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Description and Application of a NPZD Model to Forecast Hurricane Impacts to Secondary Production in Coastal Ecosystems

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Abstract

Increases in hurricane strength and frequency are forecast to occur in association with global climate changes. In coastal ecosystems the passage of a hurricane is associated with increases in nutrients that may cause subsequent increases in phytoplankton and zooplankton biomass. Zooplankton are an important food source for small fishes that are feed on by larger fishes, thus commercial and recreational fisheries could benefit from the passage of a hurricane. NPZD simulations of hurricane scenarios are used to assess the magnitude and resilience of secondary production after the passage of hurricanes with different wind speeds and directions of approach. Short-term increase and recovery of phytoplankton and zooplankton biomass after the passage of hurricanes suggests short-term increase in fish biomass, and a potential benefit to some commercial and recreational fisheries.

Keywords: NPZD model; Zooplankton; Hurricane Impacts

1. Introduction

Winds, precipitation, or storm surge from hurricane events cause an increase in nutrient concentration that impact biological production [1, 2]. In the open ocean, winds during hurricane events vertically mix the surface layer and release cold nutrient rich deep water that stimulates primary production [3].

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Enhanced primary production in estuarine and coastal systems that are affected by nutrient discharge from large rivers and land, are often from enhanced nutrient loading and run-off caused by high amounts of precipitation during a hurricane [1, 2]. In coastal waters the addition of nutrients can cause algal blooms that create environmental conditions that affect secondary production [4]. Assessing the affects of hurricanes on an aquatic ecosystem requires a consideration of the links among hurricane drivers, environmental, and biological factors.

Zooplankton are an important link in the transfer of energy that can be used as an indicator of stability within the trophic structure of marine ecosystems [5]. As the primary food source for larval fishes, zooplankton are important for sustaining many pelagic commercial and recreational fisheries [6]. In addition, zooplankton are the primary consumer of phytoplankton. Therefore fluctuation in zooplankton production may be an indicator of flux in phytoplankton and pelagic fish production. Trophic linkages between nutrients, phytoplankton, zooplankton, and fish implies that the destabilization of a linked group will affect the destabilization of the directly dependent groups. Enhanced nutrients after the passage of a hurricane may be associated with direct increase or decrease in phytoplankton and zooplankton that may be associated with an increase or decrease in fish abundance.

In anticipation of the increase in hurricane frequency and strength within the next decade [7-9], resource managers of coastal and estuarine ecosystems need a tool for forecasting the ecological impacts of hurricanes that can effectively integrate biological and environmental information collected before and after hurricane events [10]. Ecological models are an ecosystem based management tool that can be used to forecast ecological impacts [11].Through their ability to integrate in situ measurements with the theoretical assumptions of ecosystem response, ecological models can be an effective tool for developing strategies for minimizing impacts from extreme events that could be destabilizing and catastrophic on currently stressed ecosystems [11]. Biogeochemical models are a type of ecological tool that may be used to make inference about the resilience of primary and secondary production after an extreme event, such as a hurricane. Biogeochemical models make use of the trophic relationship to understand and predict the effects of nutrient flux on phytoplankton and zooplankton. These models provide a theoretical baseline for comparison with real observations, because they are based on predefined characteristic and assumptions about how the primary and secondary producers interact with the environment and each other (i.e., functional responses).

Assessing the ecological effects of hurricanes on large estuarine and coastal ecosystems requires the integration of hydrological, wind forcing, and nutrient loading factors [2]. We describe an NPZD compartmental model that assumes that fluxes in river discharge from precipitation and wind forcing are the primary causes of nutrient flux after the passage of a hurricane [3]. The model integrates *in situ* daily measures of river discharge, wind, temperature, and salinity during non-hurricane and normal seasons to simulate primary and secondary production (i.e., phytoplankton and zooplankton). Hurricane events are simualted by perturbing the *in situ* measurements and comparing phytoplankton and zooplankton from perturbed with non-perturbed simulations. Beta simulations were performed on *in situ* data to assess the behavior of the model. Section 2 is an overview of the model features including assumptions and mathematical eqautions for each compartment. Section 3 provides the nominal parameter estimates and their sensitivity. Section 4 compares the state of the model after perturbations of in situ measurements of river discharge, wind forcing, temperature, and salinity. Finally, Section 5 explains the strengths and weaknesses of the model and its application as a tool for forecasting ecosystem stability after a hurricane.

2. Model Structure and Equations

2.1. Overview

Since, nitrogen is often limited in coastal and estuarine systems, a four compartment nitrogen based nutrient, phytoplankton, zooplankton, and detritus (NPZD) model [12] was built using Mathworks's Simulink software to integrate environmental data inputs that include: wind, river discharge, temperature, depth, and salinity to simulate and compare the effects of hurricane winds and precipitation on phytoplankton and zooplankton biomass (Figure 1). The environmental data inputs and simulated biological compartments are linked by functional response equations. The model follows the flow of nitrogen (mMol Nm^{-3} d^{-1}) from nutrient sources via trophic transfer to zooplankton (i.e., nutrient uptake by phytoplankton to zooplankton grazing on phytoplankton). Hurricane wind is assumed to be the primary drivers of surface layer mixing that result in nutrient fluxes and decreased temperatures after the passage of a hurricane. Precipitation increases the rate of discharge that causes subsequent increases of nutrient loads into estuarine and coastal environments. In order to minimize the complexity of the model, impacts to phytoplankton and zooplankton biomass from light availability, turbidity, advection, and migration are not considered. Although the nutrient, phytoplankton, zooplankton, and detritus compartments are simulated, temperature, salinity, depth, wind speed, and river discharge are derived from in situ measurements. There are 28 adjustable parameters contained within the model (Table 1). Parameter values and functional response equations contained in the model are derived from literature. The compartments are discussed in more detail in the following sub-sections.

