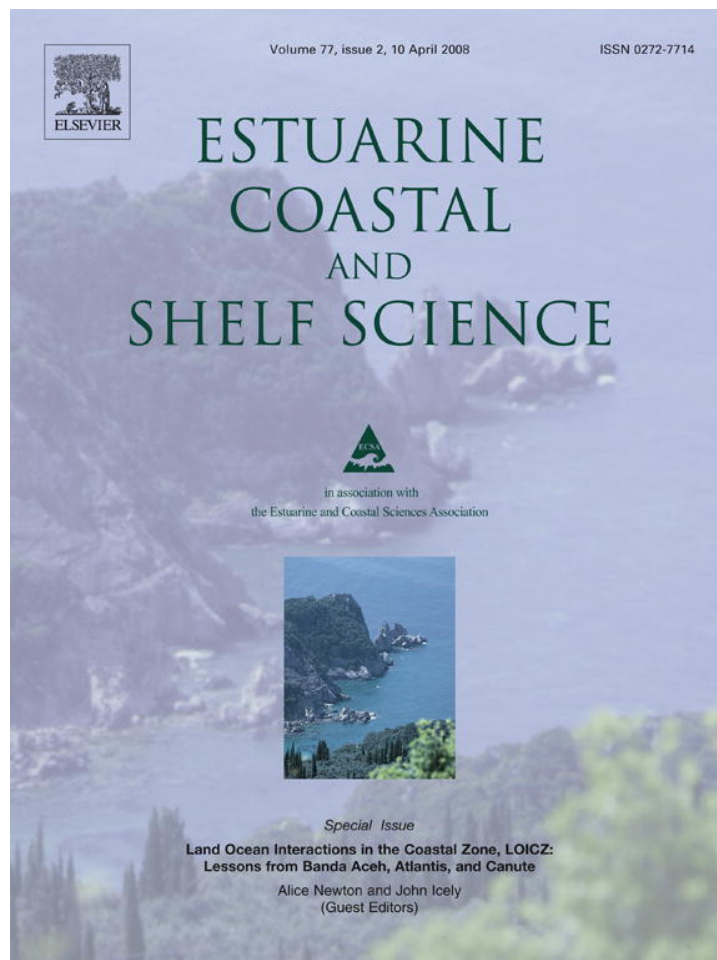


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Estuarine classification and response to nitrogen loading: Insights from simple ecological models

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Abstract

Estuaries exhibit a large range in their responses to nitrogen loadings determined in part by characteristics of the driver, such as magnitude and frequency, but also by such intrinsic characteristics as physical/chemical factors (e.g., depth, volume, hypsometry, salinity, turbidity) and biological factors (e.g., nature of ecological communities, trophic interactions). To address the richness of estuarine response to driver variables, the aim ultimately is to establish a simple estuarine classification scheme, beginning with a river-dominated subset of estuarine systems and focusing on the role of water residence time in the estuary. Residence time (or flushing time) is related to other drivers (streamflow, nutrient, and sediment loads) and drives much of the biological response of estuaries because of flushing effects on plankton, temperature, nutrients, and light. Toward this goal, nutrient–phytoplankton–zooplankton (NPZ) models have been used to examine a range of subjects including effects of nutrient limitation and zooplankton predation on phytoplankton dynamics and fish predation. This class of model can admit a wide range of behavior, including multiple steady-states and oscillatory behavior. The NPZ equations include terms for nutrient recycling, phytoplankton settling, benthic regeneration, and zooplankton mortality. Analysis of the equations suggests that both the nature of nitrogen loading (i.e., whether it is correlated with discharge or independent of it) and residence time are critical in determining the steady-state response of the system.

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Keywords: eutrophication; estuarine sensitivity; multiple stable states; nutrient cycles; estuarine dynamics; nitrogen

1. Introduction

Estuaries have been classified according to several schemes, including topography/geomorphology (Pritchard, 1952, 1967; Dyer, 1973; Hume and Herdendorf, 1988), hydrodynamics/circulation (Stommel and Farmer, 1952; Ketchum, 1954; Pritchard, 1955, 1967; Cameron and Pritchard, 1963; Hansen and Rattray, 1966), habitat type (Shaw and Fredine, 1956; Odum et al., 1974; Cowardin et al., 1979), trophic status (Bricker et al., 1999, 2003; Nobre et al., 2005) and hybrids of the above (Jay et al., 2000). Many of these are reviewed in NRC (2000). Of particular importance in managing the nutrient loads to estuaries is understanding the range of estuarine

responses to nutrient enrichments, i.e. the sensitivity of response to driver variables over a range of conditions. A variety of models exist to evaluate the response of estuaries to nutrient enrichment (reviewed in NRC, 2000). However, these are often hydrodynamically complex and site-specific, such as for the Chesapeake Bay (Cercio and Cole, 1993) or Massachusetts Bay and Jamaica Bay (Hydroqual and Normandeau Associates, 1995; Hydroqual, 1998, 2000; Signell et al., 2000). As a result, such models are extremely expensive to build, test, and run, and therefore are only available for management of very few systems (NRC, 2000). At the other extreme, for example, regression analyses across marine ecosystems have shown that log-transformed annual primary productivity is linearly related to log-transformed nitrogen (N) loading (Nixon, 1995; Nixon et al., 1996). Such models are useful in that they indicate that on average more N loading will contribute

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to more eutrophication. However, individual coastal marine ecosystems vary greatly in this response, and the “noise” inherent in these log–log relationships contains much information on the factors that determine the sensitivity of particular systems to nutrient loading. The National Research Council (NRC, 2000) concluded that, where adequate observational data exist to calibrate and verify process-based models, such models might be preferred management tools because they can include, at least in theory, a reasonably sophisticated representation of the physics, ecology, and biogeochemistry being simulated. However, the NRC also concluded that simpler statistical approaches may be more cost effective for managing most coastal marine ecosystems. We believe there is a middle ground between complex, detailed models for specific systems and cross-system statistical models. As such, this paper aims to communicate three general ideas as follows.

- Simple biogeochemical models (i.e., mathematical descriptions of the biogeochemical and ecological dynamics of estuaries) have a place in estuarine classification of sensitivity to external drivers because field observations alone may not provide sufficient information to describe coastal systems without the contextual understanding of an underlying mechanism. At the very least, such models can serve as a ‘straw man’ to test responses of alternative mechanisms.
- Even simple nonlinear models, such as the nutrient–phytoplankton–zooplankton (NPZ) models described here, exhibit a rich repertoire of behavior that may help an understanding of a great deal of the observed estuarine responses to driver variables.
- Details of the coupling between the coastal system and its watershed are critical to consider in understanding the dynamics of the ecological response of the system. Ignoring these may confound analyses, especially in cross-system comparisons.

While these points should not be controversial to the modeling community, nor to most coastal zone scientists, members of the estuarine and coastal management community may find some useful insights into ecological dynamics and management of estuaries in the examples we present below.

