

Nutrient and plankton dynamics in an intermittently closed/open lagoon, Smiths Lake, south-eastern Australia: An ecological model

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Abstract

A spatially resolved, eleven-box ecological model is presented for an Intermittently Closed and Open Lake or Lagoon (ICOLL), configured for Smiths Lake, NSW Australia. ICOLLs are characterised by low flow from the catchment and a dynamic sand bar blocking oceanic exchange, which creates two distinct phases – open and closed. The process descriptions in the ecological model are based on a combination of physical and physiological limits to the processes of nutrient uptake, light capture by phytoplankton and predator–prey interactions. An inverse model is used to calculate mixing coefficients from salinity observations. When compared to field data, the ecological model obtains a fit for salinity, nitrogen, phosphorus, chlorophyll *a* and zooplankton which is within 1.5 standard deviations of the mean of the field data. Simulations show that nutrient limitation (nitrogen and phosphorus) is the dominant factor limiting growth of the autotrophic state variables during both the open and closed phases of the lake. The model is characterised by strong oscillations in phytoplankton and zooplankton abundance, typical of predator–prey cycles. There is an increase in the productivity of phytoplankton and zooplankton during the open phase. This increased productivity is exported out of the lagoon with a net nitrogen export from water column variables of 489 and 2012 mol N d⁻¹ during the two studied openings. The model is found to be most sensitive to the mortality and feeding efficiency of zooplankton.

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1. Introduction

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 exchange with the ocean. Following a rise in the water level, these barriers are intermittently breached. Typically a narrow (<200 m), shallow (<5 m)

channel forms, connecting the lagoon to the ocean, with reduced tidal velocities when compared to permanently open estuaries (Ranasinghe and Pattiaratchi, 1999).

The open/closed cycles of ICOLLs in south-eastern Australia are not seasonal due to the intermittent nature of rainfall (EPA NSW, 2000). The timing and frequency of the entrance opening are 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 is variable, open/closed cycles are rarely predictable and therefore, ICOLLs seldom reach any long-term steady-state (Roy et al., 2001). As an added complication, 72% of NSW ICOLLs

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are now artificially opened when they reach a predefined ‘trigger’ height (DIPNR, 2004). Reasons for this include flood prevention strategies and flushing in order to minimise pollution. Due to a lack of flushing, ICOLLs are particularly prone to pollution events such as nutrient or sediment runoff.

There are few published studies of ICOLLs in south-eastern Australia. Previous studies have focused on circulation (Gale et al., 2006), morphometric analysis (Haines et al., 2006), fish assemblages (Pollard, 1994; Jones and West, 2005) and benthic fauna (Dye and Barros, 2005). This study will focus on the water column nutrient and plankton dynamics of an ICOLL. Such studies have been undertaken in South Africa (e.g. Perissinotto et al., 2000; Froneman, 2004). However, South African estuaries typically open seasonally during the wet season, rather than intermittently like those in south-eastern Australia. In order to examine the open/closed cycles of an ICOLL, field data and the output of a process based model will be analysed.

Process based models of estuarine systems have been used with much success in the past (Madden and Kemp, 1996; Murray and Parslow, 1999). Recently, process based models of estuaries (Baird et al., 2003) and the open ocean (Baird et al., 2004) have included physical limits to key ecological processes. These limits include diffusion-limited nutrient uptake by phytoplankton cells or the grazing rates of zooplankton on phytoplankton. The latter incorporates an encounter rate calculation, based on the encounter rates of particles in a turbulent fluid, which places a maximum value on the rate of ingestion. The physical limits are used until a physiological rate, such as maximum growth rate, becomes more limiting. These physical descriptions provide an alternative methodology for the formulation of the key processes in the ecological model.

This paper presents an ecological model of an ICOLL, configured for Smiths Lake, and uses physical limits to describe key ecological processes. The aims are (1) to assess model performance using field data collected over two complete open/closed cycles, (2) to examine autotrophic growth limitation, (3) to assess model sensitivity to parameter selection and (4) to produce a nitrogen budget for each open/closed phase.

2. Methods

2.1. Field location

Smiths Lake (152.519E 32.393S) is located 280 km north of Sydney, on the mid-north coast of NSW (Fig. 1). It is classified as an ICOLL, with a catchment area of 33 km² (Webb McKeown & Associates Pty. Ltd., 1998) and a fluctuating lake surface area of 9.5–9.8 km². Over the course of the study, the lake height fluctuated between 0.15 m when open and 2.24 m Australian Height Datum (AHD) when closed. For a plot of Smiths Lake bathymetry see Figure 2 from Gale et al. (2006).