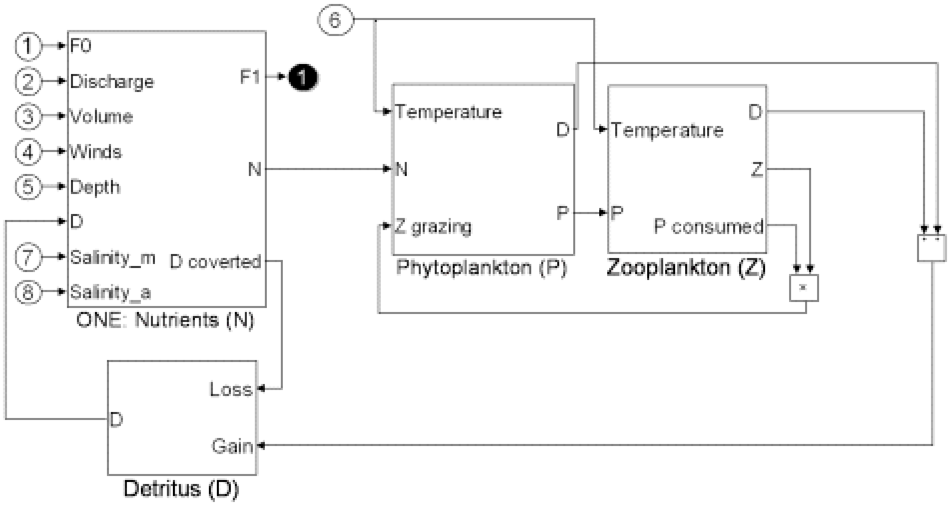


Figure 1: Block Diagram of Compartments in NPZD model. Circles with white background indicate input variables. Circle with black background indicates the flow output. Boxes indicate stocks.

Table 1. Nominal model parameters

Parameter	Symbol	Value	Unit	Reference
Bacteria Conversion Rate	β_1	0.80	d^{-1}	[12]
Phytoplankton Uptake Coefficient	κ_1	0.15	$mMolNm^{-3}$	[12]
Max. Phytoplankton Uptake Rate	μ_{max_1}	1	d^{-1}	[12]

Phytoplankton Respiration Rate	μ_{resp_1}	0.088	d^{-1}	[12]
Phytoplankton Mortality Rate	μ_1	0.072	d^{-1}	[12]
Phytoplankton Sink Rate	μ_2	0.018	d^{-1}	[12]
Phytoplankton Temperature Coefficient 1	k_{p1}	1.0		[13]
Phytoplankton Temperature Coefficient 2	k_{p2}	0.0	T°	[13]
Phytoplankton Temperature Coefficient 3	k_{p3}	2.7		[13]
Phytoplankton Temperature Coefficient 4	k_{p4}	11.9		[13]
Phytoplankton Temperature Coefficient 5	k_{p5}	40.0	T°	[13]
Phytoplankton Temperature Coefficient 6	k_{p6}	39.0	T°	[13]
Phytoplankton Temperature Coefficient 7	k_{p7}	-0.02		[13]
Zooplankton Grazing Coefficient	K_2	0.85	mMolNm^{-3}	[12]
Max. Zooplankton Uptake Rate	μ_{max_2}	0.75	d^{-1}	[12]
Zooplankton Assimilation Efficiency	β_2	0.675	%	[12]
Zooplankton Basal Respiration Coefficient	K_{resp_1}	0.071	d^{-1}	[14]
Zooplankton Active Respiration Coefficient	K_{resp_2}	0.057	d^{-1}	[14]
Zooplankton Mortality Rate	μ_3	0.025	d^{-1}	[12]
Zooplankton Excretion Rate	μ_4	0.01	d^{-1}	[12]
Predation by Larval Fish	μ_5	0.0225	d^{-1}	[12]
Zooplankton Temperature Coefficient 1	k_{z1}	1.0		[13]
Zooplankton Temperature Coefficient 2	k_{z2}	0.0	T°	[13]
Zooplankton Temperature Coefficient 3	k_{z3}	2.7		[13]
Zooplankton Temperature Coefficient 4	k_{z4}	11.9		[13]
Zooplankton Temperature Coefficient 5	k_{z5}	40.0	T°	[13]
Zooplankton Temperature Coefficient 6	k_{z6}	39.0	T°	[13]
Zooplankton Temperature Coefficient 7	k_{z7}	-0.02		[13]