1.1. Budgets and other accounting methods

Probably the simplest class of models is that based on material budgets (water, salinity, nitrogen, phosphorus, etc.). These models typically account for average or “steady-state” fluxes of materials into and out of the system of interest, often with relatively modest data requirements. Inferences about internal processes can be made based on balancing the budget. An additional attractive aspect of simple budgets and other accounting methodologies is that they are inherently linear, irrespective of the dynamics of the system: there is no attempt to describe the relationships between internal processes and external forcings (loads) beyond expressing individual fluxes as proportions of the total.

Budgets can be considered minimal models in which the process details and dynamics have been omitted, but the fundamental constraints of mass-balance have been retained. Thus, classification systems based on such approaches generally do not make use of alternate states or dynamic behaviors that are intrinsic to the system, except to determine whether fluxes are positive or negative in sign (i.e., represent net sources or sinks). For example, the Land Ocean Interactions in the Coastal Zone (LOICZ) project has used this approach successfully to infer the distributions of net ecosystem metabolism magnitude and sign (i.e., relative importance of production to respiration) of coastal ecosystems around the world (Smith et al., 2005). Numerous authors have applied steady-state nutrient budgets to coastal systems at several scales to make inferences about ecosystem structure and productivity (e.g., Boynton et al., 1995; Wulff et al., 2001).

1.2. Beyond budgets: responses of dynamic models

Most estuarine classification schemes have been based on categories representing externally based or static criteria such as trophic indices (e.g., nutrient concentrations), without consideration of potential alternate behaviors in their responses to drivers such as nutrient loads. On the other hand, even relatively simple nonlinear models can exhibit different responses to drivers, depending upon the “state” of the system, representing the wide range of estuarine responses actually observed, and thus they can provide an additional basis for classification.

An example of a simple but informative model exhibiting two alternate stable states under changes in phosphorus (P) loading is the Carpenter’s (2005) model of phosphorus dynamics in a lake. This model is essentially a simple balance between external phosphorus load and outflow, with the addition of a nonlinear, concentration-dependent cycling of phosphorus between the lake water column and its bottom sediments. To illustrate the sort of insight that can be gained from such a model beyond that of models based on input–output budget or regression approaches, a slight simplification of the Carpenter model (Appendix 1) is presented which produces the steady-state response of water column P levels to P loading shown in Fig. 1a (the case $q=8$). While the steady-state responses of water column P and sediment P to P loading are nonlinear, they are always linearly related to each other ($P = (I_p - bM)/h$; see Appendix 1 for details). The model, which is based on observations of Lake Mendota, exhibits a hysteretic relationship between loading and P concentration, as well as two alternate stable states, which suggests that lake phosphorus concentrations could abruptly ‘flip’ between high and low modes under slight changes of P load in the vicinity of threshold loading rates. The reason for this is the nonlinear relationship between nutrient recycling rate and water column P concentration (Fig. 1b). Such nonlinear kinetics (a generalization of the well known Michaelis–Menten relationship, due to the addition of an exponent parameter, q) suggest that two identical lakes with similar external P loads may exhibit very different concentrations

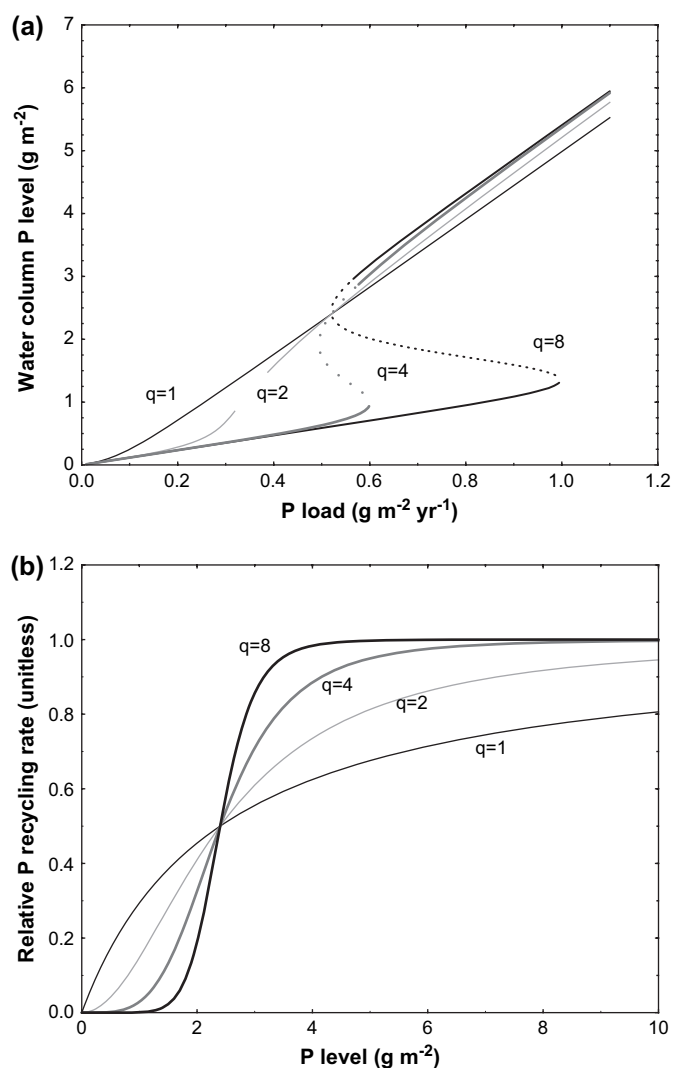


Fig. 1. (a) Response of lake water column P to P loading for various forms of recycling function (generalized Michaelis–Menten kinetics) in a simplified version of Carpenter's (2005) lake P dynamics model. Here, q is a parameter which controls the degree of nonlinearity in P recycling to P concentration; at $q = 1$, the response is conventional Michaelis–Menten dynamics; as q increases, the response increasingly resembles a step-function occurring at the half-saturation value, m . The solid lines indicate stable steady-states of water column P corresponding to the P load on the x-axis; dashed lines indicate unstable steady-state values. Circles ($q = 2$) correspond to a range of loads which yield stable oscillations. For loading rates between around 0.5 and $1 \text{ g P m}^{-2} \text{ yr}^{-1}$, two alternate stable states exist. For the other parameterizations of the recycling rate shown, this region of multiple stable states narrows or disappears altogether. (b) Generalized Michaelis–Menten function corresponding to the responses in (a). As the q parameter increases, the function changes from a standard Michaelis–Menten response ($q = 1$) toward a limiting step-function response ($q = \infty$). Carpenter used $q = 8$, based on observations in Lake Mendota.

and associated ecological indices. Clearly, a lack of awareness of such a mechanism for nonlinear or threshold “flip” responses presents a problem for those interested in developing classification systems for lakes based on some relatively easily measured parameter such as P loading. Alternate parameterizations of the P recycling rate ($q = 1, 2, 4$) show that the region of multiple stable states diminishes as recycling approaches

conventional Michaelis–Menten kinetics ($q = 1$) ultimately resulting in a single stable and approximately linear response to P loading rate (Fig. 1).

