Ecological response of an intermittently open lagoon to entrance opening regimes and catchment loads: a numerical study

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Abstract

Ecological model behaviour of an intermittently closed and open lake or lagoon (ICOLL) is analysed in order to assess the response to altered estuary forcings (catchment loads, opening regimes and lake depth), initial conditions and model parameters. Due to the low nutrient loads currently entering Smiths Lake NSW Australia, changes in the opening regime do not exhibit a strong estuarine response, however the system is sensitive to increased water depth and catchment loads. The water depth of the lagoon is shown to drive a switch from a seagrass to an algal dominated system at average depths greater than 7 m. Elevated loads ($10 \times$) of phosphorus entering the estuary increase the productivity of phytoplankton which is limited by phosphorus at lower loads. Moderate nutrient enrichment stimulates the production of seagrass, which is generally nitrogen limited and catchment loads are able to double without a decline in seagrass biomass. At elevated catchment loads, light limitation of seagrass occurs due to the increased plankton biomass and total suspended solids, and the system switches from seagrass dominated to algal dominated at loads above $5 \text{ mg N m}^{-2} \text{ d}^{-1}$ and $0.09 \text{ mg P m}^{-2} \text{ d}^{-1}$. Increasing nutrient loads

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also increase the amplitude and decrease the frequency of predator-prey cycles. In order to interpret the model output the sensitivity of different parameters and initial conditions are examined. The model showed non-linear response to variations in some parameters with the feeding efficiency of small and large zooplankton the most sensitive. For small perturbations in the initial conditions of dissolved inorganic nitrogen, phytoplankton and zooplankton biomass, ensemble members initially diverge, before converging. Periods of lake opening accelerate trajectory convergence with longer openings having the greatest effect. All simulations within the ensemble converge to the same stable oscillation within 2 open/closed phases.

Key words: eutrophication, light attenuation, opening cycle, ICOLL, plankton, seagrass, Australia, NSW, Smiths Lake

Introduction

Eutrophication is a growing problem in lakes and rivers caused by the excessive inputs of nitrogen and phosphorus (Carpenter et al., 1998). Land clearing and urbanisation can lead to eutrophication in estuarine waters as a result of increased nutrient and sediment loads entering the estuary from the catchment (Harris, 2001). Biogeochemical modelling is an important tool which can be used to assess system change and assist with management of potentially impacted systems (Webster and Harris, 2004). Nutrient exports from south-eastern Australian catchments into estuaries are generally considered small when compared to the Northern Hemisphere, resulting in oligotrophic conditions in most estuaries and coastal lagoons (Harris, 2001). Loads are highly variable due to differing levels of urbanisation and catchment flows. Total nitrogen (TN) and phosphorus (TP) loads from 24 catchments around Sydney have been shown to vary by three orders of magnitude with TN and TP increasing with population density (Harris, 2001).

Intermittently Closed and Open Lakes or Lagoons (ICOLLs) are a common type of estuary in south-eastern Australia. Of the 134 estuaries in New South Wales
(NSW), 67 (50%) are classified as intermittently open estuaries (Roy et al., 2001). ICOLLs are characterised by low freshwater inflow, leading to sand barriers (berms) forming across the entrance preventing mixing with the ocean. Increased residence time and lack of flushing makes ICOLLs particularly susceptible to pollution events such as increases in nutrient and sediment loads (Cloern, 2001; Lloret et al., 2008), yet there are far fewer studies of ICOLLs, than permanently open estuaries (Schallenberg et al., 2010). Following a rise in the water level, the sand barriers are intermittently breached. The timing and frequency of the entrance opening is related to factors such as the size of the catchment, rainfall, evaporation, the height of the berm and creek or river inputs (Roy et al., 2001). Additionally, marine currents, wave activity, weather patterns and the strength of the initial breakout will determine how long the estuary remains open to the sea. As each of these processes are variable and opening regimes are rarely predictable, ICOLLs seldom reach any long-term steady state (Roy et al., 2001). As an added complication, 72% of the estuaries in NSW are now artificially opened when they reach a predefined 'trigger' height (DIPNR, 2004). Reasons for artificial opening include flood prevention strategies and flushing in order to minimise pollution and eutrophication. However, opening events have previously resulted in unintended ecological consequences (Schallenberg et al., 2010) such as de-oxygenation, nutrient enrichment and increased chlorophyll a concentrations (Twomey and Thompson, 2001; Gobler et al., 2005; Becker et al., 2009).

Unlike permanently open estuaries which have regular tidal flushing, the opening regimes of ICOLLs are often unpredictable. There are many estuary-specific characteristics such as lake inflow, depth and catchment loads which will influence the ecology of the system after opening (Cloern, 2001). Understanding the interaction of physical and ecological processes within an ICOLL needs to be understood before decisions are made about altering the opening regimes. Biogeochemical modelling
studies of ICOLLs, such as this one, allow the examination of the ecological impacts during altered opening regimes. The model configuration used in this study emphasises the two different phases of the ICOLL cycle - open and closed - and the different hydrological processes which occur.

The ecological model examined in this study was configured for Smiths Lake and was built using a combination of physical and physiological limits to the processes of nutrient uptake, light capture by phytoplankton and predator prey interactions (Everett et al., 2007). The model outputs were assessed against field data and shown to capture the important ecological dynamics of Smiths Lake. A cost function was used to compare the field and model data, normalised by the standard deviation of the field data, to assess the fit, as per the methods of Moll (2000). The fit for salinity (0.20) and dissolved inorganic nitrogen (DIN, 0.79) were considered very good (<1 standard deviation), while dissolved inorganic phosphorus (DIP, 1.49) and chlorophyll a (1.01) were considered good fits (1-2 standard deviations, Everett et al., 2007; Moll, 2000). The simulated DIN and DIP concentrations were consistent with observations for much of the open-closed cycle. At high lake levels, DIN and DIP are underestimated. The concentration of water column DIN and DIP remains relatively constant over the course of the model simulation. Both observations and model data show very low concentrations of water column DIP (Everett et al., 2007).

Smiths Lake has a largely forested catchment with a small population and low levels of urbanisation (Webb McKeown & Associates Pty Ltd, 1998). Population pressure and increasing urbanisation will result in increased nutrient exports from the catchment. Changing rainfall patterns in south-eastern Australia (Hennessy et al., 2004; CSIRO and Bureau of Meteorology, 2007) will also alter the length and frequency of opening regimes and lake depths. As a result, there is a need for an analysis of the response of the state variables to changing estuary forcings such as nutrient loads and opening regimes.
Simple forcings models have previously been used to simulate the response of coastal lagoons to changing nitrogen loads and water residence times (Webster and Harris, 2004). Their study focussed on the response of primary producers to increasing and decreasing nitrogen loads, and how the response is altered by changes in the flushing rate of the lagoon. The model showed that the highly episodic catchment nutrient loading regimes increases the vulnerability of the lagoon (Webster and Harris, 2004). When compared with steady loading regimes, episodic loads caused phytoplankton blooms at lower catchment loads.

The behaviour of the ecological model can be used to explore the response of a broader range of ICOLLs to changing nutrient loads and opening regimes. The inorganic nitrogen load for Smiths Lake has been calculated as 0.5 mg DIN m\(^{-2}\) d\(^{-1}\) from field data (Everett, 2007) and the total nitrogen load calculated as 5 mg TN m\(^{-2}\) d\(^{-1}\) from modelled data (CSIRO, 2003). This value is low when compared with other eastern Australian estuaries due mainly to Smiths Lake’s largely forested catchment and small catchment to lake area ratio. Other estuaries in eastern Australia have much higher loads. Lake Macquarie (permanently open) and Narrabeen Lakes (ICOLL) for example, have an estimated 5% forested catchment and loads of 70 mg DIN m\(^{-2}\) d\(^{-1}\). Turros and Coila Lakes (ICOLLs), which have catchments that are 40% forested have loads of 20 mg DIN m\(^{-2}\) d\(^{-1}\) (CSIRO, 2003).

