

Plant biomass and nutrient dynamics: modelling blooming phenomenon.

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Abstract: There is an increasing public awareness of the very strong pressures that aquatic ecosystems are experiencing because of direct and indirect influences from rapid population growth. The signs that there are problems in such ecosystems are already obvious: changes in biodiversity, decreased water availability, increased salinity and general deterioration in the catchment environment. In addition, such areas already experience instances of poor water quality caused by changes in chemical nutrients from the redeployment of land for urban, industrial and agricultural uses.

Aquatic ecosystems such as catchments are essential for the health, wellbeing and diversity of the coastal and marine environment. Variations in the conditions in these environments from increased pollution, changing weather and long term climatic trends has altered the biodiversity and abundance of species found. Selner et al. (2003) documented the shift in climatic and pollution trends which are favourable for algae blooming. The National Land and Water Resources Audit also confirms this link in the Australian Catchment, River and Estuary Assessment.

Catchments comprise dynamic estuaries which currently suffer under eutrophication due to excessive nutrients from run-off and storm water input. An increase in primary production through excessive organism growth is the general outcome of an increased nutrient flux of either Phosphorus (P) or Nitrogen (N). The addition of excess nutrients to high nutrient ecosystems creates a negative response in benthic species such as seagrass because of secondary light limitation from shading due to algae blooms. In this paper, the consequences of blooming experienced in aquatic ecosystems due to changes in temperature and chemical nutrient dynamics is modelled by a Lotka-Volterra type system. The aim of this paper is to use this system to address aspects of competition between seagrass and filamentous algae.

Accounting for the dynamics of species in estuaries proves to be an effective measure of the overall risk from increased nutrient and changing temperature fluxes. Integrating this component into a whole catchment model could potentially provide a useful tool in reducing the uncertainty around optimal management practices for controlling excess nutrient loads from storm water and run-off.

Keywords: Aquatic ecosystem, blooming, integrated catchment models, Lotka-Volterra, nutrient dynamics.

1 A SIMPLE MODEL OF COMPETITION IN A MIXED ENVIRONMENT

Currently, there exists a need within integrated catchment management models to address individual system component influences on whole level management actions in order to develop a clearer understanding of the behaviour of the “natural” catchment system. Understanding the individual system components aids stakeholders (policy makers, community groups, researchers and management) in the distribution of available management resources. The National Land and Water Resources Audit have identified the need to integrate conceptual models that link catchment and estuarine use, estuarine ecology and estuary condition. In particular, linkages between catchment land use and estuary conditions are of primary interest.

Several integrated physical-ecological models exist to explore this link for aquatic ecosystems under increasing eutrophication (detailed examples may be found in Hu *et al.* (2006); Kuo *et al.* (2008) and citations therein). These models conceptualise the relationship between nutrient fluxes, temperature and phytoplankton blooming phenomena. In the Australian estuarine environment however, vertical mixing implies that temperature and nutrients can be more or less constant within the water column and this suggests that blooms are often of the filamentous types of algae rather than phytoplankton. This type of algae is not rooted to the lagoon floor and forms mats across the benthic surface layers and hence is not, in this simple model, a “moving” species. Essentially, this species obtains nutrients from the water column. This means that the population dynamics model may be considered as a two-dimensional diffusive system without advection of any species assuming that species and nutrients occupy one vertical layer. In this model, a simplified structure is assumed to gain an understanding of the dynamics of species for the well mixed environment and as such cannot be extended on as a global study. We focus on the Central Coast Catchment of New South Wales, where the environments are well mixed. Additionally, these environments are essential for filamentous algae growth, a key focus point of this paper.

The major chemical nutrient causing eutrophication depends on the ecosystem in question. In aquatic ecosystems, the literature shows that freshwater lakes are primarily Phosphorus (P) limited and marine ecosystems are primarily Nitrogen (N) limited (Howarth and Marino, 2006; Taylor *et al.*, 1995). Salinity for the estuaries considered in this paper generally ranges from 10 - 35 ppt, suggesting that the ecosystem may be N limited. This allows for an additional advantage of model simplification through the use of coupled partial differential equations for N flux.