The master driver variable in the Carpenter (2005) lake eutrophication model is P loading, though the mechanism for generating multiple stable states is the nonlinear release of phosphorus from sediment. Estuarine nutrient dynamics can show similar responses to loads, though generally the controlling nutrient has been found to be nitrogen (N) rather than P (NRC, 2000; Howarth and Marino, 2006). Very similar multiple stable state behavior in response to N loading has been observed in the N dynamics of an estuarine biogeochemical model due to the mechanism of benthic denitrification (Murray and Parslow, 1999).

In general, the response of an aquatic system to changes in loading or other drivers is the net result of several processes, each of which could exhibit a distinct nonlinear response to variations in a driving variable (Fig. 2). For example, residence time is frequently considered a “master variable” in estuarine dynamics because it can be related to several other factors such as hydraulic loading, tidal dynamics, and terrestrial sediment, organic matter and nutrient loads (Nixon et al., 1996; Smith et al., 2005), as well as factors related to ecological processes, such as phytoplankton flushing (Ketchum, 1954), dilution (Nixon, 1992), stratification (Malone, 1977; Geyer and Montgomery, 2000; Jay et al., 2000), light limitation (Cloern, 2001) and denitrification (Nixon et al., 1996). Howarth et al. (2000) found short residence times ($< 1\text{--}3$ days) to be critical in limiting the rate of gross primary production in the Hudson River estuary, presumably due to the rate of flushing of phytoplankton from the estuary compared to their growth rate. The fraction of N load denitrified in estuaries has also been shown to be related to estuarine flushing time (Nixon et al., 1996).

Below, the response of a simple estuarine model to a range of hypothetical N loadings and residence times is examined. While estuarine residence time has a complex distribution dependent on bathymetry and other factors (Sheldon and Alber, 2002), for purposes of comparing estuarine response to average residence time across estuaries, freshwater flushing time (V/Q) is used as a proxy for average residence time.

2. An NPZ model for river-dominated estuaries

A class of models somewhat more complex than either nutrient budget models or the simple two-variable model discussed above, the nutrient–phytoplankton–zooplankton (NPZ) models, have been used to examine a range of subjects including effects of nutrient limitation and zooplankton predation on phytoplankton dynamics (e.g., Steele and Henderson, 1981) and fish predation (e.g., Scheffer et al., 2001). These models exhibit a wide range of behaviors, including multiple steady-states and oscillatory behavior (Edwards and Brindley, 1999). A particular set of NPZ equations have been selected to characterize the class of estuarine systems where primary production is predominantly pelagic. An advantage of such an approach is that parameters describing various processes or flows of materials can be treated as “knobs” to examine

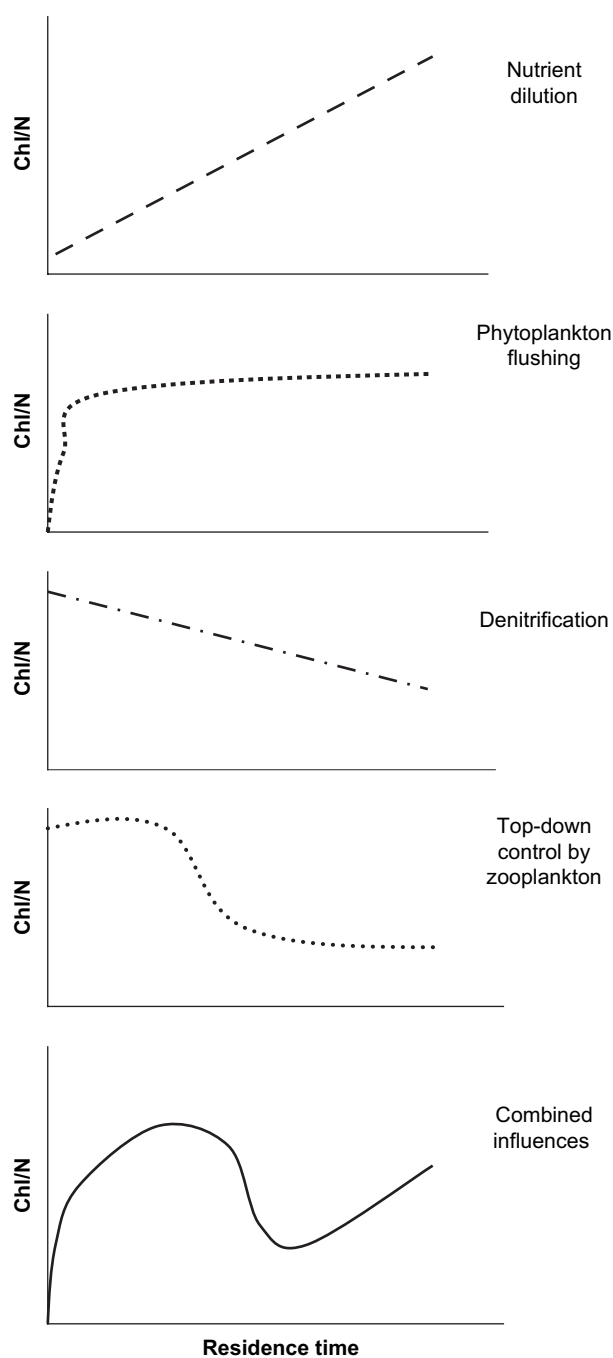


Fig. 2. Hypothesized responses of individual estuarine processes to variation in residence time as indicated by the ratio of chlorophyll to N concentration.

the effects of “switching processes on or off”, adjusting their magnitude, etc. The equations include terms for nutrient uptake and recycling, phytoplankton settling, benthic regeneration, and predation on zooplankton (Appendix 2). The NPZ model used in the preliminary investigations of estuarine response to nitrogen loading (Fig. 3) is conceptualized as a single, well-mixed compartment in which the basic interactions between nutrients (here, nitrogen), phytoplankton, and zooplankton are modeled as a set of coupled, nonlinear differential equations. The model is driven by inputs of nitrogen

both from sources that are coupled to Q (the riverine input of freshwater) by the input concentration C_N in the river and from sources that are independent of riverine flow. Below, the effects are examined of both flow-dependent and flow-independent nitrogen loads. Conceptually, the flow-dependent input can be thought of in the context of examining inter-annual variability within a given watershed (over relatively short number of years when N inputs to the watershed remain fairly constant) from non-point sources. The inputs of N that are not related to riverine flow can be thought of either in terms of point-source inputs, or alternatively average non-point source inputs over time periods of 5–6 years or more across a range of watersheds or within a given watershed over time, when the N inputs to the watersheds from human activity vary (Howarth et al., 1996). Dissolved N is lost to denitrification, to uptake by phytoplankton, and to the sea by flushing. Benthic primary producers are not considered in this version of the model. Recycling of nutrients from phytoplankton is proportional to the grazing rate of phytoplankton by zooplankton (attributable to either zooplankton excretion or “sloppy grazing”).