2.2. Nutrient

The nutrient compartment calculates nitrogen concentration as the sum of detritus released from wind induced deepening of the mixed layer and nutrient discharge (nitrogen) from an adjacent river (Equation 1). Losses to nutrients are considered to be primarily from phytoplankton uptake. The winds of hurricane induce deepening of the mixed surface layer and nutrient fluxes from detritus, while precipitation increases river discharge flow rates and nutrient loading. Wind speed measurements are used to calculate the rate of wind energy conversion (Equation 2) at each time step . The release of detritus into the nutrient compartment associated with wind induced mixed layer deepening is simulated using a logistic function. The logistic function assumes that as wind speeds increase, detrital inputs will increase until a saturation wind speed is reached. Nutrient inputs from the river are simulated by uni-directional flow (Equation 7) that incorporates freshwater residence time (FRT) at each time step [15]. Seasonal nutrient inputs from river loading are simulated by a sine function [7] (Equation 8).

$$\frac{dN}{dt} = \underbrace{D\beta_1 W_{Effects}}_{Wind} + \underbrace{R_{Loading}}_{River} - \underbrace{G_1 P}_{Phytoplankton\,Uptake} + \underbrace{RZ}_{Zooplankton\,Resp} \tag{1}$$

$$W_{Effects} = ae^{\left(-bE_{m_{day}}\right)}, \tag{2}$$

where a is a parameter that scales the y-axis intercept, b is a parameter that determines the steepness of the curve in the logistic function, and $E_{m_{day}}$ is the rate in days at which the energy in the wind becomes available for increasing the mixed layer [16].

$$E_{m_{day}} = \left(\frac{PE}{E_m}\right) 0.00027 * 24, \tag{3}$$

where PE is the potential energy of the water column and E_m is the rate in joules at which the potential energy of the water column is changed by mixing [16].

$$E_m = 0.0015\ \rho_a C_{10} U_{10}^3, \tag{4}$$

where ρ_a is the air density (1 kg m^{-3}), C_{10} is the mean wind speed measured 10 m above the sea surface, and U_{10} is the mean wind speed measured 10 m above the sea surface [16].

$$PE = mg\Delta h/2, \tag{5}$$

where m is the mass of the water column , g is the gavitational constant, and Δh is the height that a water column increases as it absorbs heat.

$$\Delta h = \alpha h \Delta T, \tag{6}$$

where α is the coefficient of thermal expansion for water ($10^{-4}\ ^\circ C^{-1}$), h is the height of the center of mass of a water column, ΔT is the increase in temperature associated with thermal expansion.

$$R_{Loading} = \frac{Freshwater_i}{dt} = \frac{Freshwater_{i+1} - Freshwater_{i-1}}{FRT} + SNC, \tag{7}$$

where FRT is the freshwater residence time, which is a steady-state estimator of residence time [15], and SNC is the seasonal nitrogen concentration which simulates the seasonal oscillations of nitrogen.

$$SNC = 40.5 + 5 * sin\left(\left(\frac{8}{365}\right) * (time + 80)\right). \tag{8}$$

$$FRT = \left(\frac{S_s - S_e}{S_s}\right)\frac{V}{Q_f}, \tag{9}$$

where S_s is the max salinity (33 psu), S_e is the average salinity, V is the total volume, and Q_f is the total freshwater input.

2.3. Phytoplankton

Phytoplankton growth is assumed to be the sum of the products of phytoplankton metabolic rates and biomass. The metabolic rates included in this compartment are nutrient uptake (G_1), respiration (μ_{resp_1}), sinking (μ_2), and mortality (μ_1) (Equation 10). While respiration, sinking, and mortality rates are single parameters (linear functions), nutrient uptake requires multiple parameters. A optimum temperature function is used to simulate the impacts of temperature on phytoplankton growth (Equation 12). Consumption rates are assumed to decrease based on deviation from an optimal temperature. In addition a Type II (Michealis-Menten) functional response, which assumes maximal uptake at nutrient saturation, is used to simulate the impacts of changes in nutrient stocks on phytoplankton uptake rates and growth (Equation 11). Respiration is simulated as the product of the respiration factor and phytoplankton at each time step. Losses to the phytoplankton stock are assumed to be from zooplankton grazing.

$$\frac{dP}{dt} = \left(\underbrace{G_1}_{Growth} - \underbrace{\mu_1}_{Mortality} - \underbrace{\mu_2}_{Sinking} - \underbrace{\mu_{resp_1}}_{Respiration}\right)P - \underbrace{G_2 Z}_{Zooplankton\,Grazing} \tag{10}$$

$$G_1 = y_1 \mu_{max_1} \frac{N}{\kappa_1 + N}, \tag{11}$$

where y_1 is the optimum temperature functional response growth rate, μ_{max1} is the maximum phytoplankton uptake rate, $\kappa 1$ is the phytoplankton uptake coefficient, and N is the nitrogen concentration.

$$y_1 = \frac{k_{p1}(T - k_{p2})^{k_{p3}}}{k_{p4}^{k_{p3}} + (T - k_{p2})^{k_{p3}}} - exp\left(k_{p7} - \left(\frac{k_{p5} - (T - k_{p2})}{k_{p5} - k_{p6}}\right)\right), \tag{12}$$

where k_{p1} scales the overall curve on the y-axis, k_{p2} is the lower temperature at which growth is zero, k_{p3} is a shape parameter for the rising part of the curve, k_{p4} is roughly analogous to the half-saturation constant, k_{p5} is the maximum temperature at which growth is positive, k_{p6} is the temperature at which growth is maximal, and k_{p7} is a shape parameter for the falling part of the curve.