The major impacts of eutrophication in estuaries are increases in nonbenthic populations (such as filamentous algae) which dominate nutrient uptake in the water columns. Benthic populations suffer the most under increased nutrient loads because of the way in which they interact with other light-reducing non-benthic populations. To model this limiting process a Lotka-Volterra competition model is formulated and solved. This model deals firstly with the increases in the chemical nutrient flux resulting from increased storm water and run-off inflow by modelling in terms of nutrient uptake by the primary ecological competitors, seagrass and filamentous algae. Secondly, the model addresses the interaction process between benthic seagrass species and floating mats of filamentous algae through the inclusion of a Lotka-Volterra interspecific competition term where reduction in benthic species increase is proportional to the amount of filamentous algae. Assumptions about secondary light limitation are made from this term with parameterisation from Cummins *et al.* (2004). The results from this term are utilised as an indicator of the potential risks arising from an increased nutrient flux and changing temperature conditions.

As an initial starting point we consider only the nutrients available at each location and form a simplified water column model. Of course this model will need to be integrated with a hydrodynamic model of transportation such as those found in Teeter *et al.* (2001). The parameters used in this paper come from known literature and are used as a guide, current bioassay and geographic studies are underway on site and we expect to have these after the summer bloom, as such some parameters are estimated in order to provide a link to the competition dynamics explored in Dunn *et al.* (2009). Additionally, we use proportional responses to govern the secondary light limitations as given in Cummins *et al.* (2004).

2 MODEL DESCRIPTION

The model is a coupled system consisting of a nutrient dynamics component and a species dynamics component. Assessment of the impacts of algae blooming phenomena for changing environmental condi-

tions is achieved using time dependant functions for the parameters in the coupled system. State variables include sources of N (DIN-dissolved inorganic N, SED-sediment N), and biomasses of floating algae and benthic seagrass. The pathways of internal biogeochemical cycling of N are detailed in the flow diagram Figure (1), adapted from Forés *et al.* (1994). The flow arrows detail the cycle paths with detritus (*DET*) cycling back into *SED* from seagrass and algae mortality. The following sections describe each component in detail.

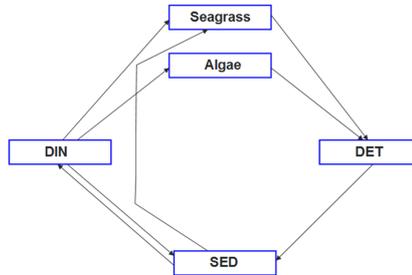


Figure 1. Nutrient state variables interactions with species.

2.1 Species Dynamics Model

The species dynamics of filamentous algae, u , and benthic seagrass, v , are coupled components governed by a general competitive Lotka-Volterra equation model. For the two-dimensional diffusive situation, the equations take the form

$$\begin{aligned}
 \frac{\partial u(x, y, t)}{\partial t} &= c_1 \Delta u(x, y, t) + u(x, y, t) [r_1(t) - \alpha_{11}u(x, y, t)] && \text{in } \Omega \\
 \frac{\partial v(x, y, t)}{\partial t} &= c_2 \Delta v(x, y, t) + v(x, y, t) [r_2(t) - \alpha_{21}u(x, y, t) - \alpha_{22}v(x, y, t)] \\
 \mathbf{n} \nabla u|_{\Gamma} &= 0 \\
 \mathbf{n} \nabla v|_{\Gamma} &= 0 \\
 u(x, y, t = 0) &= u_0 \quad v(x, y, t = 0) = v_0.
 \end{aligned}
 \tag{1}$$

where u is the biomass of the blooming species and v the biomass of the light limited benthic species. α_{ij} the competition terms with $i \neq j$ inter- and $i = j$ intraspecific competition. The c_i and $r_i(t)$ relate the diffusive rates and growth-mortality rates to the domain Ω in x, y (longitude, latitude) pairs and time t . Γ refers to the boundary of the domain, Figure 2, on which Neumann boundary conditions are imposed with \mathbf{n} the outward normal and u_0 and v_0 provide the initial distributions of u and v at $t = 0$.