Phytoplankton and zooplankton are also assumed to have exogenous sources (e.g., benthic, up-estuary or seaward “seed sources” of plankton rather than riverine sources), which can be associated to varying degrees with Q , depending upon the relative values of I_{PZ} and C_{PZ} , and they are also lost to the sea by flushing. In some circumstances, exogenous sources appear to be necessary to maintain zooplankton densities against flushing and predation. Phytoplankton uptake of N has a generalized Michaelis–Menten kinetics with respect to N; grazing of phytoplankton by zooplankton has Michaelis–Menten kinetics in phytoplankton. The standard Michaelis–Menten form ($q = 1$) has been used to date with parameters in Appendix 2. Phytoplankton are also lost from the system via sinking, and zooplankton are lost due to predation from higher trophic levels; both of these processes are assumed to be first order.

To examine the response of the model to alternative N loading rates or residence times, a modified fourth-order Runge–Kutta integration routine (cf. Press et al., 1992) is used to solve the equations to “steady-state”, where this state is defined operationally as a point at which the absolute values of the rates-of-change of each of the three state variables considered (phytoplankton and zooplankton biomass density and water column N concentration) are less than or equal to one-thousandth of the corresponding values of the state variables, i.e. their relative changes in time are small. Default parameter values used as starting points to explore model parameter space are shown in the list of model parameters in Appendix 2. Unless otherwise indicated, these are the values used in the simulations below; those indicated by “superscript a” are based on values used by Hopkinson and Vallino (1995).

In the results below, the model responses are compared against phytoplankton-based measures of trophic state suggested by expert panels as part of NOAA’s National Estuarine Eutrophication Assessment (Bricker et al., 1999): <5 , $5–20$, $20–60$ and $>60 \mu\text{g chl l}^{-1}$ for low-, medium-, high-, and hyper-eutrophic states. The NPZ model as configured

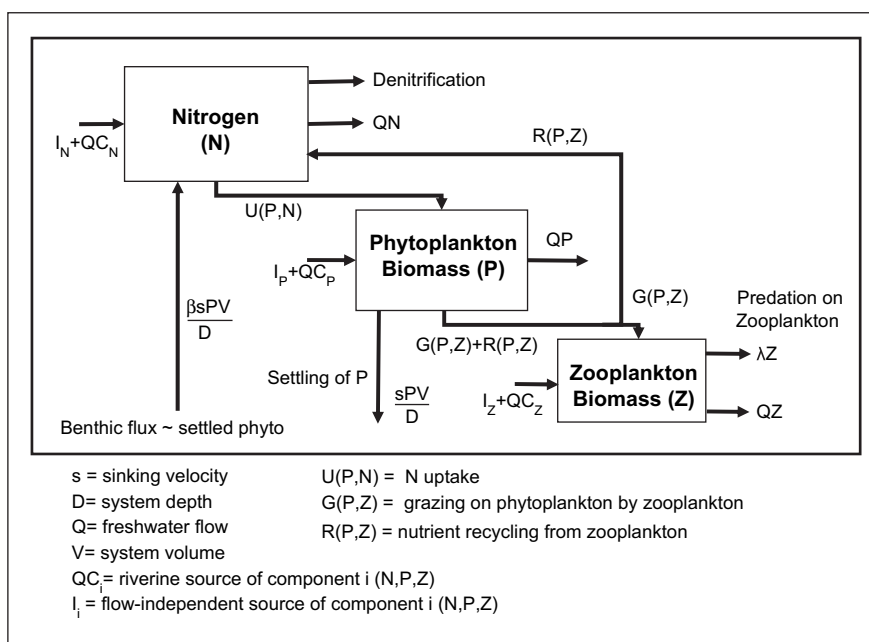


Fig. 3. Schematic diagram of NPZ compartments and the fluxes between them.

here characterizes phytoplankton biomass in its nitrogen equivalents, which correspond to values of 0.03, 0.12, and 0.37 mg N l⁻¹ for the trophic boundaries listed above, assuming a ratio of 0.165 mg chl mg⁻¹ N in phytoplankton biomass, based on the Redfield ratio (5.67 g C g⁻¹ N) and a C:Chl ratio (34 g C g⁻¹ Chl) typical of the midrange of coastal phytoplankton (Welschmeyer and Lorenzen, 1985).

Mathematical analysis of the model to date suggests that its ecological dynamics can be considered as spanning three general regimes: (1) no zooplankton are present at steady-state, (2) no phytoplankton or zooplankton are present at steady-state, or (3) both phytoplankton and zooplankton are present. The first two cases represent situations in which high flushing rates, inadequate nutrients, or other unfavorable circumstances force the elimination of one or more trophic levels. Limitation of primary productivity has been reported at low residence times – i.e. high flushing rates (Howarth et al., 2000). Case three represents a broad regime within which there remains significant variation in the ecological response to nutrient loading and flushing rates.

3. Results and discussion

While the steady-state analysis might appear artificial to managers of coastal systems because secular and seasonal variation in driver variables (climate, hydrology, and nutrient loading) prevent estuaries from reaching steady-state, the steady-state responses provide adequate representations to allow distinctions among estuaries. Apart from this, the system itself may have its own internal dynamics which prevent it from settling down to a steady-state, at least on the time scales of interest to managers.

A steady-state is achieved over a wide range of nutrient loads for the default parameter values of the model (Appendix 2). However, beyond some parameter boundaries, the *dynamics* can become considerably more complicated. Increasing load or changing other parameter values may upset the steady-state balance, resulting in oscillatory or other time-varying behavior. Fig. 4a shows two scenarios: the default scenario, in which rate of predation on zooplankton (by fish or other predators) is 15 day⁻¹, and the case in which this rate is reduced to 1/3 of the ‘default’ rate (to 5 day⁻¹). In both cases, the biology of the estuary being simulated has reached a steady-state trophic status in response to steady inputs of nitrogen. In the default scenario, phytoplankton stabilize at a borderline “high” trophic status, while in the reduced-predation scenario, they stabilize at a steady level of intermediate trophic status, due to increased levels of zooplankton associated with reduced-predation which increases the steady-state grazing of zooplankton on phytoplankton. Such steady responses to alternative scenarios are not the only behaviors exhibited for such scenarios. Fig. 4b shows the effect of increasing N concentration in riverine load from 5 to 7 mg l⁻¹ N. In this case, the default scenario (default level of predation on zooplankton) shows a steady response very similar to that in Fig. 4a. However, the decreased predation rate on zooplankton now results in dramatic oscillations around the intermediate value (note log scale). “Switching on” denitrification returns the system to steady-state corresponding to reduced zooplankton predation shown in Fig. 4a by effectively reducing the increased load, but if the N load is further increased (e.g., to 10 mg l⁻¹) the oscillatory behavior shown in Fig. 4b returns even in the presence of denitrification. This scenario illustrates that the presence of denitrifiers may not only affect the ambient concentration of nitrogen, but both short and longer term N