The Smiths Lake catchment remains relatively undeveloped. A population of 1100 people live within the catchment (Great Lakes Council, 2001). Due to low-lying development Smiths Lake is artificially opened by the local council when

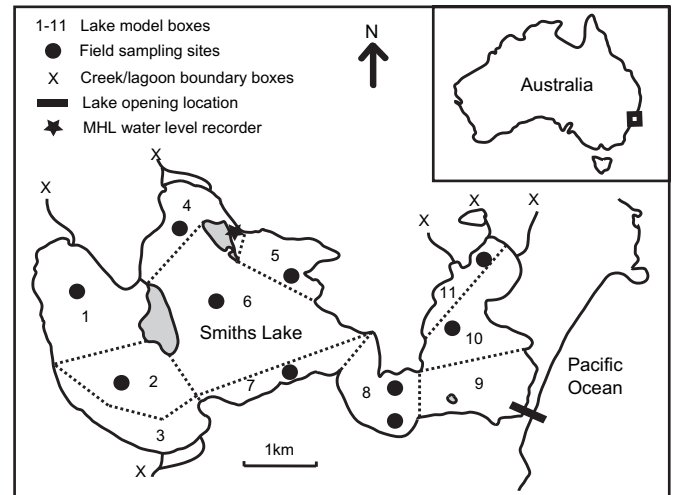


Fig. 1. Map of Smiths Lake with model boxes and sampling sites included. The ocean waters were sampled at Seal Rocks, approximately 4 km south of Smiths Lake.

it reaches 2.1 m AHD (G. Tuckerman – Great Lakes Council, personal communication, 2005).

2.2. Transport model

The model is spatially resolved to 11 lake boxes and seven boundary boxes (Fig. 1). The boundary boxes are representative of five small creeks, one small adjoining lagoon and an ocean box. The lake boxes were established to reflect sub-catchment land use and topography, lake bathymetry, benthic habitat and sampling regime. The five creeks and one lagoon flow into boxes 1, 3, 4, 10 and 11, while exchange with the ocean only occurs at box 9 (Fig. 1). Boxes 3 and 9 do not contain field sampling sites.

The transport model is forced by evaporation (E), rainfall (R) and tidal exchange (TE). The influence of each of these physical forcings depends on the open/closed state of the lake (as outlined below). The transport of water column properties between adjacent boxes is modelled as a diffusive process. The equation for the change in concentration of a tracer in box i is given by:

$$\frac{dC_i}{dt} = \sum_{j=1}^n \underbrace{\frac{k_{ij}(C_j - C_i)}{V_i}}_{\text{Diffusion process}} - \underbrace{\frac{C_i E_i}{V_i}}_{\text{Evap}} + \underbrace{\frac{C_{cr} R_i}{V_i}}_{\text{Runoff}} + \underbrace{\frac{C_{oc} TE}{V_i}}_{\text{Tidal exchange}} + \underbrace{\frac{C_i dV_i/dt}{V_i}}_{\text{Dilution}} \quad (1)$$

where C_i and C_j are the concentrations of box i and an adjoining lake box j (mol m⁻³), V_i is volume of box i (m³), k_{ij} is the transport coefficient between boxes i and j (m³ s⁻¹), E_i is evaporation from box i (m³ s⁻¹) and is negative, C_{cr} is the concentration of creek flow into box i (mol m⁻³), R_i is the flow of water off the catchment into box i (m³ s⁻¹), TE is the tidal flow into or out of the lake (m³ s⁻¹), C_{oc} is the concentration in the ocean box (mol m⁻³) and $n = 11$ is the number of lake boxes.

The transport coefficient (k_{ij}) between box i and j is calculated as:

$$k_{ij} = D \left(\frac{CSA_{ij}}{MPD_{ij}} \right) \quad (2)$$

where D is the diffusion coefficient ($\text{m}^2 \text{s}^{-1}$) calibrated from observed salinity (see Section 2.7), CSA_{ij} is the cross-sectional area between two adjoining lake boxes (m^2) and MPD_{ij} is the distance between the midpoints of the two adjoining lake boxes (m). The transport coefficient encompasses all mixing processes, including advection due to wind and tides. The important mixing processes during the open and closed phases are fundamentally different with wind mixing being dominant during the closed phase and tidal exchange becoming dominant during the open phase of the lake, hence, a different value for D is used for each phase.

2.2.1. Evaporation and rainfall

During the closed phase of the lake, evaporation is determined from the change in lake volume, when dV_i/dt is negative (i.e. lake level falling). An averaged evaporation rate of $-0.35 \text{ m}^3 \text{ s}^{-1}$ is derived from the observations during the closed phase and is applied to each box when the lake is open to the ocean (Fig. 2). This is close to a theoretical prediction for Smiths Lake of $-0.405 \text{ m}^3 \text{ s}^{-1}$ (derived from 35 mm d^{-1} (Gale et al., 2006) over a 10 km^2 lake surface area (Webb McKeown & Associates Pty. Ltd., 1998)).

Rainfall is assumed to be evenly distributed over the entire catchment and lake surface. During the closed phase of the lake, rainfall is calculated from the change in lake volume where dV/dt is positive (i.e. lake level rising). Rainfall is split into direct (R_D) and indirect (R_I) rainfall. Direct rainfall falls directly onto the lake and dilutes the water column but does not change the load of the nutrients and suspended solids. Indirect rainfall falls onto the catchment, before running into the

lake via the creeks. The nutrient concentration of runoff from the catchment is set by the model boundary conditions.