2.4. Zooplankton

Zooplankton growth is the sum of the products of zooplankton metabolic rates and biomass. The metabolic rates included in this compartment are grazing, respiration, natural mortality, and excretion (Equation 13). Single parameter multipliers are used to simulate natural mortality (μ_3), excretion (μ_4), and predation (μ_5) rates. The consumption rate is the product of multiple parameters that include the maximum assimilation efficiency and maximum grazing rate. As in the phytoplankton compartment, an optimum temperature functional response (Equation 16) is used to simulate temperature effects to grazing, and a Type II functional response is used to simulate phytoplankton concentration effects to consumption (Equation 14). Respiration rate is an exponential function of temperature (Equation 15). The basal rate is single parameter, but the active rate results from an equation that predicts specific respiration from temperature. Losses to zooplankton growth are assumed to be from icthyo-plankton predation.

$$\frac{dZ}{dt} = \left(\underbrace{\beta_2 G_2}_{Growth} - \underbrace{\mu_3}_{Mortality} - \underbrace{\mu_4}_{Excretion} - \underbrace{R}_{Respiration} - \underbrace{\mu_5}_{Predation}\right) Z, \tag{13}$$

where β_2 is the zooplankton assimilation efficiency, and G_2 is a type II functional response growth rate.

$$G_2 = y_2 \mu_{max_2} \frac{P}{\kappa_2 + P}, \tag{14}$$

where y_2 is the optimum temperature functional response growth rate, μ_{max2} is the maximum zooplankton uptake rate, $\kappa 2$ is the zooplankton grazing coefficient, and P is the phytoplankton biomass.

$$R = \kappa_{resp_1} exp(\kappa_{resp_2} * T) * 0.01, \tag{15}$$

where κ_{resp_1} is the zooplankton basal respiration coefficient, κ_{resp_2} is the zooplankton active respiration coefficient, and T is temperature.

$$y_2 = \frac{k_{z1}(T-k_{z2})^{k_{z3}}}{k_{z4}^{k_{z3}} + (T-k_{z2})^{k_{z3}}} - exp\left(k_{z7} - \left(\frac{k_{z5}-(T-k_{z2})}{k_{z5}-k_{z6}}\right)\right), \tag{16}$$

where k_{z1} scales the overall curve on the y-axis, k_{z2} is the lower temperature at which growth is zero, k_{z3} is a shape parameter for the rising part of the curve, k_{z4} is roughly analogous to the half-saturation constant, k_{z5} is the maximum temperature at which growth is positive, k_{z6} is the temperature at which growth is maximal, and k_{z7} is a shape parameter for the falling part of the curve.

2.5. Detritus

Losses to phytoplankton and zooplankton growth are accumulated in the detrital compartment and recycled into the nutrient compartment via wind mixing (Equation 17). Zooplankton loss is the sum of mortality, excretion, and unassimilated efficiency (Equation 18). Phytoplankton loss is the sum of natural mortality and sinking (Equation 19).

$$\frac{dD}{dt} = \underbrace{Z_{Loss}}_{ZooplanktonLoss} + \underbrace{P_{Loss}}_{PhytoplanktonLoss} - \underbrace{D\beta_1 W_{Effects}}_{ConversiontoNutrient} \tag{17}$$

$$Z_{Loss} = (\mu_4 + \mu_3 + ((1-\beta_2)*G_2))Z \tag{18}$$

$$P_{Loss} = (\mu_1 + \mu_2)P \tag{19}$$

3. Simulations

3.1. Overview

Nominal, parameter adjusted, nutrient, depth, and salinity adjusted non-hurricane simulations, and nutrient, depth, and salinity adjusted hurricane simulations are run to characterize the overall behavior of the model. Non hurricane simulations were run for 1400 days(approx. 4 years). Day 1 of the simulation is January 1 of the calendar year and cycles back to January 1 in 365 day intervals. Two years of daily in situ wind, temperature, and discharge measurements were used for the simulations. Fourth order Runga-Kutta numerical methods at a time step of 0.25 d^{-1} are used to solve all the differential equations. The initial condition values were obtained from the literature and adjusted. Depth, salinity, and nutrient adjusted simulations use the same time span, time step, and numerical solution as the nominal simulation, however the inputs for depth, average salinity, and nitrogen were adjusted to simulate inner shelf, mid shelf, and outer shelf environments (Table 2).

Table 2: Depth, average salinity, and nitrogen inputs used for nominal inner shelf, mid shelf, and outer shelf simulations

Simulation	Depth	Salinity (S_e)	Nitrogen
Nominal	10 m	3 psu	0 mMol Nm^{-3} d^{-1}
Inner Shelf or Estuary	10 m	3 psu	+20mMol Nm^{-3} d^{-1}
Mid Shelf	50 m	15 psu	0 mMol Nm^{-3} d^{-1}
Outer Shelf	100 m	33 psu	-20mMol Nm^{-3} d^{-1}

3.2. Sensitivity Analysis

The nominal and single parameter adjusted non-hurricane simulations were compared to assess the sensitivity and robustness of the model to parameter adjustments. Sensitivity of parameters (Table 1) was assessed by perturbation of an individual parameter value ±5%, ±10%, and ±50%. Residual sum of squares are calculated for the zooplankton compartment by comparing the results of each single parameter adjusted simulation to the results of the nominal simulation.