In this study, numerical experiments are used to examine the biological response of an estuarine model to changes in estuary forcings (opening regimes, catchment loads, lake depth), initial conditions and model parameters. The range of forcing values used in this study allow insights into the future behaviour of Smiths Lake under altered conditions, while also being used as a tool to understand other ICOLLs.
Methods

A 1-box ecological model of an intermittently open lagoon (Everett et al., 2007) is investigated. The sensitivity of the model to estuary forcings, initial values of the state variables and model parameters is examined. The sensitivity results presented here are for a 1-box configuration with an idealised lake height, flushing regime and solar radiation. A brief overview of the model is presented in the following section. For a more detailed description see Everett et al. (2007).

Transport Model

The transport model is reduced to a 1-box configuration for this study. The model is forced by evaporation ($E$), rainfall ($R$) and tidal exchange ($TE$). The equation for the change in concentration of a tracer is given by:

$$\frac{dC}{dt} = \frac{C_{cr} R_I}{V_{Runoff}} - \frac{C}{V_{Evaporation}} - \frac{C_{oc} TE}{V_{Tidal Exchange}} - \frac{C_{dV/dt}}{V_{Dilution}}$$  \hspace{1cm} (1)

where $V$ is volume ($m^3$), $E$ is evaporation ($m^3 s^{-1}$) and is negative, $C_{cr}$ is the concentration of creek flow into the model ($mol m^{-3}$), $R_I$ is the flow of water off the catchment ($m^3 s^{-1}$), $C_{oc}$ is the concentration of the ocean ($mol m^{-3}$), $\frac{dV}{dt}$ is the change in volume over time ($m^3 s^{-1}$) and $TE$ is the tidal exchange when open to the ocean ($m^3 s^{-1}$).

Ecological Model

The ecological model contains 17 state variables (Table 1). With the exception of state variables relating to phosphorus and total suspended solids, nitrogen is the basic currency of the state variables. The autotrophs (phytoplankton, epiphytes and seagrass) gain all their nutrients from the water column, with the exception of seagrass which is also able to draw nutrients from the sediment. Dissolved inorganic nitrogen, unflocculated phosphorus, and total suspended solids enter the system from
the catchment. Total suspended solids and flocculated and unflocculated phosphorus
sink out of the water column into the sediment. Depending on water column and
sediment pore water concentrations, $DIN$ and $DIP$ are able to diffuse back into the
water column from the sediment. Small and large zooplankton grow by feeding on
small and large phytoplankton respectively.

In the model, light is attenuated through the water column, epiphytes and seagrass sequentially. The light model is adapted from Baird et al. (2003). The proportion of the downward solar radiation (mol photon m$^{-2}$ s$^{-1}$) available as photosynthetically available radiation (PAR) is assumed to be 43% (Fasham et al., 1990).

The realised growth rate ($\mu_x$) of each autotroph is determined by the minimum of the physical limit to the supply of nitrogen, phosphorus and light, and the maximum metabolic growth rate of an organism:

$$\mu_x = (\mu_{\text{nitrogen}}, \mu_{\text{phosphorus}}, \mu_{\text{light}}, \mu_{\text{max}})$$

The four autotrophs in the model have fixed internal stoichiometric requirements. Phytoplankton (small and large) and epiphytic microalgae adopt the Redfield ratio (C:N:P) of 106:16:1 (Redfield, 1958), while seagrass adopt a seagrass-specific ratio of 474:21:1 (Duarte, 1990). The light requirements of all the autotrophs are fixed at 10 photons per carbon atom (Kirk, 1994).

Growth rates of phytoplankton, epiphytic microalgae and seagrass

Phytoplankton are divided into two size classes - small ($PS$) and large ($PL$). Phytoplankton cells obtain nutrients from the surrounding water column and absorb light as a function of the average available light in the water column and their absorption cross section. The maximum rate (s$^{-1}$) at which a phytoplankton cell can obtain nutrients through diffusion from the water column is given by:

$$\mu_{PS,N} = \frac{\psi_{PS}D_NDIN}{m_{PS,N}}$$
where $\psi_{PS}$ is the diffusion shape factor (m cell$^{-1}$), $D_N$ is the molecular diffusivity of nitrogen (m$^2$ s$^{-1}$), and $m_{PS,N}$ is the nitrogen cell content of small phytoplankton cells (mol N cell$^{-1}$). Phosphorus uptake is calculated in a similar manner. The diffusion shape factor ($\psi$) in this study is for a sphere and is calculated as $4\pi r$, where $r$ is the radius of the cell (m).

The light-limited growth rate of small phytoplankton (and similarly for large phytoplankton) is given by:

$$\mu_{PS,I} = \frac{I_{AV}aA_{PS}}{m_{PS,I}}$$

(4)

where $I_{AV}$ is the average light field in the water column (mol photon m$^{-2}$ s$^{-1}$), $aA$ is the absorption cross-section of the cell (cell$^{-1}$ m$^2$), and $m_{PS,I}$ is the required moles of photons per phytoplankton cell (mol photon cell$^{-1}$).

In the model, seagrass grows on the benthos and the epiphytes grow on both the surface of the seagrass and the benthos. Both seagrass and epiphytes absorb water column nutrients through the same effective diffusive boundary layer which occurs along their surface. Nutrient uptake is divided between both epiphytes and seagrass by a ratio termed the seagrass uptake fraction ($\eta$). In the model, seagrass are able to extract nutrients from both the water column and the sediment. The zooplankton biomass is not modelled explicitly here, but is implied to be proportional to the aboveground biomass. Priority in nutrient uptake is given to the water column, however nutrient limitation in the seagrass only occurs when the combined sediment and water column nutrients do not meet demand.

The nitrogen limited growth rate for epiphytes is given as:

$$\mu_{EP,N} = \frac{D_N}{BL}(1 - \eta)DIN \frac{1}{EP}$$

(5)

where $D_N$ is molecular diffusivity of nitrogen, $BL$ is the boundary layer thickness, $\eta$ is the seagrass uptake fraction and $DIN$ is the water column concentration.
of dissolved inorganic nitrogen. Phosphorus limited growth rate is calculated in a similar manner.

When formulating seagrass dynamics, fluxes are calculated per m². As a result, to convert the water column uptake to a growth rate requires division of the uptake rate by the biomass. The nitrogen (and similarly for phosphorus) limited uptake rate (s⁻¹) for seagrass is the sum of the water column and the sediment uptake and is given as:

$$\mu_{SG,N} = \frac{D_N}{BL} \eta_DIN \frac{1}{SG} + \frac{\mu_{max}^{SG} DIN_{sedconc}}{k_{SG,N}}$$  \hspace{1cm} (6)$$

where $\mu_{max}^{SG}$ is the maximum growth rate of seagrass (s⁻¹), DIN_{sedconc} is the sediment concentration of nitrogen and $k_{SG,N}$ is the half saturation constant for nitrogen uptake in seagrass.

Light is available to the epiphytes after it passes through the water column, and to the seagrass after passing through the epiphytic layer. The light limited growth rate for epiphytes and seagrass respectively is given as:

$$\mu_{EP,I} = \left( I_{bot} - I_{belowEP} \right) \frac{16}{1060} \frac{1}{EP}$$  \hspace{1cm} (7)$$

$$\mu_{SG,I} = \left( I_{belowEP} - I_{belowSG} \right) \frac{21}{4740} \frac{1}{SG}$$  \hspace{1cm} (8)$$

where $I_{BOT}$ is PAR at the bottom of the water column, $I_{belowEP}$ and $I_{belowSG}$ is the light below the epiphytes and seagrass layers respectively, 16:1060 and 21:4740 is based on the Redfield and Duarte Ratio (Duarte, 1990; Redfield, 1958) and a 10:1 photon:carbon ratio (Kirk, 1994).