When the lake is open, volume change is primarily due to tides and cannot be used to estimate runoff. Instead, rainfall is derived from a 0.5 mm tipping bucket rain gauge operated by Manly Hydraulics Lab at the same location as the lake height recorder. A comparison of dV/dt and the rain gauge measurements during the closed phase gives a runoff coefficient (R_{CO}) of 0.3.

2.2.2. Tidal exchange

During the open phase, volume change is used to calculate the flow of ocean water into and out of the lake. Oceanic exchange is only introduced for the eastern-most box (box 9), which has an interface with the oceanic box. Exchange occurs between box 9 and the rest of the lake as per Eq. (1). During the open phase the outgoing (negative) water transport ranges between -10 and $-50 \text{ m}^3 \text{ s}^{-1}$ and incoming (positive) water transport approaches 50 – $100 \text{ m}^3 \text{ s}^{-1}$. The height difference inside the lake, between tidal cycles, is in the order of 10–40 cm.

2.3. Light model

Averaged six hourly, 2° resolution shortwave downward solar radiation (W m^{-2}) was obtained from the NOAA–CIRES Climate Diagnostic Centre and linearly interpolated in space to Smiths Lake (152.519E, 32.393S) and further interpolated in time. In the model, light is attenuated through the water column, epiphytes and seagrass sequentially. The light model is adapted from Baird (2001). The proportion of the downward solar radiation ($\text{mol photons m}^{-2} \text{ s}^{-1}$) available as photosynthetically available radiation (PAR) is assumed to be 43% (Fasham et al., 1990).

2.4. Ecological model

The ecological model contains 17 state variables (Table 1). With the exception of state variables relating to phosphorus and total suspended solids, moles of nitrogen is the basic currency of the state variables. The autotrophs (phytoplankton, epiphytes and seagrass) gain their nutrients from the water column, with the exception of seagrass which is also able to draw nutrients from the sediment (Fig. 3). Dissolved inorganic nitrogen ($1.1 \times 10^{-2} \text{ mol N m}^{-3}$), unflocculated phosphorus ($1 \times 10^{-4} \text{ mol P m}^{-3}$), and total suspended solids ($1 \times 10^{-2} \text{ kg TSS m}^{-3}$), 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.

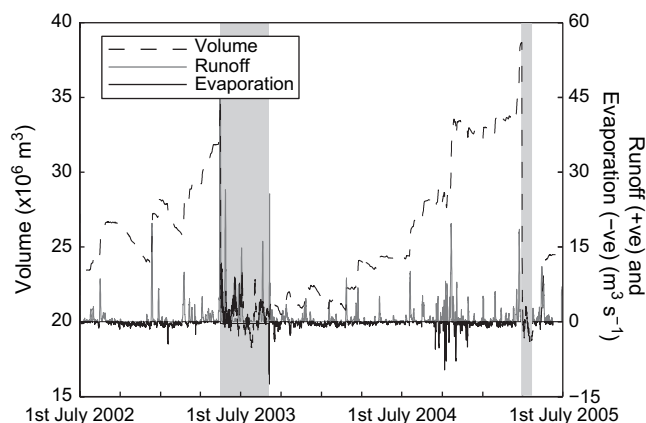


Fig. 2. Estimated lake volume ($\times 10^6 \text{ m}^3$) and forcing functions — runoff ($\text{m}^3 \text{ s}^{-1}$) and evaporation ($\text{m}^3 \text{ s}^{-1}$) for the entire model simulation (July 2002–July 2005). The lake was open from 15 May–3 September 2003 (as shown in grey shading) and then again 29 March–23 April 2005. During this time it becomes tidal. The fluctuations in lake volume during the closed phase represent a balance between runoff and evaporation.

Table 1

Biological state variables used in the model. The mean and range of initial conditions after the model spin-up are presented. Ocean boundary conditions and their symbol and units are also shown

State variable	Symbol	Mean values (and range) of initial conditions	Ocean boundary condition	Units
Dissolved inorganic nitrogen	DIN	7.3 (4.8–7.8) × 10 ⁻⁴	9.5 × 10 ⁻⁴	mol N m ⁻³
Dissolved inorganic phosphorus	DIP	5.1 (4.5–5.5) × 10 ⁻⁶	1.0 × 10 ⁻⁴	mol P m ⁻³
Small phytoplankton	PS	1.1 (0.5–1.4) × 10 ⁻⁴	1.6 × 10 ⁻⁴	mol N m ⁻³
Large phytoplankton	PL	3.3 (3.1–5.1) × 10 ⁻⁴	2.1 × 10 ⁻⁴	mol N m ⁻³
Small zooplankton	ZS	9.8 (9.4–10) × 10 ⁻⁴	1.5 × 10 ⁻⁴	mol N m ⁻³
Large zooplankton	ZL	1.1 (0.9–1.1) × 10 ⁻³	1.5 × 10 ⁻⁴	mol N m ⁻³
Epiphytic and benthic microalgae	EP	8.4 (7.0–13) × 10 ⁻⁵	0	mol N m ⁻²
Seagrass	SG	6.0 (0–8.2) × 10 ⁻²	0	mol N m ⁻²
Refractory detritus	RD	21 (0.27–34) × 10 ⁻²	0	mol N m ⁻²
Sediment dissolved inorganic nitrogen	DIN _{sed}	3.3 (0.2–20) × 10 ⁻²	0	mol N m ⁻³
Unfloculated phosphorus	P _{unfloc}	2.7 (1.8–4.3) × 10 ⁻⁷	0	mol P m ⁻³
Floculated phosphorus	P _{floc}	2.0 (0.1–4.2) × 10 ⁻⁸	0	mol P m ⁻³
Sediment dissolved inorganic phosphorus	DIP _{sed}	1.8 (1.6–1.9) × 10 ⁻³	0	mol P m ⁻³
Unfloculated sediment phosphorus	P _{sed_unfloc}	3.1 (2.7–3.2)	0	mol P m ⁻³
Floculated sediment phosphorus	P _{sed_floc}	5.6 (4.8–5.8)	0	mol P m ⁻³
Unfloculated total suspended solids	TSS _{unfloc}	5.2 (5.0–5.3) × 10 ⁻³	0	kg TSS m ⁻³
Floculated total suspended solids	TSS _{floc}	2.2 (1.5–2.6) × 10 ⁻⁵	0	kg TSS m ⁻³