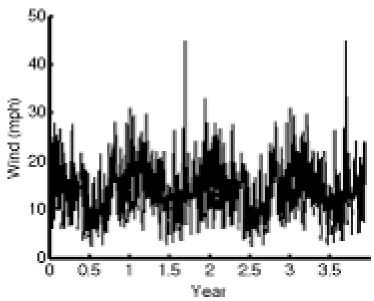
3.3. Hurricane Simulation

Hurricane simulations are compared with nominal non-hurricane simulation results to characterize the resilience and stability of the phytoplankton and zooplankton compartments after hurricane passage. Perturbation of *in situ* measures of wind to category 4 hurricane wind strength for 4 days at the end of July were used to simulate the impacts of hurricane wind on nutrients, phytoplankton, and zooplankton. While pertubations can be imposed at anytime during the 1400 days runtime (approx. 4 years), test simulation of this hurricane event were imposed during the second year of a typical hurricane season, which starts June 1st and ends November 31st (a time range of approximately 150 days). The second year was used to reduce flux associated with initial condition values, observed in preliminary nominal non-hurricane simulations.

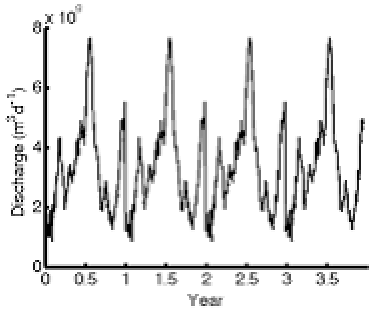
4. Results

4.1. Nominal Simulation: Environmental Inputs

The environmental inputs used in the simulations display an overall annual cyclic pattern for discharge rates, wind speeds, and temperatures (Figure 2). Discharge rates ranged between 1.5 $\times 10^{-8}$ and 8×10^{-8} m^3 d^{-1} (Figure 2a). The highest and lowest discharge rates are observed in the middle and beginning of each year, respectively. Wind speeds typically ranged between 3 and 30 mph with the higher speeds observed in the beginning of the year and lower speeds observed in the middle of the year (Figure 2b). Anomalous peaks of 50 mph wind speeds are observed around years 1.8 and 3.8. Temperatures ranged between 21 and 32 °C are observed at the beginning and middle of the year, respectively (Figure 2c).



(a)



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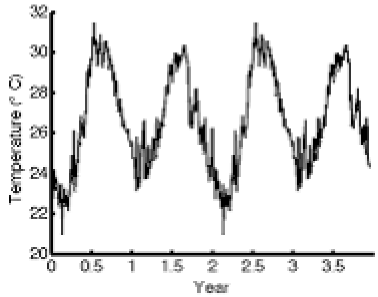
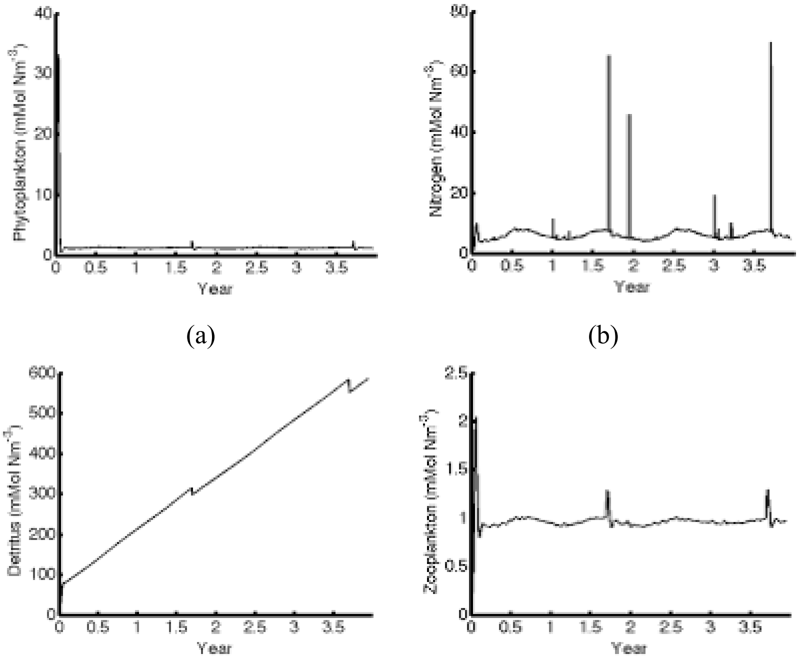


(c)

Figure 2: Nominal simulation environmental inputs: (a) river discharge, (b) wind speed, and (c) temperature.