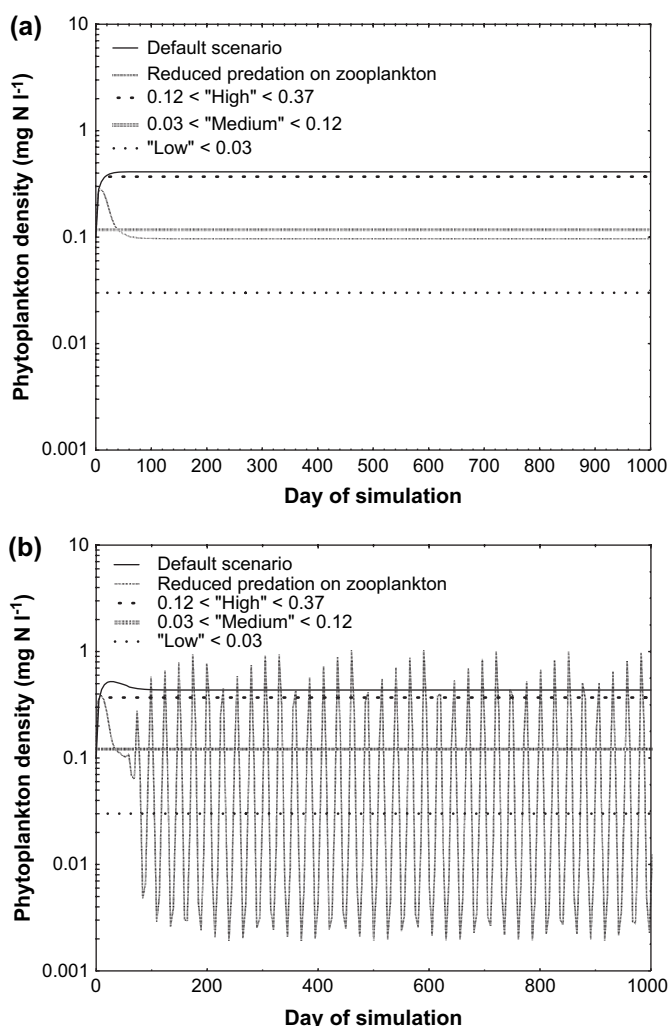


Fig. 4. Phytoplankton concentration vs. time assuming a nitrogen concentration of 5 mg l⁻¹ in riverine flow and a zooplankton predation coefficient of 0.05 instead of the default value of 0.15. Phytoplankton rapidly settles down to a steady-state value. (b) as in (a), except that the nitrogen concentration in river flow has increased to 7 mg l⁻¹. The result is stable oscillations of phytoplankton, due to the lack of top-down damping by zooplankton predators.

dynamics as well. It is important to note some results of sensitivity analyses: while the specific loads at which the phytoplankton levels begin to fluctuate depend on the specific values of other parameters (e.g., the half-saturation rate of nitrogen uptake), qualitatively, the transitional behavior remains.

The interaction of specific functional groups, such as denitrifiers, with “bottom-up controls” can be significant to the steady-state response of estuaries to nutrient loading. Fig. 5a shows the steady-state response of N concentration, phytoplankton and zooplankton biomass densities to increasing nitrogen loading for the default scenario ($\tau = 100$ days) in the absence of denitrification. “Switching on” denitrification (Fig. 5b) is manifest not only in a reduced N concentration of the estuary, but in reduced phytoplankton and zooplankton densities as well. In these simulations, at loading rates above 40 t day⁻¹ N the difference is enough to shift phytoplankton densities from above the indicated “high” trophic status boundary to well below it.

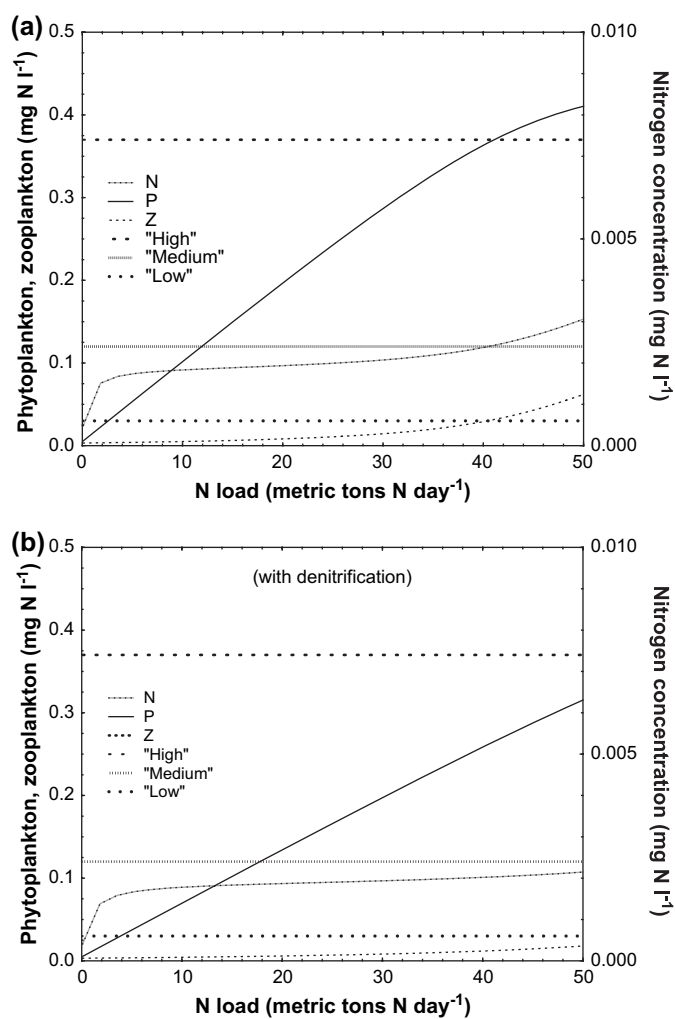


Fig. 5. Simulated steady-state response of nitrogen (N), phytoplankton (P) and zooplankton (Z) to increasing nutrient loads assuming a system flushing time of 100 days. (a) The simulated response to loading in the absence of denitrification. (b) Response with the addition of a residence-time-dependent denitrification rate (Nixon et al., 1996). Removal of nitrogen from the system suppresses phytoplankton and zooplankton, and changes the eutrophication status of the estuary, especially at high loading rates.