A linear mortality is applied to epiphytes ($\zeta_{EP}$) and a quadratic mortality is applied to seagrass ($\zeta_{SG}$) as a closure term for the benthic autotrophs. A resorption coefficient ($\omega_{SG}$) is appended to the mortality term of the seagrass to represent the
detainment of nutrients as carbon is lost through blade death (Hemminga et al., 1999). When seagrass die, the remaining nutrients after resorption breakdown into refractory detritus (RD) before breaking down further and being released into the water column as DIN and DIP.

Zooplankton Grazing

In the model small zooplankton graze on small phytoplankton as shown below (and similarly large zooplankton graze on large phytoplankton):

\[ \mu_{ZS} = \frac{\mu_{ZS}^{max} PS}{K_{ZS} + PS} \]  

(9)

where \( \mu_{ZS}^{max} \) is the maximum growth rate of small zooplankton (s\(^{-1}\)) and \( K_{ZS} \) is the half saturation constant of small zooplankton growth (mol N m\(^{-3}\)). A quadratic mortality for zooplankton is selected on the assumption that the biomass of zooplankton will be proportional to their predator.

Initial Conditions

The model is run for a period of one closed and one open cycle to allow the model to reach a quasi steady-state before commencing the model simulations. The initial conditions of the spin-up are set from the ocean boundary conditions for water column state variables. The initial biomass of epiphytes and seagrass is based upon the literature (Duarte, 1990, 1999) and the mapped seagrass coverage in Smiths Lake (West et al., 1985). Initial conditions for sediment state variables are derived from Baird et al. (2003), Murray and Parslow (1997) and Smith and Heggie (2003). The values at the end of this ‘spin-up’ are used as the initial conditions for the model (Table 1).

Lake Boundary Conditions

Nutrients (DIN and \( P_{unfloc} \)) and TSS\( _{unfloc} \) enter the lake through runoff from the catchment. Nutrients (DIN and DIP) and plankton (PS, PL, ZS and ZL) enter
from the ocean when the lake is open. Nutrient concentrations are interpolated from field sampling in the creeks (catchment) and at Seal Rocks Beach (oceanic). The boundary conditions for $DIN$ and $P_{unflocc}$ from the catchment are $1.08 \times 10^{-2} \text{ mol N m}^{-3}$ and $9.03 \times 10^{-5} \text{ mol P m}^{-3}$ respectively. The boundary condition of $TSS_{unflocc}$ from the catchment is $0.1 \text{ kg TSS m}^{-3}$ (Baird et al., 2003). Oceanic boundary conditions are found in Table 1.

Idealised Configuration

In this study, the transport model is used in an idealised single box configuration. During a control simulation, the lake height increases linearly from 0.4 m to 2.0 m Australian Height Datum (AHD) over 10 months which corresponds to average depths of 1.9 - 3.5 m (Fig. 1). After 10 months, the ICOLL opens to the ocean and drains for 48 hours to a lake height of 0.4 m AHD. A sinusoid tidal exchange is imposed for 2 months, with amplitude of 0.05 m. This cycle is repeated until a steady oscillation is reached ($< 10$ years).

The depths and sinusoidal amplitude used in the model are chosen to be representative of the average lake cycle and flushing rates of Smiths Lake observed over the last 10 years (Everett, 2007). Due to intermittent rainfall, there is a large variability in open/closed phases. On average the lake stays open for 62 days (from lake height data courtesy of Manly Hydraulics Laboratory). Depending on the height difference between Smiths Lake and the ocean, it takes 36-48 hours to drain and begin flushing with the ocean.

A constant solar radiation is maintained throughout the simulations to prevent any seasonal effects influencing the sensitivity analysis. The solar radiation in the model is $95 \text{ W m}^{-2}$ and is derived from the yearly mean of averaged 6 hourly, $2^\circ$ shortwave downward solar radiation, linearly interpolated in space to Smiths Lake (152.519E, 32.393S - data courtesy of the NOAA-CIRES Climate Diagnostic Centre). The control simulations in the following sections refer to a model run with no changes
made to estuary forcings, initial conditions or parameters.

**Estuary Forcing**

*Catchment Load:* In order to examine the response of the model to varying catchment loads of dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP) and total suspended solids (TSS), the loads are changed by 0.1×, 0.5×, 2.0×, 10× and 100× the control values. This is undertaken in seven different combinations of DIN, DIP, TSS, DIN+DIP, DIN+TSS, DIP+TSS and DIN+DIP+TSS. The control values for DIN, DIP and TSS are 0.5 mg N m$^{-2}$ d$^{-1}$, 0.009 mg P m$^{-2}$ d$^{-1}$ and 0.033 g TSS m$^{-2}$ d$^{-1}$. The inflow concentrations for DIN and DIP are determined from sampling of five creeks entering Smiths Lake. The value for TSS is based upon Baird et al. (2003).

*Opening Regimes:* The current study varies the duration of the entire open/close cycle and the duration of the open phase to examine the effect on plankton and seagrass dynamics within Smiths Lake. The open/closed cycle duration is the total time between two successive closed phases (i.e. one complete open and closed cycle) and is undertaken at 12, 18, 24, 36, 48 and 60 months. The open duration is the total time the lake is open to the ocean and is undertaken by 7, 14, 30 and 60 days, making a total of 20 simulations (5 cycles × 4 open phases).

*Lake Depth:* In order to examine the sensitivity of the model to lake depth, simulations are run with depths, when open to the ocean, of 0.4 m AHD (control simulation - representative of Smiths Lake), 2.5, 5 and 10 m AHD. These heights (AHD) correspond to average lake depths over the whole simulation of 2.5, 4.5 7.0 and 12.0 m. During these simulations the same rate of lake rise is maintained, hence these simulations do not alter the catchment inflow.

*Initial Condition Sensitivity*

The initial conditions for DIN, PS, PL, ZS and ZL are randomly varied and the effect on the model is examined for three ensembles of ten members each.
three ensembles have open durations of two months, one month and two weeks. The initial conditions are varied based on a uniform random distribution with a mean of zero and a maximum of no more than the concentration of $DIN (4 \times 10^{-4} \text{ mol N m}^{-3})$, which is the state variable with the lowest concentration. This formulation is used to prevent the initial conditions of state variables from taking negative values, while also keeping the total mass constant.

**Parameter Sensitivity**

A sensitivity analysis of all model parameters is undertaken by varying each parameter by 10%, 25% and 50% and analysing the change in each state variable (Table 2). Results for the 14 most sensitive parameters are presented here. The results from the 5th year of the simulation (by which time the model had reached a steady oscillation) are analysed for changes in the state variables, by comparison with the control simulation. Results of the parameter sensitivity are compared with the 11-box model of Smiths Lake Everett et al. (2007). The standardised sensitivity of each state variable to each parameter (Murray and Parslow, 1997) is calculated as:

$$\text{Normalised Sensitivity} = \frac{V(1.1 p) - V(0.9 p)}{V(p)0.2}$$  \hspace{1cm} (10)

where $V(1.1 p)$ is the mean value of the state variable $V$ when parameter $p$ is increased by 10% and $V(0.9 p)$ is the mean value when the parameter is decreased by 10%. $V(p)$ is the mean value of the state variable when there is no change in the parameter. If the normalised sensitivity is close to 1, the change in $V$ is proportional to the change in $p$. If the sensitivity is close to 2, $V$ is proportional to $p^2$. 