4.2. Nominal Simulation: Compartments

Nominal simulations of nutrient, phytoplanton, and zooplankton compartments show stable nonlinear limit cycles, in which there is a return to the origional orbit despite daily variation in the environmental inputs (Figure 3). In contrast, detritus displays an unstable, noncyclic, and linearly increasing pattern. However, there are spikes observed in nutrients that are not seen in the phytoplankton and zooplankton biomass. A series of small spikes in the nutrient compartment are observed between 1 and 1.5 years, and 3 and 3.5 years (Figure 3a). Three large spikes are observed in the nutrient compartment at years 1.8, 2, and 3.8. These spikes appear to coincide with wind speeds of around 30 mph or above. In the phytoplankton and zooplankton compartments spikes in biomass are observed that coincide with the spikes in wind speed and nutrients at years 1.8 and 3.8. These spikes in biomass are higher in phytoplankton than zooplankton. In the detritus compartment dips are observed at years 1.8 and 3.8 that coincide with the peaks in wind speed, nutrient, phytoplankton and zooplankton. These spikes in nutrients and dips in detritus are due to the models functional response of winds on the release of detritus into the nutrient compartment. Despite large increases in phytoplankton and zooplankton at the beginning of the simulation, biomass within these compartments stablizes after 45 days from the start of the simulation. With the exception of the biomass peaks, phytoplankton and zooplankton do not fluctuate more than ±10% of 1.5 and 0.6 mMol Nm^{-3} d^{-1}, respectively. The detritus compartment displays a linear increase with time and is not at equilibrium.

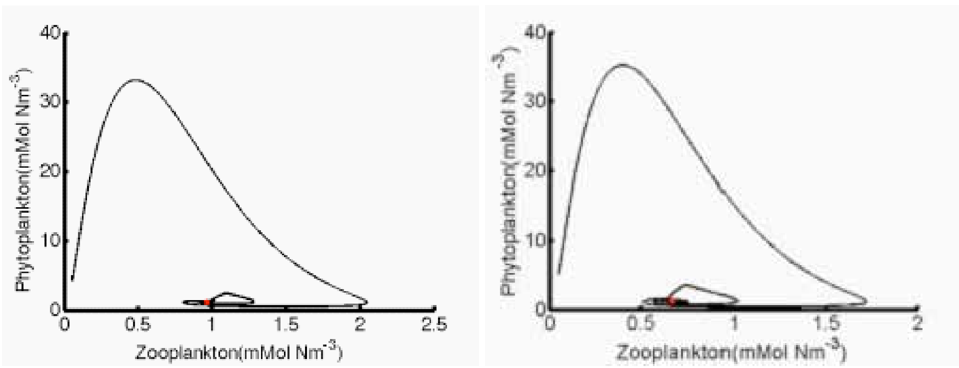


(a) (b) (c) (d)

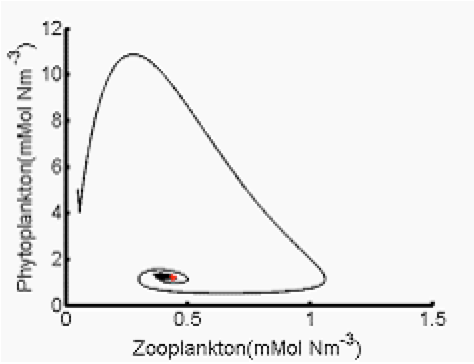
Figure 3: Nominal simulation results for (a) nutrients, (b) phytoplankton, (c) zooplankton, and (d) detritus.

4.3. Non Hurricane depth, salinity, and nutrient Adjusted Simulations

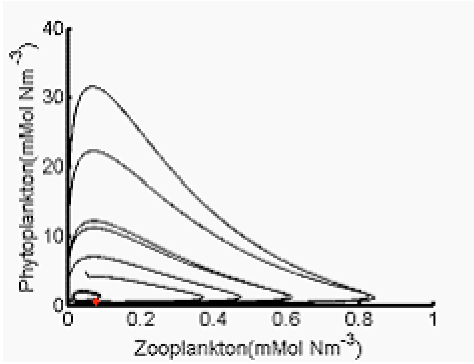
Phytoplankton and zooplankton display at a combined increase in depth and salinity, and decrease in nutrients (Figure 4). An increase in nutrients, only, to +20 mMol Nm^{-3} d^{-1} causes a 30%-40% increase over nominal phytoplankton and zooplankton values during the beginning of the simulation that stabilizes to values slightly larger than observed in the nominal simulation. Increasing the depth to 50 m and salinity to 15 psu results in a smaller increase in phytoplankton and zooplankton during the beginning of the simulation that stabilizes to values slightly smaller than observed in the nominal simulation. An unstable cyclic state is observed with an increase in depth to 100m, increase in salinity to 33 psu, and decrease in nutrients to -20 mMol Nm^{-3}.



(a) (b)



(c)



(d)

Figure 4: Zooplankton vs. phytoplankton plots show a cyclic equilibrium state for (a) nominal simulations and adjusted by depth, salinity, and nitrogen: (b) 10m, 3psu, and +20mMol Nm^{-3} d^{-1} ; (c) 50m, 15psu and 0 mMol Nm^{-3} d^{-1}; and (d) 100m, 33psu, and -20mMol Nm^{-3} d^{-1}.

4.4. Single Parameter Sensitivity Analysis

The zooplankton compartment is more sensitive to adjustments of the zooplankton and phytoplankton temperature coefficients 5(k_{p5} , k_{z5})and 6 (k_{p6} , k_{z6}), which are the temperature values that zooplankton grazing is positive and maximal, respectively (Table 3). A rank of mean residual sum of squares (MS) shows that adjustments to the zooplankton temperature coefficient 6 (k_{z6}) have the greatest average variance and adjustments zooplankton predation by larval fish (μ_5) have the lowest average variance among similarly treated parameters.

Table 3: Single parameter nominal model sensitivity analysis.