The steady-state response of the estuarine plankton to N loading also varies strongly with flushing time, but the effects of nutrient loading can be complicated in cases where N loading is correlated with flushing. For any given watershed where the inputs of nitrogen from human activity are relatively constant over time, the load of nitrogen in the river is highly correlated with discharge, and thus is inversely correlated with flushing time. On the other hand, nitrogen fluxes in rivers, compared across watersheds or averaged over several years, are strongly controlled by the inputs of nitrogen to the watersheds from human activity (Howarth et al., 1996, 2006; Boyer et al., 2002). While riverine freshwater flow is related to nitrogen fluxes in rivers at both short and longer time scales (Howarth et al., 2006), because of the influence of nitrogen inputs, freshwater flow is not strongly correlated with nitrogen fluxes when comparing across river basins or examining long-term trends in nitrogen fluxes even in river basins where non-point sources of nitrogen dominate.

Fig. 6a, b shows the response of phytoplankton and zooplankton to several different N loading scenarios over a range of residence times. For a specified N loading rate (independent of Q and flushing time), steady-state phytoplankton density initially increases linearly with flushing time, eventually reaching a plateau and even declining somewhat from the maximum at intermediate residence time for high loading rates (Fig. 6a). The asymptotic behavior is evidently due to zooplankton grazing. At low flushing times (<20 days) the system can only support low steady-state zooplankton biomass densities, but sufficient phytoplankton biomass to support relatively large densities of zooplankton is permitted at longer time scales (Fig. 6b). This is further supported by the effect of denitrification, which when “switched on” in the model (Fig. 7), results in a dramatic decline in phytoplankton and especially zooplankton densities. The effect of the flushing time-dependent denitrification rate on plankton densities is especially strong at the high end of the range of time scales examined (>60 days).

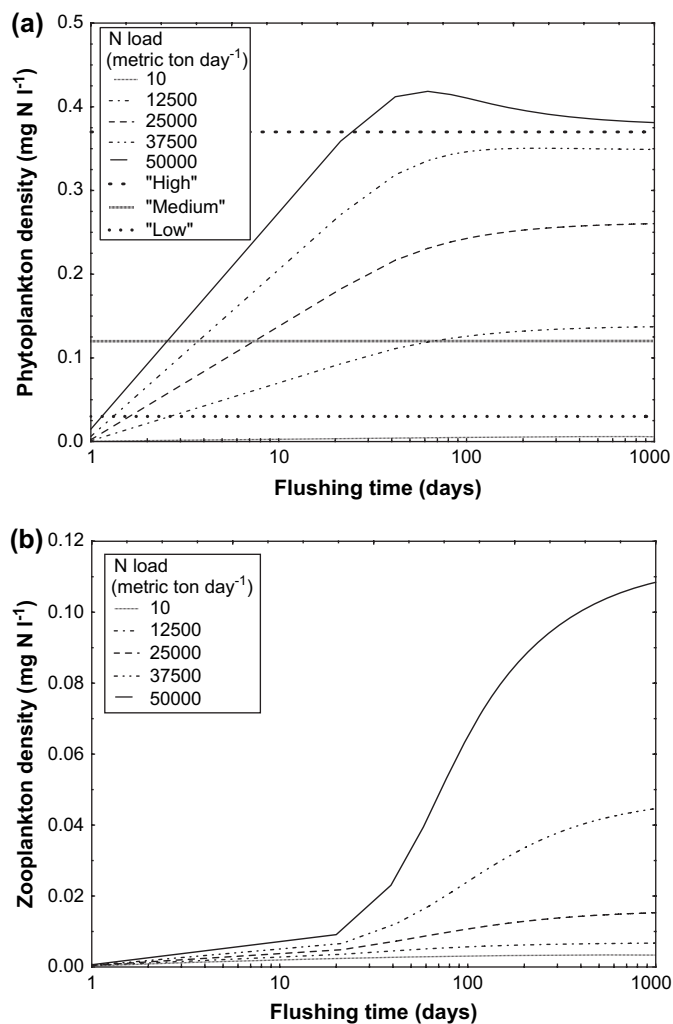


Fig. 6. (a) Simulated steady-state response phytoplankton vs. flushing time at differing nitrogen loading rates (metric tons N day⁻¹). At the highest levels of loading, phytoplankton levels decline from a peak at an intermediate flushing time. (b) Longer time scales permit more extensive grazing by zooplankton, resulting in higher zooplankton densities.

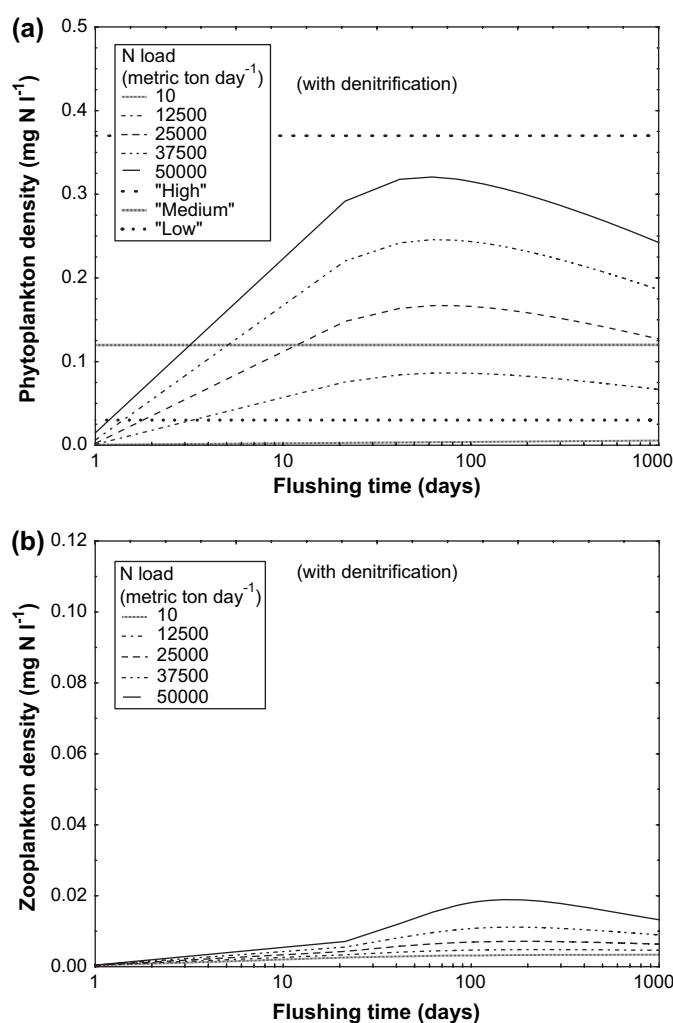


Fig. 7. (a) Simulated steady-state response phytoplankton vs. residence time at differing nitrogen loading rates with the assumption of a flushing time-dependent denitrification rate. In this scenario, denitrification suppresses phytoplankton level due to nutrient limitation, especially at longer time scales. (b) Zooplankton densities are correspondingly limited due to lower phytoplankton biomass.