2.4.1. Initial conditions

The model was 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 were set from the ocean boundary conditions for water column state variables. The initial biomass of epiphytes and seagrass was based upon the literature (Duarte, 1990; Duarte and Chiscano, 1999) and the mapped seagrass coverage in Smiths Lake (West et al., 1985). Initial conditions for sediment state variables were derived from Murray and Parslow

(1997), Baird (2001), and Smith and Heggie (2003). The values at the end of this ‘spin-up’ were used as the initial conditions for the model (Table 1).

2.4.2. 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 were interpolated from field sampling in the creeks (catchment) and at Seal Rocks Beach (oceanic). The boundary conditions for DIN and P_{unfloc} from the catchment are 1.08 × 10⁻² mol N m⁻³ and 9.03 × 10⁻⁵ mol P m⁻³, respectively. The boundary condition of TSS_{unfloc} from the catchment is 0.1 kg m⁻³ (Baird, 2001). Oceanic boundary conditions are found in Table 1.

2.4.3. Autotrophic growth

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

$$\mu_x = \min(\mu_{\text{nitrogen}}, \mu_{\text{phosphorus}}, \mu_{\text{light}}, \mu_{\text{max}}) \tag{3}$$

The four autotrophs within 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

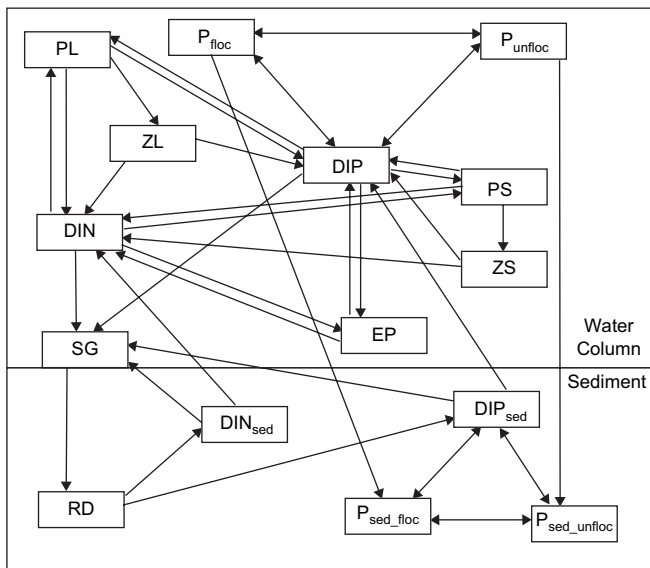


Fig. 3. Schematic of ecological model showing interactions between the biological state variables. Suspended solids (TSS_{unfloc} and TSS_{floc}) are not shown. Abbreviations are given in Table 1.

requirements of the autotrophs are fixed at 10 photons per carbon atom (Kirk, 1994).

2.4.3.1. Growth rates of phytoplankton. 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:

$$\mu_{PS,N} = \frac{\psi_{PS} D_N \text{DIN}}{m_{PS,N}} \quad (4)$$

where ψ_{PS} is the diffusion shape factor ($m \text{ cell}^{-1}$), 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 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:

$$\mu_{PS,I} = \frac{I_{AV} \overline{aA}_{PS}}{m_{PS,I}} \quad (5)$$

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

2.4.3.2. Growth rates of epiphytic microalgae and seagrass. 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 (η). In the model, seagrass are able to extract nutrients from both the water column and the sediment. The belowground 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 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:

$$\mu_{EP,N} = \frac{D_N}{BL} (1 - \eta) \text{DIN} \quad (6)$$

where D_N is molecular diffusivity of nitrogen, BL is the boundary layer thickness, η is the seagrass uptake fraction and DIN is the water column concentration of dissolved inorganic nitrogen, and similarly for phosphorus (Tables 2 and 3).