Parameter	Symbol	MS
Zooplankton Temperature Coefficient 6	k_{z6}	6.2018e+4
Phytoplankton Temperature Coefficient 6	k_{p6}	6.1861e+4
Phytoplankton Temperature Coefficient 5	k_{p5}	5.8399e+4
Zooplankton Temperature Coefficient 5	k_{z5}	5.7860e+4
Max. Zooplankton Uptake Rate	μ_{max_2}	5.0927e+4
Zooplankton Temperature Coefficient 1	k_{z1}	4.8879e+4
Zooplankton Assimilation Efficiency	β_2	4.8879e+4
Phytoplankton Temperature Coefficient 1	k_{p1}	4.8780e+4
Max. Phytoplankton Uptake Rate	μ_{max_1}	4.8780e+4
Zooplankton Basal Respiration Coefficient	k_{resp_1}	4.6654e+4

Phytoplankton Respiration Rate	μ_{resp_1}	4.6579e+4
Phytoplankton Temperature Coefficient 3	k_{p3}	4.6555e+4
Zooplankton Temperature Coefficient 3	k_{z3}	4.6551e+4
Phytoplankton Mortality Rate	μ_1	4.6535e+4
Zooplankton Temperature Coefficient 4	k_{z4}	4.6457e+4
Phytoplankton Temperature Coefficient 4	k_{p4}	4.6456e+4
Phytoplankton Sink Rate	μ_2	4.6454e+4
Phytoplankton Temperature Coefficient 2	k_{p2}	4.6452e+4
Zooplankton Temperature Coefficient 2	k_{z2}	4.6446e+4
Phytoplankton Temperature Coefficient 7	k_{p7}	4.6446e+4
Zooplankton Temperature Coefficient 7	k_{z7}	4.6446e+4
Bacteria Conversion Rate	β_1	4.6446e+4
Zooplankton Excretion Rate	μ_4	4.6446e+4
Zooplankton Mortality Rate	μ_3	4.6444e+4
Zooplankton Active Respiration Coefficient	K_{resp_2}	4.6432e+4
Zooplankton Grazing Coefficient	K_2	4.6413e+4
Phytoplankton Uptake Coefficient	K_1	4.6107e+4
Predation by Larval Fish	μ_5	4.5408e+4

4.5. Hurricane Simulations

Depth, salinity, and nutrient adjusted hurricane simulations *in situ* winds were perturbed to category 4 hurricane wind levels (Figure 5) show differences in recovery times (Figure 6). asociated combined increase in depth to 100 m and salinity to 33 psu, and decrease in nutrients of 20 mMol Nm^{-3}. The zooplankton compartment of the nominal simulation with an adjusted increase in nutrients of 20 mMol Nm^{-3} showed a peak increase of 1 mMol Nm^{-3} in zooplankton and recovery to the non-pertubed simulation equilibrium state within 3 months (Figure 6). An increase of 1 mMol Nm^{-3} and recovery to the non-perturbed simulation equilibrium state within 3 months was also displayed in the zoplankton compartment of the nominal simulation with an adjusted increase in depth to 50m and salinity to 15psu (Figure 6).The nominal simulation with an adjusted increase in depth to 100m, increase in salinity to 33psu, and decrease in nutrients to -20 mMol Nm^{-3} showed a 0.1 increase in zooplankton over the non perturbation immediately after the wind perturbation and a subsequent larger peak that lags behind a peak of non perturbed simulation (Figure 6).The pertubed adjusted simulations in all cases have equilibrium states that do not differ from the non-perturbed adjusted simulations.

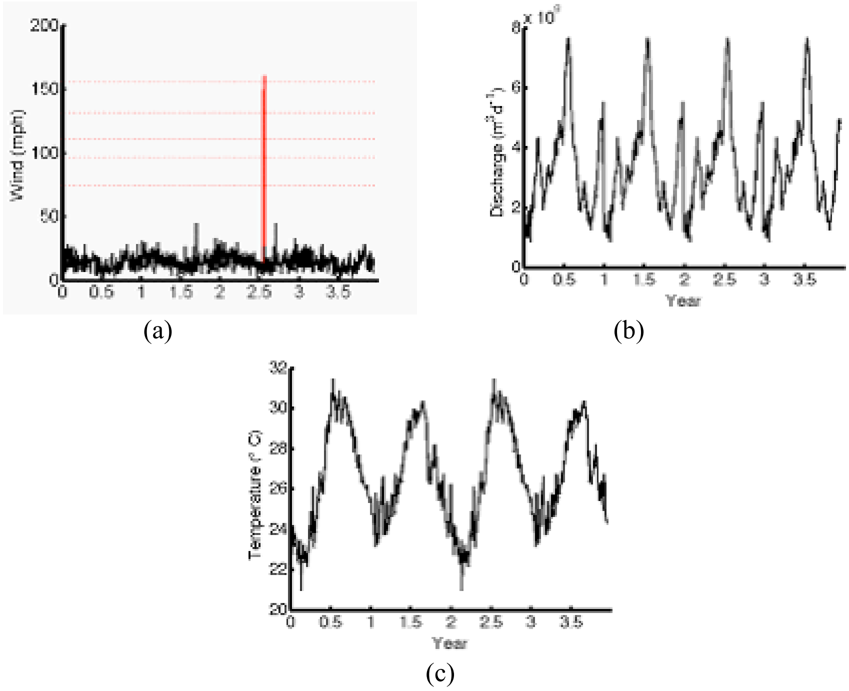


Figure 5: Nominal simulation environmental inputs: (a) river discharge, (b) wind speed, and (c) water temperature