In contrast to the previous cases where nitrogen loads were independent of flow, cases were also explored in which loads are correlated with flow, holding riverine concentrations constant so that loads are varied by changing river flow (Fig. 8). Here, riverine N concentration is held constant, and therefore N loads are inversely correlated with flushing times; that is, as flushing time increases, riverine flow (and so N load) decreases. The response is very different to the alternative approach considering N inputs independent of flow, showing declining phytoplankton levels as flushing time increases because N load decreases with flushing time.

This distinction is important for cross-system comparisons because the relationship between nutrient loading and residence time can be confounding.

From the standpoint of analyzing the interaction of nutrient load and flushing time across systems, nutrient loading rates could appear to be largely independent of flushing time either

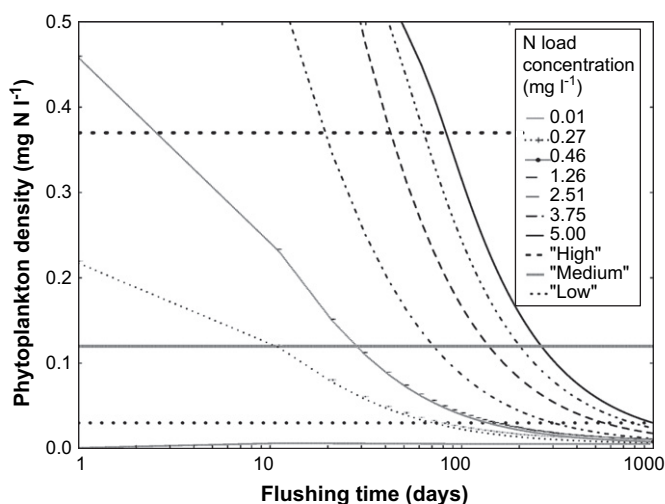


Fig. 8. Simulated steady-state response in phytoplankton vs. flushing time at differing nitrogen concentration levels (mg N l^{-1}) assumed in riverine flow to the system. As flushing time increases, flow decreases along with associated N loads, and phytoplankton levels decline.

because they are independent of flow (steady point-source discharge directly to the estuary, or using a constrained set of catchments of approximately equal area) or because the analysis spans a range of estuaries of varying volumes unrelated to the magnitude of riverine inflows. A NOAA data set (Smith et al., 2003) comparing characteristics of North American estuaries across systems reveals a few interesting relationships (all using log-transformed data, $n = 91$). There is essentially no relationship between residence time and N load scaled per area of watershed ($r = 0.17$) or between freshwater flow per area and N load per area ($r = 0.12$). Thus for a set of watersheds of roughly the same area, N loads appear to be independent of residence time. This is consistent with the finding that human-controlled N inputs to the river basin are the major control on average fluxes of N in river at multi-year time scales (Howarth et al., 1996, 2006; Boyer et al., 2002). If the N loads are not scaled by watershed area, there are strong correlations between freshwater flow and estimated N load ($r = +0.80$) because of the range of contributing areas, but weaker negative correlations between estuarine exchange time and estimated N load ($r = -0.30$), due to the effect of volume variation of receiving waters. In such cases, nutrient loads that are primarily riverine in origin and correlated with streamflow can be negatively correlated with estuarine flushing time in any one system, but may not appear to be correlated across systems because of the effect of varying system volume. In the world of estuarine typology, the implications are significant, given the difference in response between flow-independent and flow-dependent nutrient loads.

4. Conclusions

The model system presented here represents a simple, single-compartment, single-layer “cartoon” of the biological dynamics of an estuary. It is worth noting that while this model

is relatively simplistic and minimal in its parameterization, even simpler budget based models have been useful in cross-systems comparisons and coastal typologies (Crossland et al., 2005). These simple models can exhibit a variety of behaviors in response to different levels of environmental drivers, such as freshwater flow or nutrient load, including various steady-states, regular oscillations, and irregular fluctuations that may inform classification of coastal ecosystems sensitivity.

One may ask the degree to which simple models should be used to predict estuarine behavior. More complex models could consider distinctions between nutrient sources (e.g., explicit consideration of atmospheric and oceanic terms), include multiple layers (Gordon et al., 1996), additions of size structured plankton or functional groups (Moloney and Field, 1991; Armstrong, 1999), light and temperature (Cloern, 2001; Geyer et al., 2000), other nutrients (Justic et al., 1995; Conley, 2000; Howarth and Marino, 2006), N fixation (Howarth et al., 1999), and competition for light (Huisman et al., 2004). Models that incorporate some of these factors (cf Andersen, 1997; Armstrong, 2003) have been developed. While such models are often used to examine hypotheses about ecological mechanisms, they tend to be site- or process-specific and not general enough for guiding the more general task.

The responses of the simple, mechanistically-based models to variations in external drivers suggest dynamics to consider when trying to interpret data and classify estuarine systems. These include: hysteresis and other nonlinear responses, multiple stable states, the potential for instability and oscillations, and interactions of processes. As such, simple models can be powerful tools for guiding data collection and analyses, and for characterizing estuarine response within and across estuarine types, because they can suggest how processes might shape those responses.

It is clear, though, that even relatively simple nonlinear models can exhibit a wide repertoire of behaviors, and one must guard against inferring unrealistic behaviors obtained from poor parameter estimates or combinations. For example, some marine food chain models have exhibited spurious oscillations or extinctions in regions of parameter space where observations suggest that they should not occur (Armstrong, 1994, 2003; Hurtt and Armstrong, 1996, 1999). To partially address this issue, a parameter sensitivity analysis is performed to examine the range of model behavior as parameters change. The analyses suggest that steady-state behavior of the NPZ model (Appendix 2) is relatively insensitive to two key parameters: the nutrient half-saturation constant and phytoplankton growth rate. Where model *dynamics* may depend on specific values of parameters, the steady-state behavior is more robust, lending some credibility to analysis of long-term responses.

In summary, tools like this NPZ model can help assess complex responses of estuaries to multivariate drivers associated with climate change, land-use change, and other anthropogenic effects, and that this provides a logical and flexible basis for categorizing estuarine sensitivity to these drivers.

Some insights have been gained into estuarine responses to a range of flushing times and N loads; the response depends, among other things, upon whether the load is dependent on or independent of freshwater inflows, and thus directly on the nature of the N source to the estuary. Such a model-based approach should provide further insights into sound environmental management of estuaries, and lead to more intelligent assessment of potential impacts of human activities.