When formulating seagrass dynamics, fluxes are calculated per m^2 . As a result, to convert to a growth rate requires division of the uptake rate by the biomass. The nitrogen limited

uptake rate (s^{-1}) for seagrass from the water column and the sediment, respectively, is given as:

$$\mu_{SG,N}^{WC} = \frac{D_N}{BL} \eta \text{DIN} \frac{1}{SG} \quad (7)$$

$$\mu_{SG,N}^{SED} = \frac{\mu_{SG}^{\max} \text{DIN}_{\text{sedconc}}}{K_{SG,N}} \quad (8)$$

where μ_{SG}^{\max} is the maximum growth rate of seagrass (s^{-1}), $\text{DIN}_{\text{sedconc}}$ is the sediment concentration of nitrogen and $K_{SG,N}$ is the half-saturation constant for nitrogen uptake in seagrass.

The nitrogen (and similarly for phosphorus) limited growth rate for seagrass is given as:

$$\mu_{SG,N} = \mu_{SG,N}^{WC} + \mu_{SG,N}^{SED} \quad (9)$$

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:

$$\mu_{EP,I} = (I_{\text{bot}} - I_{\text{belowEP}}) \frac{16}{1060} \frac{1}{EP} \quad (10)$$

$$\mu_{SG,I} = (I_{\text{belowEP}} - I_{\text{belowSG}}) \frac{21}{4740} \frac{1}{SG} \quad (11)$$

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

The rate of change for epiphytes and seagrass is given by:

$$\frac{dEP}{dt} = \mu_{EP} EP - \underbrace{\zeta_{EP} EP}_{\text{Mortality}} - \underbrace{\frac{dA/dt}{A} EP}_{\text{Lake area correction term}} \quad (12)$$

$$\frac{dSG}{dt} = \mu_{SG} SG - \underbrace{\zeta_{SG} SG^2 \omega_{SG}}_{\text{Quadratic mortality}} - \underbrace{\frac{dA/dt}{A} SG}_{\text{Lake area correction term}} \quad (13)$$

A lake area correction term is applied to epiphytes and seagrass in order to conserve mass when the lake surface changes with lake height, and is necessary due to the coarseness of the model boundary.

A quadratic mortality of seagrass (ζ_{SG}) is used as a closure term for the benthic autotrophs. A resorption coefficient (ω_{SG}) is appended to the mortality term of the seagrass to represent the retainment 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 .

Table 2

Parameter values for the ecological model. To improve readability, ecological parameters are given with time units of days, but appear in the text with units of seconds

Parameter	Value
Cell radius of PS	$r_{PS} = 2.5 \times 10^{-6}$ m
Cell radius of PL	$r_{PL} = 1.0 \times 10^{-5}$ m
Cell radius of ZS	$r_{ZS} = 4.0 \times 10^{-6}$ m
Cell radius of ZL	$r_{ZL} = 1.0 \times 10^{-3}$ m
Cell radius EP	$r_{EP} = 5.0 \times 10^{-6}$ m
Maximum growth rate of PS	$\mu_{PS}^{\max} = 1.86$ d ⁻¹ (Tang, 1995)
Maximum growth rate of PL	$\mu_{PL}^{\max} = 1.00$ d ⁻¹ (Tang, 1995)
Maximum growth rate of ZS	$\mu_{ZS}^{\max} = 1.94$ d ⁻¹ (Hansen et al., 1997)
Maximum growth rate of ZL	$\mu_{ZL}^{\max} = 0.27$ d ⁻¹ (Banse and Mosher, 1980)
Maximum growth rate of EP	$\mu_{EP}^{\max} = 0.34$ d ⁻¹ (Fong and Harwell, 1994; Plus et al., 2003)
Maximum growth rate of SG	$\mu_{SG}^{\max} = 0.1$ d ⁻¹ (Baird et al., 2003)
Mortality rate of ZS	$\zeta_{ZS} = 94.78$ (mol N m ⁻³) ⁻¹ d ⁻¹
Mortality rate of ZL	$\zeta_{ZL} = 2.09 \times 10^{-4}$ (mol N m ⁻³) ⁻¹ d ⁻¹
Mortality rate of EP	$\zeta_{EP} = 0.05$ d ⁻¹
Mortality rate of SG	$\zeta_{SG} = 4.22$ (mol N m ⁻²) ⁻¹ d ⁻¹ (Duarte, 1990)
N content of PS, PL, EP	$m_{PS,N}, m_{PL,N}, m_{EP,N} = N_{RED}/C_{RED} 1.32V^{0.758}$ mol N cell ⁻¹ (Baird et al., 2003)
P content of PS, PL, EP	$m_{PS,P}, m_{PL,P}, m_{EP,P} = P_{RED}/C_{RED} 1.32V^{0.758}$ mol P cell ⁻¹ (Baird et al., 2003)
I content of PS, PL, EP	$m_{PS,I}, m_{PL,I}, m_{EP,I} = I_{RED}/C_{RED} 1.32V^{0.758}$ mol I cell ⁻¹ (Baird et al., 2003)
Diffusion shape factor	$\psi = 4\pi r$ m cell ⁻¹ (Baird et al., 2004)
PS absorption cross-section	$\bar{a}_{PS} = 1.015 \times 10^{-11}$ cell ⁻¹ m ² (Baird et al., 2003)
PL absorption cross-section	$\bar{a}_{PL} = 1.726 \times 10^{-10}$ cell ⁻¹ m ² (Baird et al., 2003)
EP absorption cross-section	$\bar{a}_{EP} = 4.779 \times 10^{-11}$ cell ⁻¹ m ² (derived from Baird et al., 2003)
SG absorption cross-section	$\bar{a}_{SG} = 14.01$ m ² (mol N) ⁻¹
Rate of RD Breakdown	$r_{RD} = 0.1$ d ⁻¹ (Murray and Parslow, 1997)
Feeding efficiency of ZS	$\beta_{ZS} = 0.31$ (Hansen et al., 1997)
Feeding efficiency of ZL	$\beta_{ZL} = 0.34$ (Hansen et al., 1997)
Clearance rate of ZS	$C_{ZS} = 5.6$ m ³ mol N d ⁻¹ (Murray and Parslow, 1997)
Clearance rate of ZL	$C_{ZL} = 1.12$ m ³ mol N d ⁻¹ (Murray and Parslow, 1997)
Fraction SG _N :EP _N absorption	$\eta = 0.83$ (Cornelisen and Thomas, 2002)
SG _N resorption	$\omega_{SG} = 0.3$ (Stapel and Hemminga, 1997; Hemminga et al., 1999)
Sinking rate of P _{floc} /TSS _{floc}	$w_{P_{floc}} = 5$ d ⁻¹ and $w_{TSS_{floc}} = 5$ d ⁻¹ (Baird, 2001)
Sinking rate of P _{unfloc} /TSS _{unfloc}	$w_{P_{unfloc}} = 5$ d ⁻¹ and $w_{TSS_{unfloc}} = 5$ d ⁻¹ (Baird, 2001)
Rate of TSS flocculation	$r_{floc}^{\max} = 0.01$ d ⁻¹ (Baird, 2001)
P absorption/desorption	$P_{abs,r} = 1$ d ⁻¹ (Baird, 2001)
P absorption coefficient	$P_{abs,co} = 2$ m ³ kg ⁻¹ (Baird, 2001)
Sediment porosity	$poros = 0.547$ (Baird, 2001)
Sediment–water column exchange	$sedxch = 1 \times 10^{-10}$ m ² s ⁻¹ (Baird, 2001)
Half-saturation constant of ZS	$K_{ZS} = 1.1 \times 10^{-3}$ mol N m ⁻³
Half-saturation constant of ZL	$K_{ZL} = 0.7 \times 10^{-3}$ mol N m ⁻³
Nitrogen half-saturation constant of SG	$K_{SG,N} = 3.6 \times 10^{-4}$ mol N m ⁻³
Phosphorus half-saturation constant of SG	$K_{SG,P} = 1.0 \times 10^{-4}$ mol P m ⁻³

