameter (ESD).

₂₀ The medium zooplankton are parameterized as small to medium bodied copepods ($0.2 - 2mm$ ESD), and

₂₁ the large zooplankton are parameterized as large copepods/krill ($2 - 20mm$ ESD). The parameterization of

₂₂ trophic interactions relies primarily on the allometric and bioenergetics relationships described in (refs. **???**),

₂₃ and the model was calibrated to ensure quantitative consistency with large-scale planktonc food web dynam-

24 ics, including patterns in primary and meso-zooplankton production (**?**). COBALT estimates zooplankton

25 mortality rates using a density dependent closure term (**?**). This mortality term accounts for all zooplankton

26 production that is not consumed by other zooplankton, and hence represents feeding by higher predators and

27 other sources of mortality that are not resolved explicitly. This density dependence has empirical support

28 (e.g. **?**) and reflects an assumption that the biomass of predators responds to the biomass of prey.

29 COBALT is linked to the size-based food web model described herein in an "off-line" fashion. This is done

30 at the phytoplankton level: information about phytoplankton from COBALT is used to drive the dynamics

31 of the size-based food web model. Like COBALT, the size-based food web model estimates the biomasses of

32 meso-zooplankton, and their feeding rates on phytoplankton. Hence, we have two independent measures of

33 zooplankton dynamics, one from COBALT and one from the size-based food-web model. As a consequence

34 it is possible to force the size-based model's zooplankton feeding rates to match COBALT's.

35 The size-based food web model is comprised to four major animal groups: zooplankton, a planktivorous

36 fish, a piscivorous fish and benthic invertebrates. Zooplankton are modeled a simple biomass pools, within

37 an inflow of biomass dictated by COBALT's fluxes. Hence, in the size-based model we do not model

38 zooplankton feeding on phytoplankton mechanistically (i.e. with a Type II feeding function as is done in

39 COBALT). However, by tracking the biomass of zooplankton in both the size-based food-web model and

40 COBALT, measures of off-line coupling accuracy can be made. Simply put, the quotient of zooplankton

41 biomass from COBALT and the size-based food-web model.

42 Population dynamics for the remaining groups - piscivore, planktovore and benthic invertebrate - are modeled

43 in a more ecologically explicit manner, following the *size-structured* formulation of Van Leeuwan et al.

44 2008. The population of each group is modeled as a collection of size-classes, with smaller classes growing

45 (somatically) into larger size classes. The size-structured model is general, being applied to each group with

46 no difference in model-structure. It is mainly the choice of parameters that defines the different groups.

The rate of change of biomass density ($g\ m^{-2}$) for the smallest size classes in either the piscivore, planktivore or benthic groups is:

$$\frac{dB_i}{dt} = \sum_{\substack{j \neq i}}^{N-1} (1 - \kappa_j)\nu_j B_j - \kappa_i \gamma_i B_i - d_i B_i, \tag{1}$$

where $i = 1$, the index of the smallest size-class in a given group. The first term on the right-hand-side is the total amount of newborn fish or crustacean biomass (i.e. summed over all larger size classes) 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 is used somatic growth, hence $1 - \kappa$ is the energy invested in the production of larvae/eggs. The total amount of newborn biomass recruiting to the first size-class is the summation of larvae/egg production over all larger size-classes (index j not i to N the total number of size-classes in a given group). The second term is the loss of biomass 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 biomass due to natural mortality.

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

$$\frac{dB_i}{dt} = \kappa_{i-1}\gamma_{i-1}B_{i-1} - \kappa_i \gamma_i B_i - (1 - \kappa_i)\nu_i B_i - d_i B_i, \tag{2}$$

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

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

$$\nu_i = \lambda I_i - T_i, \tag{3}$$

where λ is the food assimilation efficiency ($g_i\ g_i^{-1}$), I is the biomass consumed ($g_j\ g_i\ d^{-1}$) and T is

68 biomass-specific metabolic costs $(g_i \ g_i^{-1} \ d^{-1})$. The energy available for somatic growth is:

69
$$\gamma_i = \frac{\nu_i - \frac{1}{\kappa_i}d_i}{1 - z_i^{(1-d_i)/(\kappa_i \nu_i)}}, \tag{4}$$

70 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

71 final body size that a particular life stage encompasses and hence reflects the size range that an individual

72 has to grow through before maturing to the next stage.