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Results

Catchment Load Response

*Plankton Dynamics:* Phosphorus is the limiting nutrient for the growth of small and large phytoplankton in the control simulations. Simulations run at $0.1\times$ and $2\times$ the control phosphorus load result in only a small deviation from the values of $PS$ and $PL$ during the control simulations (Fig. 2A,B). There is no change in the overall shape of the oscillation. When the phosphorus load is increased by $10\times$ and $100\times$, there is an increase in the frequency and amplitude of the oscillations (Fig. 2A,B). There is an associated increase in the yearly productivity of $PS$ and $PL$ from 19.3 and 10.8 mmol m$^{-3}$ yr$^{-1}$ at $2\times$ DIP loads to 34.7 and 26.3 mmol m$^{-3}$ yr$^{-1}$ respectively at $10\times$ DIP loads (Fig. 2C,D). The change in oscillation structure corresponds with a switch in the growth limitation of $PS$ (Fig. 3A,C) and $PL$ (Fig. 3B,D) from predominately phosphorus limited to nitrogen and maximum growth rate limited. In both $2\times$ and $10\times$ simulation (Fig. 3) $PS$ and $PL$ are out of phase, with the growth of $PS$ limited by nitrogen when its biomass is increasing and by its maximum growth rate when the biomass is decreasing. The opposite is true of $PL$, which is limited by its maximum growth rate as its biomass is increasing and by nitrogen when its biomass is decreasing.

*Seagrass:* Seagrass is nitrogen limited during the control simulations and the addition of $10\times$ and $100\times$ DIN load increases the seagrass biomass (Fig. 4A). These scenarios show no discernible difference in the light attenuation of phytoplankton and light availability for seagrass (Fig. 4C,D).

The addition of $10\times$ DIN + DIP and DIN + TSS load show little change in the seagrass light availability, however the addition of DIP allows the phytoplankton biomass, and therefore phytoplankton light attenuation, to increase (Fig. 4G). The addition of DIN allows the seagrass to obtain a higher biomass (Fig. 4E,I). The addition of DIN + DIP loads results in a small decrease in seagrass light availability.
(Fig. 4H). At higher loads the $SG$ light availability oscillates, coinciding with the oscillation of phytoplankton biomass and light attenuation. The addition of $100 \times DIN + DIP$ and $DIN + TSS$ loads (Fig. 4E,I) results in an increase in biomass during the shallower open phases when seagrass is maximum growth rate limited (not shown). There is a reduction in biomass during the closed phases (Fig. 4E), when seagrass becomes light limited (not shown). This is a result of decreased light availability to seagrass (Fig. 4H) due to an increase in the phytoplankton light attenuation (Fig. 4G).

The simultaneous addition of $DIN + DIP + TSS$ at $100 \times$ control loads results in a permanently lower seagrass biomass of $0.014$ mol N m$^{-2}$ (Fig. 4M) due to the reduction in light availability at the bottom of the water column (Fig. 4P).

**Opening Regimes**

There is an increasing $DIN$ concentration in simulations with short open/close cycle durations (Fig. 5A). The highest mean $DIN$ concentrations occur during the 1 year cycle, and are consistent across all open phases. The highest mean $DIP$ values occur at an open/closed cycle duration of 5 years and an open duration of 60 days (Fig. 5B). $PS$ and $PL$ both increase in biomass as the open duration increases (Fig. 5C,D). The highest biomass of $PS$ occurs during simulations with a long open duration (60 days) and long open/closed cycle duration (5 years), while the highest biomass of $PL$ occurs during simulations with long open phases (30-60 days) and short open/closed cycle duration (1 year). The highest biomass of $ZS$ and $ZL$ occurs during simulations with long open phases (60 days) (Fig. 5E,F). The highest mean biomass of $SG$ is $0.037$ eutrophication N m$^{-2}$ and occurs during the 5 year open/closed cycle (Fig. 5G). The duration of the open phase does not substantially affect the mean $SG$ biomass.
Lake Depth

For simulations with an average lake depth of greater than 7 m, there is a reduction of up to 97% in seagrass biomass when compared to the control simulations (Fig. 6H). At depths of 4.5 and 7 m, there is no discernible difference in SG biomass from the 2.5 m control simulations. In simulations with depths greater than 7 m, PS and PL more limited by their maximum growth rate as opposed to phosphorus limitation, when compared to simulations with depths of 2.5 and 4.5 m (Fig. 7 Col 1,2). At average depths of greater than 7 m, there is a more sudden shift in seagrass and epiphytic growth limitation from phosphorus and nitrogen respectively, to light limitation (Fig. 7 Col 3,4). This results in a reduced growth rate for seagrass (Fig. 8F) which in turn allows more nutrients to be available for increased phytoplankton growth (Fig. 8A,B).

Initial Conditions

An ensemble of 10 members with different initial conditions of each of the state variables shows large standard deviations during the first year (Fig. 9A). However, the mean standard deviation of state variables (DIN, DIP, PS, PS, ZS and ZL) is reduced almost 10 fold between the first (9.6×10^{-5}) and the second closed phase (1.4×10^{-6}). The 2 month long open phase acts to accelerate the trajectory convergence of the model. The model is subsequently run for simulations with shorter open phases (1 month and 2 weeks). These simulations take longer to converge but by the end of the second open phase the mean standard deviation is 2.4×10^{-6} and 3.7×10^{-5} respectively (Fig. 9B,C). Convergence within two phases illustrates the importance of steady states in the model behaviour and provides confidence that using the 5th year is a meaningful comparison of these states.

Parameter Sensitivity

The sensitivity of the parameters is investigated using a normalised sensitivity derived from a power law relationship. The feeding efficiency of ZS \( (\beta_{ZS}) \) and ZL
(β_{ZL}) and the mortality of ZS (ζ_{ZS}) and EP (ζ_{EP}) are the most sensitive parameters in this configuration of the model (Table 3). DIP, phytoplankton, zooplankton and epiphytes are relatively sensitive to the radii of PS and PL when compared to the sensitivity of many other parameters in the model. The nine most sensitive parameters are investigated further by running the same simulations with changes in the value of the parameters of ± 25 and 50% (Table 4).

The non-linearity of the model is illustrated by changes in the normalised sensitivity as the percentage change of the parameter is increased. State variable-parameter combinations with changes of more than 0.1 between simulations are considered to have different sensitivities at different magnitudes of permutation and are highlighted in Table 4. The parameters which exhibited the greatest change in normalised sensitivity when changed by 25 and 50% are r_{PL}, ζ_{EP}, β_{ZS} and β_{ZL}. The control parameter values for r_{PL} and ζ_{EP}, are 1 \, \mu m and 0.05 \, d^{-1} respectively (Table 2) with a range (±50%) of 0.5-1.5 \, \mu m and 0.25-0.75 \, d^{-1} respectively. The control parameter values for β_{ZS} and β_{ZL} are 0.31 and 0.34 respectively (Table 2) with a range (±50%) of 15.5-46.5 and 17-51 respectively. The model responds in a relatively linear manner to the other parameters tested (Table 2).

**Discussion**

In this paper we have undertaken numerical experiments with changes in estuarine forcings, parameter values and initial conditions from an assessed configuration of Smiths Lake, Australia. It is not possible to co-vary all these factors simultaneously. As an example we have not simultaneously co-varied opening regimes and catchment loads. By examining each estuarine response in isolation, we gain less complicated, yet revealing, insights into the behaviour of intermittently open estuaries, while not deviating significantly from the assessed model.
**Catchment Load Response**

**Plankton Dynamics:** The responses of plankton communities and biomass to eutrophication in coastal lagoons are not well documented (Rissik et al., 2009). Phytoplankton and zooplankton biomass in intermittently open estuaries is generally low during times of little freshwater influx and therefore small nutrient loads (Grange and Allanson, 1995; Froneman et al., 2000). Plankton biomass was higher in estuaries following freshwater pulses and their accompanying nutrient loads (Wooldridge, 1999; Froneman et al., 2000). Similar responses are seen in this study with elevated loads ($10^\times$) of phosphorus entering the estuary increasing the productivity of phytoplankton which is limited by phosphorus at lower loads. This increase in productivity allows the biomass of $PS$ and $PL$ to turn over more quickly and hence decrease the period of oscillation and increase the amplitude (Fig. 2). The high availability of non-limiting $DIN$ and light, combined with a high growth rate compared with other state variables allows phytoplankton to quickly take advantage of any additional phosphorus which becomes available in the water column. Similarly Edwards and Brindley (1996) found that under increasing nutrient loads in an NPZ model produced stable predator-prey (limit) cycles of greater amplitude.