2.4.4. Zooplankton grazing

In the model, small zooplankton graze on small phytoplankton and large zooplankton graze on large phytoplankton as shown below:

$$\mu_{ZS} = \frac{\mu_{ZS}^{\max} PS}{K_{ZS} + PS} \quad (14)$$

where μ_{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). The change in the zooplankton population becomes:

$$\frac{dZS}{dt} = \mu_{ZS}\beta_{ZS}ZS - \underbrace{\zeta_{ZS}ZS^2}_{\text{Quadratic mortality}} \quad (15)$$

where μ_{ZS} is the growth rate of small zooplankton (s⁻¹), β_{ZS} is the feeding efficiency of small zooplankton and ζ_{ZS} is the

quadratic mortality coefficient of small zooplankton ((mol N m⁻³)⁻¹ s⁻¹). Of this mortality, $\mu_{ZS}\beta_{ZS}$ is transferred directly to the small zooplankton, and $\mu_{ZS}(1-\beta)ZS$ is released directly into the water column as available nutrients. A quadratic mortality for zooplankton was selected on the assumption that the biomass of zooplankton will be proportional to their predator.

Table 3
Physical constants used in the model

Constant	Symbol and value
Molecular diffusivity of N	$D_N = 1.95 \times 10^{-9}$ m ² s ⁻¹ (Li and Gregory, 1974)
Molecular diffusivity of P	$D_P = 0.734 \times 10^{-9}$ m ² s ⁻¹ (Li and Gregory, 1974)
Diffusion boundary layer thickness	$BL = 1 \times 10^{-3}$ m
N uptake coefficient	$S_N = \frac{D_N}{BL} = 1.95 \times 10^{-6}$ m s ⁻¹
P uptake coefficient	$S_P = \frac{D_P}{BL} = 0.734 \times 10^{-6}$ m s ⁻¹

2.4.5. Phosphorus and total suspended solids dynamics

Phosphorus and total suspended solids are divided into flocculated and unflocculated phosphorus (P_{floc} and P_{unfloc}) and TSS (TSS_{floc} and $\text{TSS}_{\text{unfloc}}$), respectively. Phosphorus and total suspended solids enter the model from the creeks in the unflocculated form. The rate of flocculation of TSS, and hence phosphorus, is a discontinuous function of salinity as per Baird (2001). In the water column, phosphorus is involved in a reversible absorption/desorption reaction with both flocculated and unflocculated phosphorus (Baird, 2001). Nutrients are released from the sediment as a function of the difference in nutrient concentration between the water column and the sediment.