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Appendices

Appendix 1. A simplified variant of Carpenter’s (2005) lake P dynamics model

Carpenter (2005) described a three variable model of phosphorus dynamics in a lake and its watershed which exhibits two stable states under changes in P loading. Without significant changes to the qualitative behavior of the model we can eliminate one of the variables (watershed soil P concentration) and assume P loading to the lake (I_p) as a parameter, thus:

$$\frac{dP}{dt} = I_p - (s + h)P + rMf(P) \quad (\text{a1.1})$$

$$\frac{dM}{dt} = sP - bM - rMf(P) \quad (\text{a1.2})$$

where

$$f(P) = \frac{P^q}{m^q + P^q}$$

= relative rate of recycle of phosphorus from sediment to water column (unitless)

where P = mass of P in the water column per unit lake area (g m^{-2}); M = mass of P in the lake sediments per unit lake area (g m^{-2}); I_p = watershed loading of P to the lake ($\text{g m}^{-2} \text{ yr}^{-1}$); s = sedimentation rate of P ($\text{g m}^{-2} \text{ yr}^{-1}$); h = outflow rate of P from lake ($\text{g m}^{-2} \text{ yr}^{-1}$); b = permanent burial rate of sediment P ($\text{g m}^{-2} \text{ yr}^{-1}$); r = maximum rate of

P recycling/unit sediment P (yr^{-1}); q = dimensionless parameter in generalized Michaelis–Menten function used to describe P recycling; m = “1/2-saturation” parameter in generalized Michaelis–Menten function used to describe P recycling.

Default parameter values used by Carpenter are as follows: $s = 0.7$; $h = 0.15$; $b = 0.001$; $r = 0.019$; $q = 8$.

Assuming steady-state, and adding Eqs. (a1.1) and (a1.2), we obtain a linear relationship between M and P : $0 = I_p - hP - bM$, which is easily rearranged to solve for the corresponding value of M in terms of P and I_p .

Appendix 2. A simple NPZ model

The nutrient–phytoplankton–zooplankton system described in Section 2 of the text can be written as a set of mass-balance equations in the following form:

$$V \frac{dN}{dt} = I_N + Q(C_N - N) - U(P, N) + R(P, Z) + V \frac{\beta s P}{D} - \text{Denitr} \quad (\text{a2.1})$$

$$V \frac{dP}{dt} = I_P + Q(C_P - P) + U(P, N) - G(P, Z) - R(P, Z) - V \frac{sP}{D} \quad (\text{a2.2})$$

$$V \frac{dZ}{dt} = I_Z + Q(C_Z - Z) + G(P, Z) - \lambda V Z \quad (\text{a2.3})$$

The equations describe homogeneous compartments of concentrations of nitrogen (N), phytoplankton (P), and zooplankton (Z), subject to discharge from terrestrial sources (Q), discharge-independent loading (I_i , $i = N, P, Z$), discharge-dependent loading (QC_i), flushing of nitrogen, phytoplankton and zooplankton from the system to the open sea (QN, QP, QZ), uptake of nitrogen by phytoplankton (U), grazing of phytoplankton by zooplankton (G), recycling of a portion of the grazed phytoplankton nitrogen (R).

The complete set of model parameters and their default values used for this study is shown below:

| | |
|--|-------------------|
| V , system volume (m^3) | 1.0E + 09 |
| D , system depth (m) | 5 |
| Q , riverine inflow ($\text{m}^3 \text{ day}^{-1}$) | 1.0E + 07 |
| C_N , N concentration in riverine load ($\text{mg l}^{-1} \text{ N}$) | 5.00 |
| C_P , P biomass concentration in riverine load ($\text{mg l}^{-1} \text{ C}$) | 0.05 |
| C_Z , Z biomass concentration in riverine load ($\text{mg l}^{-1} \text{ C}$) | 0.05 |
| I_N , flow-independent N load (g N day^{-1}) | 0.0 |
| I_P , flow-independent P source (g C day^{-1}) | 0.0 |
| I_Z , flow-independent Z source (g C day^{-1}) | 0.0 |
| ν_N , maximum phytoplankton growth rate (day^{-1}) | 2 ^a |
| k_N , Phytoplankton growth half-saturation constant ($\text{mg l}^{-1} \text{ N}$) | 0.03 ^a |
| ν_P , Maximum zooplankton grazing rate (day^{-1}) | 1 ^a |
| k_P , Zooplankton grazing half-saturation const ($\text{mg l}^{-1} \text{ C}$) | 0.4 ^a |
| q , Generalized Michaelis–Menten exponent (unitless) | 1 |
| b , Phytoplankton C required per unit grazer C (unitless) | 1 |
| α , Fraction of grazing recycled (unitless) ($0 < \alpha < 1$) | 0.7 |

(continued on next page)

(continued)

| | |
|--|------|
| β , Fraction of benthic flux recycled (unitless) ($0 < \beta < 1$) | 0.1 |
| s , Phytoplankton sinking rate (m day^{-1}) | 0.5 |
| λ , 1st order predation coefficient on zooplankton (day^{-1}) | 0.15 |
| Initial condition, $N(0)$ ($\text{mg l}^{-1} \text{N}$) | 0.10 |
| Initial condition, $P(0)$ ($\text{mg l}^{-1} \text{C}$) | 0.10 |
| Initial condition, $Z(0)$ ($\text{mg l}^{-1} \text{C}$) | 0.10 |

^a Hopkinson and Vallino, 1995.

P and Z biomass are conventionally tracked in carbon units (i.e., g C m^{-3} or mg C l^{-1}) but, for convenience, are reported here in nitrogen units (i.e., mg N l^{-1}) assuming a fixed C:N ratio, as described in Section 2.

For this analysis, $U(P,N)$ is considered to be in the form of a generalized Michaelis–Menten relation in N and proportional to P, i.e., $U(P,N) = VP(v_N N^q / (k_N^q + N^q))$ (here, $q = 1$ is assumed). Grazing, $G(P,Z)$, is regarded as proportional to Z, and has been considered either as a generalized Michaelis–Menten in P or proportional to P ($G(P,Z) = (1 - \alpha)VZ(v_P P^q / (k_P^q + P^q))$ or $G(P,Z) = (1 - \alpha)Vv_P PZ$). The nutrient recycling term $R(P,Z)$ is proportional to G , i.e., $R(P,Z) = \alpha / (1 - \alpha)G(P,Z)$. The grazing loss to phytoplankton biomass is $G + R$, i.e., either $VZ(v_P P^q / (k_P^q + P^q))$ or $v_P V PZ$. Denitrification has been characterized by Nixon et al. (1996) in terms of the percent of terrestrial N load, i.e.:

$100(\text{Denitr}/I_N) = 20.8 \log(\tau_{\text{mo}}) + 22.4$ where Denitr = rate of denitrification, I_N = nitrogen load to the system, τ_{mo} = flushing time (months). This relationship is used for denitrification as a function of nitrogen load and residence time.

There are similarities to Carpenter's P dynamics model in the structure and mathematical form of the above equations, though for the parameter space examined to date, observations on transitions between alternate stable states have not been investigated.

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