2.2 Nutrient Dynamics Model

The nutrient dynamics model links the dissolved inorganic N and the sediment N, with the species dynamics model given in section 2.1. For the two-dimensional situation, the nutrient dynamics take the form

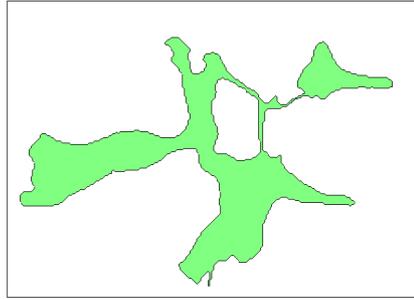


Figure 2. The boundary and domain Γ of Avoca Lagoon.

$$\begin{aligned} \frac{\partial n_1(x, y, t)}{\partial t} &= -f_1 n_1(x, y, t) + f_2 n_2(x, y, t) - V_{11} u(x, y, t) - V_{12} v(x, y, t) && \text{in } \Omega \\ \frac{\partial n_2(x, y, t)}{\partial t} &= f_1 n_1(x, y, t) - f_2 n_2(x, y, t) + d(u + v) - V_{22} v(x, y, t) && (2) \\ \mathbf{n} \nabla n_1 &= 0 \\ \mathbf{n} \nabla n_2 &= 0. \end{aligned}$$

where n_i are the dissolved inorganic N (DIN) and sediment N (SED) available for uptake from u and v . The input of N into the system from storm water and run-off is given by a where the possibility exists for $a = a(x, y, t)$. The coefficients β_{ij} model the uptake and transformation of the n_i into species u and v biomass and the constant d provides for the detritus (DET) contribution from dead or decaying u and v . Flux between pelagic and benthic compartments balance each other out. It is reasonable to assume that both n_i will have flow across the boundary Γ so Neumann boundary conditions are imposed with ψ_0 constant. Observations at Avoca Lagoon also indicate the inflow of N into the system has no observable shift in species growth because maximum uptake of N has already been exceeded, however inclusion of the hydrodynamic model could address this point further.

3 PARAMETERISATION

Species biomass of u and v and standing stocks of n_i are given in kg m^{-2} . Parameter values are adapted from known literature cited in Table 1 but data collection is currently underway and values should only be used as an indicator of general behaviour. Growth as a function of temperature for filamentous algae (FA) and seagrass are bell-shaped and adapted from Kiirikki *et al.* (1998) such that

$$\begin{aligned} g_1(n_1, T) &= \mu_1 V_1 \exp\left(\frac{b_1 * T_m}{1 - b_1} + T\right) * \ln\left(b_1 + \frac{1 - b_1}{T_m} * T\right) + T_m - T \\ g_2(n_1, n_2, T) &= \mu_2 \left(V_1 \exp\left(\frac{b_2 * T_o}{1 - b_2} + T\right) * \ln\left(b_2 + \frac{1 - b_2}{T_o} * T\right) + T_o - T + V_2 \exp\left(\frac{b_3 * T_o}{1 - b_3} + T\right) * \ln\left(b_3 + \frac{1 - b_3}{T_o} * T\right) + T_o - T \right) \end{aligned} \quad (3)$$

where the μ are the maximum growth rates for species, the b 's are the coupling constants for growth and temperature, T , and $T_{o,m}$ are the optimal temperatures for growth. Here $r_i = g_i - d_i$ with d_i species mortality.