2.5. Numerical techniques

The model equations are integrated in time using a 4th–5th order Runge–Kutta integrator, with a relative and absolute tolerance of 10^{-8} , and a maximum time step of 3 h. The transport and ecological equations are integrated sequentially to allow separate integration of the respective equations.

2.6. Sampling methods

Ten sites on Smiths Lake were sampled from October 2002 through to June 2005 (Fig. 1). At each site, salinity was measured at 1 m depth intervals through the water column using a calibrated Yeo-Kal 611 conductivity, temperature, depth unit. Water samples ($n = 2$) were collected from 20 cm below the surface for analysis of ammonium (NH_4^+), oxidised nitrogen (NO_2^- and NO_3^-), phosphate (PO_4^+) and chlorophyll *a* (as per Moore et al., 2006). Nutrient concentrations were determined using the American Public Health Association Method 4500 modified for oxidised nitrogen, ammonia and phosphate on the Lachat Instruments autoanalyser. The practical quantification limits for this method are 0.07 mol m^{-3} for oxidised nitrogen, 0.14 mol m^{-3} for ammonia, and 0.03 mol m^{-3} for phosphate. Six creek and lagoon sites (Fig. 1) were also sampled for nutrients in order to estimate catchment loads.

Zooplankton biomass data were determined by towing an in situ optical plankton counter (OPC-2T) in both the eastern and the western basins of Smiths Lake as per the methods of Moore and Suthers (2006). The OPC-2T (Focal Technologies, Inc., Dartmouth, Canada) records equivalent spherical diameters of particles that pass through the instrument in a 0.5 s interval. The particle sizes are recorded digitally into 4096 bins and the biomass used to assess the model is the sum of that obtained between the particle sizes of 360–1521 μm . Particle volumes are converted to carbon content using $0.126 \times 10^6 \text{ g C cell}^{-1} = 1 \text{ m}^3 \text{ cell}^{-1}$ (Hansen et al., 1997), and to nitrogen content using the Redfield C:N ratio of $6.625 \text{ mol mol}^{-1}$.

2.7. Transport coefficient calibration

Salinity measured in the field was used to calibrate the diffusion coefficient (D) of the transport model. A cost function

was used to compare the field and model salinity, normalised by the standard deviation of the field data, to assess the fit, as per the methods of Moll (2000). Due to the different dominant processes involved in mixing, separate values of D were obtained for the open and closed phases.

The cost function is calculated as:

$$C = \frac{\sum_{t=1}^{n_t} \sum_{s=1}^{n_s} (M_{ts} - F_{ts}) / \sigma_s}{n_t n_s} \quad (16)$$

where M_{ts} is the value of the model at time t and site s , F_{ts} is the corresponding value of the in situ field data, σ_s is the standard deviation of the in situ field data for a particular site over time and n_t and n_s are the number of temporal and spatial data points, respectively. The cost function gives an indication of the goodness of fit between the model and the field data. As per Moll (2000), the results of the cost functions are described as: very good <1 standard deviation, good: 1–2 standard deviations, reasonable: 2–5 standard deviations, poor: >5 standard deviations. The diffusion coefficients used in the model were $9 \text{ m}^2 \text{ s}^{-1}$ (closed) and $85 \text{ m}^2 \text{ s}^{-1}$ (open) with a calculated cost of 0.20 (very good).

2.8. Sensitivity analysis

A sensitivity analysis was undertaken by varying each parameter in the model by 10% and analysing the change in each state variable. The model was run under ‘idealised conditions’ for 365 days, with the lake height increasing linearly from 0.4 m to 2.0 m. The results from the final 275 days (75%) of the scenario were analysed for changes in the state variables, by comparing to a ‘control’ simulation with no changes in the parameters.

The sensitivity of each state variable to each parameter (as derived from Murray and Parslow, 1997) was calculated as:

$$\text{Sensitivity} = \frac{V(1.1p) - V(0.9p)}{V(p)0.2} \quad (17)$$

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

3. Results

Smiths Lake opened to the ocean twice during the study period (Fig. 2). The lake initially closed prior to the study on 29 June 2002. Sampling began on 13 October 2002. The lake remained closed for approximately 10 months before opening on 15 May 2003 at a lake height of 2.1 m and salinity of 20 (Fig. 4A). The lake remained opened for approximately 110 days before closing with a salinity of 35. The lake remained closed for a period of almost 2 years before opening again