This model produced strong predator-prey cycles that are typical of numerical models (Edwards and Brindley, 1996). At high loads ($10^\times$ and $100^\times$), the oscillations of $PS$ and $PL$ are out of phase. $PS$ is nitrogen limited when the biomass is increasing and maximum growth rate limited when it is decreasing, while $PL$ is the opposite. Even though the maximum biomass increases throughout the closed phase, the switch in growth limitation always occurs at the same place on the curve rather than at the same water column $DIN:DIP$ ratio. The switch between nitrogen and maximum growth rate limitation occurs at the same time in alternate cycles of $PS$ and $PL$. That is, when $PS$ changes from nitrogen limited to maximum growth rate limited, $PL$ changes from maximum growth rate limited to nitrogen limited. This dynamic
is driven by $PL$, which is able to draw down the most $DIN$ from the water column
(as a result of its higher biomass), resulting in $PS$ becoming nitrogen limited. The
switch in $PS$ growth limitation to nitrogen limitation corresponds with the lowest
point of $DIN$ concentration (not shown).

**Seagrass:** The modelled seagrass biomass is relatively insensitive to changes in
the catchment loads of up to $2\times$. Up to these loads the biomass of seagrass stays
relatively constant and is not influenced by changes in light availability. A $10\times$
increase in catchment loads of $DIN$ (even in the presence of $10\times$ increase in $DIP$
and/or $TSS$) doubled the seagrass biomass to $0.11 \text{ mol N m}^{-2}$ at the end of the five
year simulation when compared to the $2\times$ simulation ($0.05 \text{ mol N m}^{-2}$). Under these
conditions there is only a small increase in light attenuation by the phytoplankton
and non-phytoplankton component of the water column. These simulations illustrate
the importance of light for seagrass growth.

The addition of $100\times$ the limiting nutrient for seagrass (nitrogen) allowed seagrass
to attain a higher biomass, however the addition of $100\times$ loads of phosphorus (the
limiting nutrient for phytoplankton), led to a bloom in phytoplankton which resulted
in reduced light availability to the seagrass (Fig. 4). The same occurred when the
levels of $TSS$ are increased $100\times$, which also increased the light attenuation of the
water column.

In both these light-limiting scenarios the seagrass is able to recover during the
open phases when the lake level is low and flushing occurs with cleaner oceanic
water. In contrast, the addition of $DIN + DIP + TSS$ at $100\times$ levels resulted in the
collapse of the seagrass to $0.014 \text{ mol N m}^{-2}$, with very little recovery during the 2
months that the lake is open to the ocean. In this scenario, the light attenuation of
the water column (phytoplankton and non-phytoplankton components) is increased
beyond what could be flushed out of the estuary during the open phase, and the
estuary switches to an alternative state (Scheffer and Carpenter, 2003).
Benthic macrophytes, such as seagrass, are extremely important in the functioning of coastal lagoons. Benthic macrophytes are able to intercept nutrients from the water column, which is often sufficient to maintain reduced nutrient concentrations in the overlying water column (Grall and Chauvaud, 2002). As the macrophytes become stressed from increased nutrient and sediment loads, long-term retention of organic matter will decline, and be replaced by algal blooms and unattached ephemeral algae (McGlathery et al., 2007; Duarte, 1995; Valiela et al., 1997). Shallow lagoons, such as Smiths Lake, are at greater risk as there is a smaller volume of water into which to absorb the nutrient loads, but also, the photic zone generally reaches to the benthos, and so the macrophytes play a larger role in controlling the overlying water column than in deeper systems (McGlathery et al., 2007). Seagrass is especially important during closed phases of ICOLL’s, when phytoplankton blooms cannot be flushed out. If seagrass dominates the primary production of the lagoon, and nutrients will be bound by plant tissue, rather than by phytoplankton, slowing the nutrient release back into the water column (McGlathery et al., 2007).

Moderate nutrient enrichment stimulates the production of the benthic macrophytes in this study. This converges to the well-documented response at higher loads where benthic macrophytes reduce their distribution and production within the ecosystem through light limitation (Borum and Sand-Jensen, 1996; Smith and Schindler, 2009). Due to the shallow depths of Smiths Lake, and the low catchment loads (even at 10×), light limitation only becomes growth limiting for SG after 180 days of a 1 year closed phase. The reduction in biomass is small, and is less than the increase during the first half of the cycle. Hence, the overall change in seagrass biomass is positive, even in cycles with light limitation.

*Opening Regimes*

In Smiths Lake, PS and PL are generally growth limited by phosphorus, and SG is growth limited by nitrogen (Everett et al., 2007). Changes in the nutrient
availability of \( \text{DIN} \) and \( \text{DIP} \) drive changes in the biomass of the seagrass and phytoplankton respectively. Due to the availability of \( \text{DIN} \) in the water column throughout the closed phases, a longer closed phase results in an increased biomass of \( \text{SG} \) (Fig. 5). The ocean provides an additional source of \( \text{DIP} \) to supplement the low \( \text{DIP} \) in the lake. Therefore, the longer the lake is open to the ocean, the higher the mean biomass of phosphorus-limited phytoplankton. Similar responses of increased phytoplankton biomass during opening events have occurred in Australia (Twomey and Thompson, 2001) and the USA (Gobler et al., 2005), and were attributed to oceanic nutrient addition and sediment nutrient release respectively. The longer the cycle duration is, the longer the lake must stay open to the ocean to maintain the same biomass of \( \text{DIP} \), \( \text{PS} \) and \( \text{EP} \) (Fig. 5B,C,G). A reduction in the length of the open phase, for a given cycle duration, results in a reduced average biomass of \( \text{DIP} \), \( \text{PS} \) and \( \text{EP} \). Within this study however, these increases in biomass do not increase the phytoplankton biomass enough to significantly decrease the light availability to the \( \text{SG} \). As a result \( \text{SG} \) maintains a large biomass at all opening regimes. This is mainly due to the severe phosphorus limitation of phytoplankton which prevents significant blooms, and the low \( \text{TSS} \) loads due to the highly forested catchment.

At the present loads entering Smiths Lake there is no decline in \( \text{SG} \) biomass or blooms or \( \text{PS} \) or \( \text{PL} \) as a result of changes in the lake cycle duration or open phase duration. Schallenberg et al. (2010) highlights that the relationship between opening regimes and eutrophication depends on multiple factors specific to each lagoon. Longer residence times generally favour phytoplankton dominance (McGlathery et al., 2007; Valiela et al., 1997), however due to the nutrient limitation within Smiths Lake, increased residence time does not have as large an impact as is expected. Contrary to initial expectations, the biomass of \( \text{SG} \) is not decreased by an increased residence time and an accumulation of nutrients (Fig. 5). Because phytoplankton and \( \text{SG} \) are limited by two different nutrients, changes in their biomass rarely occur
simultaneously. The opening phases are driving DIP availability through oceanic enrichment, and DIN accumulation during the closed phases is driving DIN availability. If changes in the stoichiometry of the catchment loads were to occur (not considered in this study), it is expected that residence time will have a much more substantial influence.