Nutrient uptake is formulated by Michaelis-Menten kinetics with the reaction rate V related to the substrate concentration S with K_m and V_{max} the Michaelis constant and the maximum rate respectively given by

$$V_i = \frac{V_{i \max} [n_i]}{K_i + [n_i]} \quad (4)$$

Table 1. Model parameters

Symbol	Unit	Description	Value	Note
c_1	(d ⁻¹ m ⁻²)	FA dispersal rate	-	
c_2	(d ⁻¹ m ⁻²)	Seagrass dispersal rate	-	
r_1	(d ⁻¹)	FA growth/mortality rate	$r_1(n_1, T), d$	Kiirikki et al. (1998)
r_2	(d ⁻¹)	Seagrass growth/mortality rate	$r_1(n_1, T), d$	Kiirikki et al. (1998)
α_{11}	(kg ⁻¹ d ⁻¹)	Intraspecific competition term (FA)	0.313	$\alpha \propto DET_u$
α_{21}	(kg ⁻¹ d ⁻¹)	Interspecific/Light reduction competition term	0.2067	Cummins et al. (2004)
α_{22}	(kg ⁻¹ d ⁻¹)	Intraspecific competition term (seagrass)	0.602	$\alpha \propto DET_v$
f_1	(d ⁻¹)	Net exchange of DIN and SED	0.0691	Forés et al. (1994)
f_2	(d ⁻¹)	Net exchange of SED and DIN	0.8410	Forés et al. (1994)
d	(d ⁻¹)	Detritus contribution to SED	0.8050	Forés et al. (1994)
V_{11}	(d ⁻¹)	Uptake of DIN to FA biomass	0.60	Estimated
V_{12}	(d ⁻¹)	Uptake of DIN to seagrass biomass	0.0413	Forés et al. (1994)
V_{22}	(d ⁻¹)	Uptake of DET to seagrass biomass	0.5013	Forés et al. (1994)
μ_1	(d ⁻¹)	FA max growth rate	1.07	Kiirikki et al. (1998)
μ_2	(d ⁻¹)	Seagrass max growth rate	0.125	Hillman et al. (1995)
T_m	(°C)	Optimum temperature for FA growth	27.5	Observation
T_o	(°C)	Optimum temperature for Seagrass growth	25	Hillman et al. (1995)
b_i	(d ⁻¹)	Coupling constants for growth	(1.06, 1.04, 1.05)	Kiirikki et al. (1998)

The initial distribution of $n_1^0 = 0.037$ and $n_2^0 = 0.1658$ are inferred as uniform distribution across (x, y). Numerical simulations are carried out via the finite element method with triangular mesh.

4 MODEL APPLICATION

A conceptual simulation was carried out on Avoca Lagoon, NSW, Australia. The lagoons of the Central Coast are typically characterized by N limitation and previous biological and chemical observations at this lagoon showed increasing N concentration, declining seagrass biomass Mackenzie et al. (2010) and summer blooming of filamentous algae. The model is initialised with uniform distributions of u , v , n_1 and n_2 and temperature belonging to the interval from 15 to 31 degrees Celsius. We simulated with estimated parameters at this stage to gain an indication of the systems overall behaviour.

4.1 Behaviour of the System

Results indicate that the simulations produce behaviour that is consistent with the observations of competition systems given by Dunn et al. (2009) and citations therein. The current high N in Avoca Lagoon has significant impact on the filamentous algae which dominates the water column and dissolved inorganic N uptake and consequently has dire consequences for benthic seagrasses due to proportional light limitation from blooming (given as the intraspecific term in Equation 1). The domination of species that uptake nutrients from the water column can be seen as a result of high flux of N from the sediment to the water column meaning increased nutrient availability. Figure (3) indicates the relationship between temperature and species. Figure 3(a) Indicates favourable conditions for filamentous algae as the temperature rises to the optimal T_0 with Figure 3(b) representing the functions r_1 and r_2 impact on u and v .