Consumption

74 Consumption of prey biomass is dealt with in slightly different ways for the piscivore, planktivore and benthic

75 groups. The piscivore is able to feed on all groups, including itself, and the biomass specific feeding rate of

76 any given piscivore size-class i is modeled using a multi-prey Type II feeding function:

77
$$I_i = \sum_{j}^{N} \frac{a_i B_j \phi_{ij}}{1 + a_i \tau_i \sum_{j}^{N} B_j \phi_{ij}}, \tag{5}$$

78 where a_i is 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

79 one individual of size-class i, in terms of body-weight, to digest a unit of biomass of prey j $(d \ g_j \ g_i)$. Here,

80 j indexes all size-classes in all groups, and it is a diet-preference factor ϕ_{ij} that determines how much of any

81 given prey, piscivore i eats. Diet preferences are defined using empirical predator-prey mass ratios (PPMRs).

82 Specifically, $PPMR$ values are taken from the empirical gut-content analysis of **?**, who defined a mean

83 PPMR $\psi = 3$, with a PPMR standard deviation $\sigma = 1.3$. Similar to **??**, ϕ_{ij} values were then assumed to

84 be a Gaussian function of the logarithm of predator and prey body masses, $\hat{s}_i$ and $\hat{s}_j$ respectively, with a

85 maximum value when the PPMR is ψ and a standard deviation σ: $\phi_{ij} = 1/(\sigma \sqrt{2\pi}) \cdot exp(-(\hat{s}_i - \hat{s}_j - \psi)/2\sigma^2)$

86 when $\hat{s}_i - \hat{s}_j > 0$, otherwise $\phi_{ij} = 0$.

87   In contrast to the piscivore, the planktivore eats only zooplankton:

$$I_i = \frac{a_i(Z_1 + Z_2)}{1 + a_i\tau_i(Z_1 + Z_2)}, \tag{6}$$

89   where in this case i indexes only the planktivore size-classes, and it is evident that we assume all planktivore

90   size-classes eat all zooplankton, both medium and large, without preference.

91   The benthic invertebrate feeds on detrital matter accumulating on the sea-floor, which is modeled explicitly:

$$\frac{dW}{dt} = D - S - \sum_i^N I_i, \tag{7}$$

93   where W is the biomass pool of detrital matter on the sea-floor ($g \ m^{-2}$), D is the flux of detrital matter

94   from the water column ($g \ m^{-2} \ d^{-1}$; this is given by COBALT as an offline component), S is the rate of

95   sedimentation of this biomass ($g \ m^{-2} \ d^{-1}$; again a rate given by COBALT) and I_i is the consumption by

96   the detritivore of size-class i of which there are N. Like consumption elsewhere, a Type II feeding function

97   is used:

$$I_i = \frac{a_i W}{1 + a_i\tau_i W}, \tag{8}$$

99   where i indexes only the detritivore size-classes.

Offline coupling and Numerical Integration

Parameterization

102   The list of

103 RESULTS

104 DISCUSSION

105 ACKNOWLEDGEMENTS

Tables

Parameters:	Description	Example values	Units
s_i	body mass of predator i	1,100,1000	g
s_j	body mass of preferred prey j	0.001,0.1, 1	g
l_i	body length of i	0.03,0.12,0.25	m
ν_i	i's swimming speed	1700,5000,8500	$m\ day^{-1}$
V_i	volumetric search rate of i	3.8, 1.8, 1.2	$m^3 day^{-1} g^{-1}$
ϕ_{ij}	vulnerability of prey	[0,1]	$-$
τ_{ij}	time for i to handle j	5.7×10^{-5}, 0.028, 0.56	$days$

Variables:			
B_i	biomass density of size-class i	–	$g\ m^{-3}$
c_i	consumption rate of i	–	day^{-1}
d_i	predation mortality rate of i	–	day^{-1}
m_i	metabolic rate of i	0.006, 0.002, 0.001	day^{-1}
μ_i	natural mortality rate of i	0.006, 0.0002, 0.0001	day^{-1}
J_i	flux of size-class i	–	$g\ m^{-3}\ day^{-1}$

Constants:			
λ	Conversion efficiency	0.7	%
N	Number of size classes	15	#

Table 1: Table of model variables, parameters and constants posed in terms of size classes i and j, a predator and its most preferred prey respectively. Values were chosen for a 1g, 100g and 1000g sized predator, and all values are calculated assuming $12^{o}C$ temperature. Handling times were calculated using the formula in **?**.