Lake Depth

Water depth is shown to be important as it drives a switch from a seagrass dominated system to an algal dominated system at average depths greater than 7 m (Fig. 6). As would be expected due to the reduced light penetration at these increased depths, the biomass of seagrass is reduced as the system becomes dominated by plankton. The increased frequency of oscillations of phytoplankton and zooplankton in simulations with greater depths is a result of their increased growth rate due to the availability of nutrients that occurs with the decline of seagrass biomass. Interestingly, the epiphytes also reduce in biomass becoming light limited at depths greater than 7 m (Fig. 7). This is despite the fact that they require less light than seagrass per carbon, and the same light as phytoplankton (Redfield, 1958; Kirk, 1994; Duarte, 1990). Phytoplankton do not become light limited as they have first access to the light and absorb light at the average light availability through the entire water column, whereas epiphytes are at the bottom of the water column. Sensitivity analysis of depth changes of this extent (>7 m) are an important consideration, allowing the model formulation to be applicable for use in other estuaries.

Assimilative Capacity of Smiths Lake

Based upon the results of the catchment load scenarios, Smiths Lake can assimilate more than the current nutrient and sediment loads without large changes in the ecosystem. If it is assumed that any catchment load increases will equally affect DIN, DIP and TSS, the catchment loads are able to double without either a detrimental effect to seagrass, or forcing a switch to an alternative plankton-dominated
system. At loads of $10 \times$, there is a change in oscillation frequency and size; however there is a further increase in seagrass biomass suggesting the increase in plankton biomass is not fundamentally changing the ecosystem. At loads of $100 \times$ however, there is a definite switch to a plankton dominated system, and large declines in seagrass biomass. There is also an associated build-up in water column nutrients. As nutrients are entering the lake in the same DIN:DIP ratios, the plankton remains growth limited by phosphorus, however the seagrass becomes light limited. Smiths Lake’s assimilative capacity is in part determined by its small catchment area to lake area ratio of 2:1 (Haines et al., 2006), its predominately forested catchment (Webb McKeown & Associates Pty Ltd, 1998) and its large biomass of seagrass which is likely to play an important role in intercepting water column nutrients and enhancing the lagoons resistance to eutrophication (McQuatters-Gollop et al., 2009). If Smiths Lake loads increase to levels similar to more urbanised estuaries (10-100×), simulations suggest that the system would switch to an alternate state, from seagrass dominated to microalgal dominated. As a result residence time and opening/closing cycles would play a greater role in determining ecosystem state.

Parameter Sensitivity

In order to interpret the model output, it is important to also consider the sensitivity of different parameters. A sensitivity analysis provides a measure of the sensitivity of changes in model parameters with respect to changes in the state variables of interest (Jorgensen and Bendoricchio, 2001). Sensitivities are usually examined at a few different levels which are decided upon based on prior knowledge about the parameter. If a parameter or forcing is found to be sensitive, more effort can be put into making sure the parameter is accurate. The parameters to which the model state variables are most sensitive are the feeding efficiency of $ZS (\beta_{ZS})$ and $ZL (\beta_{ZL})$ and the mortality of $ZS (\zeta_{ZS})$ and $EP (\zeta_{EP})$. For the majority of state variable-parameter combinations, the normalised sensitivity for the state variables
is small (< 1) up to a ± 50% change in parameter values. The non-linearity of
β_{ZS} and β_{ZL} at parameter changes of ± 25 and 50% is shown by a large change
in the normalised sensitivity to phytoplankton biomass (Table 4). The normalised
sensitivity for β_{ZS} increased from -1.28 to -1.78 for PS and β_{ZL} increased from -1.15
to -1.35 for PL. There is a relatively large degree of uncertainty surrounding the
parameter values for feeding efficiency (β_{ZS} = 0.31 and β_{ZL} = 0.34), however, the
values chosen in this study are extracted from a compilation of 27 field studies on 33
different species (Hansen et al., 1997). The range of values for β_{ZS} and β_{ZL} in those
studies is 0.10-0.42 and 0.23-0.45 respectively. By varying these model parameters
by up to ± 50%, the sensitivity for the entire range of possible values from Hansen
et al. (1997) is captured. Within the study there was one exception with a value of
0.10 which fell below the minimum value for β_{ZS}. This value could be considered an
outlier, given its distance of more than two standard deviations from the mean.

The predators of zooplankton are not represented explicitly in this model but their
dynamics are approximated by the closure term. The closure terms can significantly
affect the dynamics of an ecological model (Edwards and Yool, 2000; Steele and Hen-
derson, 1992). In this study a quadratic mortality is implemented which represents
grazing from a predator whose biomass is proportional to that of the zooplankton
(Edwards and Yool, 2000). Nevertheless, the quadratic form of model closure does
not necessarily increase stability or reduce oscillatory behaviour (Edwards and Yool,
2000). Therefore it is not surprising that the quadratic mortality coefficients of ZS
and ZL are the most sensitive parameters in the model (For further discussion of the
relative costs and benefits of different closure terms, refer to Steele and Henderson
(1992) and Edwards and Yool (2000)).

The sensitivity of ζ_{ZS} and ζ_{ZL} is greatly reduced in the simulations presented in
this paper when compared to their sensitivity in the 11-box model of Smiths Lake
(Everett et al., 2007). The difference is that the current study utilises a 1-box model
with idealised physical configuration (idealised inflow and incoming solar radiation).

Due to the quadratic formulation of the mortality term any values for zooplankton biomass in the 11-box configuration which are above the mean value, would have been magnified, leading it to appear more sensitive than in the 1-box configuration. Therefore, the sensitivity of $\zeta_{ZS}$ and $\zeta_{ZL}$ may be underestimated in this and other studies which smooth out the patchiness of zooplankton biomass.

Zooplankton has been shown to be the most poorly simulated state variable in aquatic biogeochemical models (Arhonditsis and Brett, 2004). One suggested reason for this is the need to convert observed zooplankton data from units of individuals per volume to units of carbon or nitrogen per volume. A second possible reason is that entire zooplankton life-histories need to be fully simulated to achieve accurate representation (Arhonditsis and Brett, 2004). A possible shortcoming of this model is that it contains both these potential sources of error. Of the 27 field studies mentioned above (Hansen et al., 1997), the feeding efficiencies of only two studies are a direct measure of nitrogen efficiency, the modelled variable in this study. In all other cases, the values are given in units of volume, dry weight or carbon content (Hansen et al., 1997). Also, in this study zooplankton growth is exponential, which is characteristic of micro-zooplankton, rather than age structured, as is characteristic of macro-zooplankton (Baird and Suthers, 2007). Therefore, life histories are not explicitly modelled in this study, apart from the two different size classes - small and large zooplankton.

Summary

A previously developed and assessed model of Smiths Lake, Australia, is used to investigate the ecosystem response to changes in estuarine forcings and biological parameters for a broader range of idealised ICOLLs. There is little change in estuarine response for small changes in depth and catchment loads due to the relatively small loads and low light attenuation under current Smiths Lake conditions.
Larger load increases, as would be applicable in other estuaries, exhibit a switch in estuarine condition resulting in a decline in seagrass biomass and large changes in predator-prey cycles.

Acknowledgements

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Table 1: The 17 state variables used in the ecological model. The initial conditions and ocean boundary conditions and their symbol and units are also shown.