The 2D model indicates the basic patterns of increasing populations due to optimal temperature as seen in Figure 3 which presents the results of simulations under various average temperatures. Results of intraspecific competition as a proxy for light competition for benthic species has two results; one for the short term and one for the long term. In the short term the benthic seagrass has a decreased growth rate which presents a slow decline in the rate of overall population increase; see Figure 3(c) (of course this

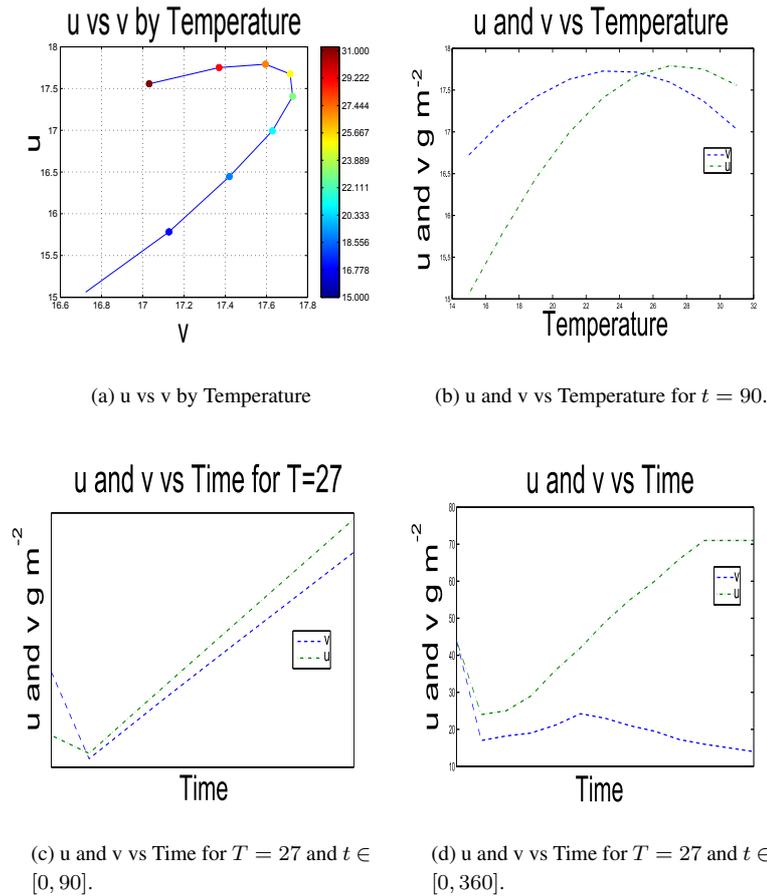


Figure 3. Temperature effects on population dynamics ($c_1 = 1.1$, $c_2 = 0.5$, $r_1 = 1.5097$, $r_2 = 0.2392$, $d_i = 0$).

interpretation is based on model assumptions rather than data collection). In the long term, as well as a decreased growth rate of benthic species, the model output produced surprising results with the possibility of decline in seagrass due to competition or recovery based on the temperature changes across the seasons. If temperature favours seagrass growth $T \leq T_m$ then the decline in seagrass is slowed and its existence is extended. This has implications for management procedures and practices where timing is a crucial consideration.

5 CONCLUSIONS AND FUTURE WORK

Modelling of blooming phenomenon in well mixed environments is an important process and a consideration that needs to be made in order to improve catchment modelling of systems especially where filamentous algae dominates. This paper includes a simplified model which looks at the dynamics of competition between a bloom of filamentous algae and a benthic species. Generalised results indicate that species interactions in the initial months of blooming slow the rate of increase of benthic species. This work is limited by the use of uniform populations, proportional intraspecific competition and temperature distributions. Future work is necessary to classify the recovery of the seagrasses as temperatures decline which is currently underway at Avoca Lagoon. This will allow for parameterisation and calibration.

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