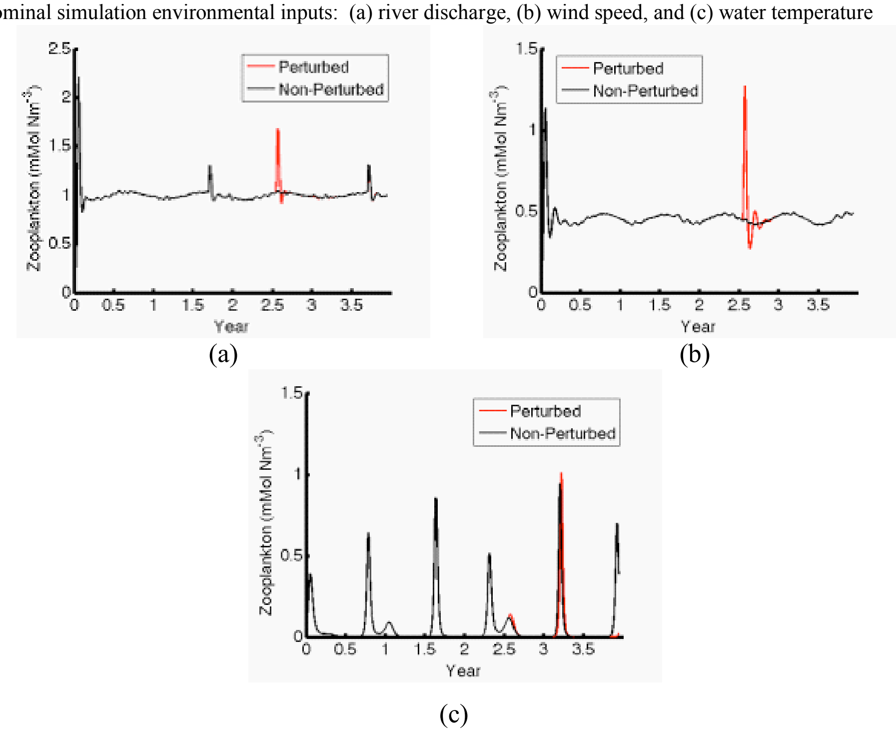


Figure 6: Zooplankton plots show recovery to nominal results for simulations adjusted by depth, salinity, and nitrogen: (a) 10m, 3psu, and +20mMol Nm^{-3} d^{-1}; (b) 50m, 15psu and 0 mMol Nm^{-3} d^{-1}; and (c) 100m, 33psu, and -20mMolm^{-3} d^{-1}.

5. Discussion

In general the robustness of the model to the adjustments of nominal parameter estimates and perturbation of *in situ* environmental inputs indicates that the model could be used to simulate estuarine and marine coastal systems. Phytoplankton and zooplankton compartments consistently return to the equilibrium stability of the nominal simulation at depths up to 50m. Sensitivity analysis suggests that biologically important feeding and mortality parameters can be increased or decreased as much as 50% over nominal values without concern for the loss of equilibrium stability. β simulations show that the model recovers and maintains cyclic equilibrium and stablilizes after short-term perturbations of in situ environmental input in combination with adjustments to depth, salinity, and nutrient conditions. Robustness of the nominal model to parameter adjustments and perturbation of in situ data suggests the utility of the model to simulate the effects of hurricanes on primary and secondary production in estaurine and nearshore to midshelf coastal systems.

During spring and fall, peaks are observed in phytoplankton and zooplankton production in estuarine and coastal ecosystems. NPZD nominal simulations show cyclic phytoplankton and zooplankton production that mimics seasonal patterns. However, adjustments in nutrients, depth, and/or salinity may result in large deviations from the seasonal patterns of phytoplankton and zooplankton production that must be considered.

Due to differences in phytoplankton and zooplankton feeding and mortality rates among different estaurine or coastal habitat, the robustness of this NPZD model to parameter adjustments suggests its utility to simulate and compare different estaurine and coastal habitat.

This NPZD models can be used to explore the mechanistic effects of hurricane winds and/or precipitation on primary and secondary biological production in estaurine and coastal ecosystems.Winds can cause enhanced production of zooplankton directly via advection [17] or indirectly by stimulating growth through vertical mixing. In the case of this model, the effects of wind are indirect. Adjusted β category 4 hurricane wind simulations suggest that phytoplankton and zooplankton production a relatively short-term recovery (weeks to months). The impacts on phytoplankton and zooplankton biomass are often short-term [18].

As the frequency and intensity of hurricane events increases, the ability to estimate response and recovery of large coastal ecosystems to hurriccane events will enable managers to better mitigate the impacts to commercial and recreational fishery resources. Typical analysis of hurricane impacts is based on before and after comparisons of observations. While these comparisons may tell us about differences, they do not provide a quatitative method of explore the mechanisms that cause the differences. The results of a NPZD model hurricane simulations can be compared against in situ observations and quantify differences among mechanistic inferences. Although ecological models may not perfectly replicate the response and recovery, managers can use them to the quantify physical and biological processes into a standard unit.

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