<table>
<thead>
<tr>
<th>State Variable</th>
<th>Symbol</th>
<th>Initial Conditions</th>
<th>Ocean Boundary Condition</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dissolved Inorganic Nitrogen</td>
<td>DIN</td>
<td>$7.3 \times 10^{-4}$</td>
<td>$9.5 \times 10^{-4}$</td>
<td>mol N m$^{-3}$</td>
</tr>
<tr>
<td>Dissolved Inorganic Phosphorus</td>
<td>DIP</td>
<td>$5.1 \times 10^{-6}$</td>
<td>$1.0 \times 10^{-4}$</td>
<td>mol P m$^{-3}$</td>
</tr>
<tr>
<td>Small Phytoplankton</td>
<td>PS</td>
<td>$1.1 \times 10^{-4}$</td>
<td>$1.6 \times 10^{-4}$</td>
<td>mol N m$^{-3}$</td>
</tr>
<tr>
<td>Large Phytoplankton</td>
<td>PL</td>
<td>$3.3 \times 10^{-4}$</td>
<td>$2.1 \times 10^{-4}$</td>
<td>mol N m$^{-3}$</td>
</tr>
<tr>
<td>Small Zooplankton</td>
<td>ZS</td>
<td>$9.8 \times 10^{-4}$</td>
<td>$1.5 \times 10^{-4}$</td>
<td>mol N m$^{-3}$</td>
</tr>
<tr>
<td>Large Zooplankton</td>
<td>ZL</td>
<td>$1.1 \times 10^{-3}$</td>
<td>$1.5 \times 10^{-4}$</td>
<td>mol N m$^{-3}$</td>
</tr>
<tr>
<td>Epiphytic and Benthic Microalgae</td>
<td>EP</td>
<td>$8.4 \times 10^{-5}$</td>
<td>0</td>
<td>mol N m$^{-2}$</td>
</tr>
<tr>
<td>Seagrass</td>
<td>SG</td>
<td>$6.0 \times 10^{-2}$</td>
<td>0</td>
<td>mol N m$^{-2}$</td>
</tr>
<tr>
<td>Refractory Detritus</td>
<td>RD</td>
<td>$21 \times 10^{-2}$</td>
<td>0</td>
<td>mol N m$^{-2}$</td>
</tr>
<tr>
<td>Sediment Dissolved Inorganic Nitrogen</td>
<td>DIN$_{sed}$</td>
<td>$3.3 \times 10^{-2}$</td>
<td>0</td>
<td>mol N m$^{-2}$</td>
</tr>
<tr>
<td>Unflocculated Phosphorus</td>
<td>$P_{unfloc}$</td>
<td>$2.7 \times 10^{-7}$</td>
<td>0</td>
<td>mol P m$^{-3}$</td>
</tr>
<tr>
<td>Flocculated Phosphorus</td>
<td>$P_{floc}$</td>
<td>$2.0 \times 10^{-8}$</td>
<td>0</td>
<td>mol P m$^{-3}$</td>
</tr>
<tr>
<td>Sediment Dissolved Inorganic Phosphorus</td>
<td>DIN$_{sed}$</td>
<td>$1.8 \times 10^{-3}$</td>
<td>0</td>
<td>mol P m$^{-2}$</td>
</tr>
<tr>
<td>Unflocculated Sediment Phosphorus</td>
<td>$P_{sed,unfloc}$</td>
<td>3.1</td>
<td>0</td>
<td>mol P m$^{-2}$</td>
</tr>
<tr>
<td>Flocculated Sediment Phosphorus</td>
<td>$P_{sed,floc}$</td>
<td>5.6</td>
<td>0</td>
<td>mol P m$^{-2}$</td>
</tr>
<tr>
<td>Unflocculated Total Suspended Solids</td>
<td>TSS$_{unfloc}$</td>
<td>$5.2 \times 10^{-3}$</td>
<td>0</td>
<td>kg TSS m$^{-3}$</td>
</tr>
<tr>
<td>Flocculated Total Suspended Solids</td>
<td>TSS$_{floc}$</td>
<td>$2.2 \times 10^{-5}$</td>
<td>0</td>
<td>kg TSS m$^{-3}$</td>
</tr>
</tbody>
</table>
Table 2: Parameter values for the ecological model. The ranges tested in the sensitivity analysis are shown in column 2 and 3. N/T = Not Tested.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>10% Range</th>
<th>50% Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cell radius of $PS$</td>
<td>$r_{PS} = 2.5 \times 10^{-6}$ m</td>
<td>2.25-2.75 $\times 10^{-6}$</td>
<td>1.25-3.75 $\times 10^{-6}$</td>
</tr>
<tr>
<td>Cell radius of $PL$</td>
<td>$r_{PL} = 1.0 \times 10^{-5}$ m</td>
<td>0.9-1.1 $\times 10^{-6}$</td>
<td>0.5-1.5 $\times 10^{-6}$</td>
</tr>
<tr>
<td>Cell radius of $ZS$</td>
<td>$r_{ZS} = 4.0 \times 10^{-6}$ m</td>
<td>3.6-4.4 $\times 10^{-6}$</td>
<td>N/T</td>
</tr>
<tr>
<td>Cell radius of $ZL$</td>
<td>$r_{ZL} = 1.0 \times 10^{-3}$ m</td>
<td>0.9-1.1 $\times 10^{-3}$</td>
<td>N/T</td>
</tr>
<tr>
<td>Cell radius $EP$</td>
<td>$r_{EP} = 5.0 \times 10^{-6}$ m</td>
<td>4.5-5.5 $\times 10^{-6}$</td>
<td>N/T</td>
</tr>
<tr>
<td>Mortality rate of $ZS$</td>
<td>$\zeta_{ZS} = 94.78$ (mol N m^{-3})^{-1} d^{-1}</td>
<td>85.30-104.26</td>
<td>47.39-142.17</td>
</tr>
<tr>
<td>Mortality rate of $ZL$</td>
<td>$\zeta_{ZL} = 18.03$ (mol N m^{-3})^{-1} d^{-1}</td>
<td>16.23-19.83</td>
<td>9.02-27.05</td>
</tr>
<tr>
<td>Mortality rate of $EP$</td>
<td>$\zeta_{EP} = 0.05$ d^{-1}</td>
<td>0.045-0.055</td>
<td>0.025-0.075</td>
</tr>
<tr>
<td>Mortality rate of $SG$</td>
<td>$\zeta_{SG} = 4.22$ (mol N m^{-2})^{-1} d^{-1}$ (Duarte, 1990)</td>
<td>3.80-4.64</td>
<td>2.11-6.33</td>
</tr>
<tr>
<td>Rate of $RD$ Breakdown</td>
<td>$RD = 0.1$ d^{-1}$ (Murray and Parslow, 1997)</td>
<td>0.09-0.11</td>
<td>N/T</td>
</tr>
<tr>
<td>Feeding efficiency of $ZS$</td>
<td>$\beta_{ZS} = 0.31$ (Hansen et al., 1997)</td>
<td>0.28-0.34</td>
<td>0.155-0.465</td>
</tr>
<tr>
<td>Feeding efficiency of $ZL$</td>
<td>$\beta_{ZL} = 0.34$ (Hansen et al., 1997)</td>
<td>0.31-0.37</td>
<td>0.17-0.51</td>
</tr>
<tr>
<td>Sinking rate of $P_{floc}$</td>
<td>$w_{P_{floc}} = 5$ d^{-1}$ (Baird et al., 2003)</td>
<td>4.5-5.5</td>
<td>N/T</td>
</tr>
<tr>
<td>Sinking rate of $P_{unfloc}$</td>
<td>$w_{P_{unfloc}} = 5$ d^{-1}$ (Baird et al., 2003)</td>
<td>4.5-5.5</td>
<td>N/T</td>
</tr>
</tbody>
</table>
Table 3: Normalised sensitivity when parameters are varied by 10%. The rows represent the parameters changed, and the columns the state variables examined. The values in bold are the parameters with a normalised sensitivity greater than $|0.4|$.

<table>
<thead>
<tr>
<th></th>
<th>$DIN$</th>
<th>$DIP$</th>
<th>$PS$</th>
<th>$PL$</th>
<th>$ZS$</th>
<th>$ZL$</th>
<th>$EP$</th>
<th>$SG$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_{PS}$</td>
<td>-0.04</td>
<td>-0.43</td>
<td>0.68</td>
<td>-0.52</td>
<td>0.64</td>
<td>-0.62</td>
<td>-0.44</td>
<td>-0.01</td>
</tr>
<tr>
<td>$r_{PL}$</td>
<td>-0.04</td>
<td>-0.52</td>
<td>-0.59</td>
<td>0.57</td>
<td>-0.58</td>
<td>0.71</td>
<td>-0.53</td>
<td>-0.01</td>
</tr>
<tr>
<td>$r_{ZS}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$r_{ZL}$</td>
<td>0</td>
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<td>0</td>
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<td>0</td>
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<tr>
<td>$r_{EP}$</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>$\zeta_{ZS}$</td>
<td>-0.01</td>
<td>-0.15</td>
<td>1.05</td>
<td>-0.14</td>
<td>-0.01</td>
<td>-0.22</td>
<td>-0.15</td>
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</tr>
<tr>
<td>$\zeta_{ZL}$</td>
<td>-0.01</td>
<td>-0.17</td>
<td>-0.2</td>
<td>0.52</td>
<td>-0.18</td>
<td>0.06</td>
<td>-0.17</td>
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<tr>
<td>$\zeta_{SG}$</td>
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<tr>
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<tr>
<td>$sedxch$</td>
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<td>0.03</td>
<td>0.04</td>
<td>0.03</td>
<td>-0.01</td>
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<tr>
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<td>-1.28</td>
<td>0.18</td>
<td>0</td>
<td>0.25</td>
<td>0.18</td>
<td>-0.01</td>
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<tr>
<td>$\beta_{ZL}$</td>
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<td>0.24</td>
<td>0.24</td>
<td>-1.11</td>
<td>0.26</td>
<td>0.09</td>
<td>0.25</td>
<td>0.02</td>
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<tr>
<td>$w_P^{loc}$</td>
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<tr>
<td>$w_P^{unfloc}$</td>
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Table 4: Table of normalised sensitivity at the 25 (and 50% - in brackets) levels for the 8 most sensitive parameters from Table 3. Bold represents the parameters whose sensitivity changed by more than 0.1 from 10 to 25% or 25 to 50%.

<table>
<thead>
<tr>
<th></th>
<th>DIN</th>
<th>DIP</th>
<th>PS</th>
<th>PL</th>
<th>ZS</th>
<th>ZL</th>
<th>EP</th>
<th>SG</th>
</tr>
</thead>
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<td>$r_{PS}$</td>
<td>0.04 (-0.04)</td>
<td>-0.48 (-0.50)</td>
<td>0.65 (0.63)</td>
<td>-0.53 (-0.50)</td>
<td>0.63 (0.62)</td>
<td>-0.58 (-0.58)</td>
<td>-0.49 (-0.51)</td>
<td>-0.01 (0)</td>
</tr>
<tr>
<td>$r_{PL}$</td>
<td><strong>-0.04 (-0.39)</strong></td>
<td>-0.47 (-0.48)</td>
<td>-0.57 (-0.58)</td>
<td>0.62 (0.61)</td>
<td>-0.54 (-0.56)</td>
<td>0.61 (0.65)</td>
<td>-0.47 (-0.48)</td>
<td>-0.01 (-0.01)</td>
</tr>
<tr>
<td>$\zeta_{ZS}$</td>
<td>-0.01 (-0.01)</td>
<td>-0.15 (-0.18)</td>
<td>1.03 (1.02)</td>
<td>-0.12 (-0.11)</td>
<td>0 (0)</td>
<td>-0.22 (-0.21)</td>
<td>-0.15 (-0.18)</td>
<td>0 (-0.01)</td>
</tr>
<tr>
<td>$\zeta_{ZL}$</td>
<td>-0.01 (0)</td>
<td>-0.14 (-0.09)</td>
<td>-0.14 (-0.11)</td>
<td>0.48 (0.49)</td>
<td>-0.16 (-0.11)</td>
<td>0.03 (-0.05)</td>
<td>-0.14 (-0.09)</td>
<td>-0.02 (-0.02)</td>
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<tr>
<td>$\zeta_{EP}$</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td><strong>-1.07 (-1.33)</strong></td>
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<td>$\zeta_{SG}$</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
<td>0 (0)</td>
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<tr>
<td>$\beta_{ZS}$</td>
<td>0.01 (0.03)</td>
<td>0.18 (0.3)</td>
<td><strong>-1.28 (-1.78)</strong></td>
<td>0.14 (0.25)</td>
<td>0 (0.09)</td>
<td>0.27 (0.22)</td>
<td><strong>0.18 (0.30)</strong></td>
<td>-0.01 (0.01)</td>
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<tr>
<td>$\beta_{ZL}$</td>
<td>0.02 (0.02)</td>
<td>0.25 (0.30)</td>
<td>0.25 (0.31)</td>
<td><strong>-1.15 (-1.35)</strong></td>
<td>0.27 (0.33)</td>
<td>0.10 (0.11)</td>
<td>0.25 (0.30)</td>
<td>0.03 (0.02)</td>
</tr>
</tbody>
</table>
Figure 1: Plot of the average lake depth (m) of the idealised model formulation against time (days). The same cycle is repeated each year. The average depth of the lake is taken from lake depth measurements and is different to the Australian Height Datum (AHD), which is the reference datum for altitude measurement in Australia. The inserted box shows the sinusoidal oscillation which occurs during the open phase.
Figure 2: Biomass of A) PS, B) PL (mol N m$^{-3}$), productivity of C) PS, D) PL (mol N m$^{-3}$ d$^{-1}$) in response to changes to the phosphorus load entering the estuary. The lines represent the changes to the phosphorus load of 2x, 10x and the Control). The grey shaded areas represent the time the lake is open to the ocean.
Figure 3: Growth limitation of PS (A, C) and PL (B, D) in response to changes to the phosphorus load entering the estuary. In plots A/B (2× increase in DIP Catchment Loads) and C/D (10× increase in DIP Catchment Loads), the line shows the biomass and the colour of the line represents the process that limits growth (nitrogen uptake, phosphorus uptake, light capture or maximum metabolic rate). The grey shaded areas represent the time the lake is open to the ocean.
Figure 4: Sensitivity of seagrass to changing catchment loads. Columns give seagrass biomass (mol N m\(^{-2}\)), water column light attenuation (m\(^{-1}\)), phytoplankton light attenuation (m\(^{-1}\)) and seagrass light availability (mol photon m\(^{-2}\) s\(^{-1}\)). Rows show catchment load simulations of DIN, DIN + DIP, DIN + TSS and DIN + DIP + TSS. The grey shaded areas represent the time the lake is open to the ocean.
Figure 5: The contours represent the mean biomass of the state variables at a lake opening height of 3.5 m. The mean value is calculated from the final closed phase. The white crosses show the location of the mean simulation values used to create the contours.
Figure 6: The biomass of $DIN$, $DIP$, $PS$, $PL$, $ZS$, $ZL$, $EP$ and $SG$ for simulations as the lake depth is changed. The lines represent the changes in estuary depth from 2.5, 4.5, 7 and 12 m. The grey shaded areas represent the time the lake is open to the ocean.
Figure 7: Biomass of $PS$, $PL$, $EP$ and $SG$ (columns 1-4 respectively) coloured by process limiting growth rate. Depth simulations of 2.5, 4.5, 7 and 12 m are plotted across the rows. The line shows the biomass and the colour represents the growth limitation options of nitrogen, phosphorus, light and maximum metabolic rate. The grey shaded areas represent the time the lake is open to the ocean.
Figure 8: The realised growth rate for $PS$, $PL$, $ZS$, $ZL$, $EP$ and $SG$ as the lake depth is changed. The colours represent the changes in estuary depth from 2.5, 4.5, 7 and 12 m. The grey shaded areas represent the time the lake is open to the ocean.
Figure 9: The standard deviation of state variable biomass for 10 ensemble members for the first 3 years of the simulation. The plots represent A) 2 week open phase, B) 1 month open phase and C) 2 month open phase. The lines represent the 6 state variables of *DIN*, *DIP*, *PS*, *PL*, *ZS* and *ZL*. The grey shaded areas represent the time the lake is open to the ocean.