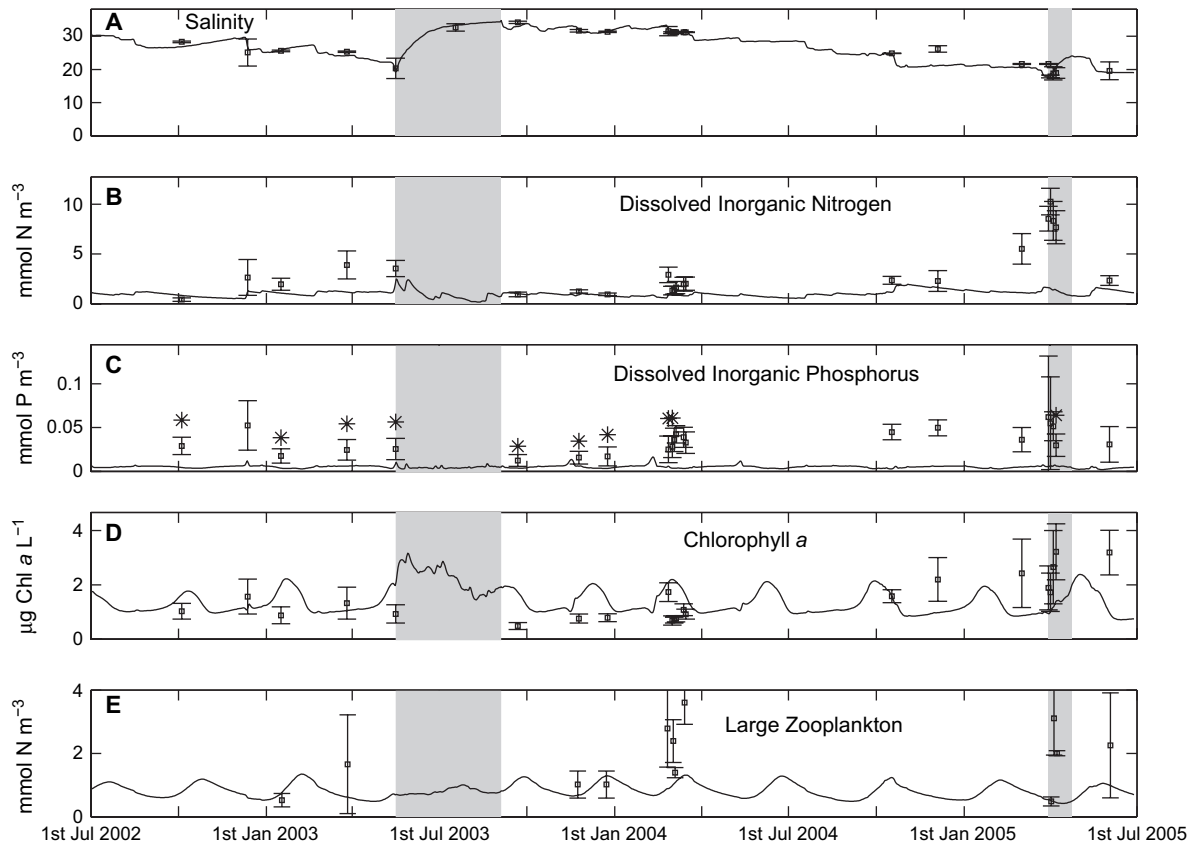


Fig. 4. The solid line represents the volume-weighted, spatial mean of (A) salinity, (B) dissolved inorganic nitrogen (mmol N m^{-3}), (C) dissolved inorganic phosphorus (mmol P m^{-3}), (D) chlorophyll *a* ($\mu\text{g chl } a \text{ L}^{-1}$), and (E) large zooplankton (mmol N m^{-3}) over the time of the simulation (July 2002–July 2005). The data points (\square) and error bars show the mean and standard deviation of the field data and the shaded area denotes when the lake is open to the ocean. The mean data points marked with an asterisk (*) have some or all values which are below the detection limit of the nutrient autoanalyser.

on 29 March 2005 at a height of 2.2 m and salinity of 18. It remained open for approximately 21 days, reaching a maximum salinity of 24. The final field sampling was undertaken 40 days after the lake closed.

The simulated DIN and DIP concentrations are consistent with observations for much of the open–closed cycle (Fig. 4B,C). 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 with values ranging from 0.15×10^{-3} to $2.5 \times 10^{-3} \text{ mol N m}^{-3}$ and 0.2×10^{-5} to $1.6 \times 10^{-5} \text{ mol P m}^{-3}$, respectively (Fig. 4B,C). Both observations and model data show very low concentrations of water column DIP. The results of the cost function for salinity, DIN, DIP and chlorophyll *a* were 0.20, 0.79, 1.49 and 1.01, respectively. It was expected salinity would have the best fit (very good) as the mixing model was calibrated from this data. The fit for DIN was also considered very good, while DIP and chlorophyll *a* are considered good fits.

3.1. Model budget

During the first opening, there is an overall (catchment and ocean) net import of DIN (Fig. 5B). When only the import from the ocean is considered (754 mol N d^{-1}), there is a net export of DIN during the opening. During the second opening (Fig. 5D), there is a net export of DIN, even when the

catchment inputs are included. There is also a net export of phytoplankton and zooplankton during both open phases. When individual size classes are examined, there is a net import of PL during the second opening (Fig. 5D).

3.2. Autotrophic growth limitation

Little change in growth limitation occurs between the open and closed phases for each of the autotrophic state variables (Table 4). PS is mainly limited by phosphorus availability and to a lesser extent by its maximum growth rate. During the closed phase, PL and EP are limited only by phosphorus. During the open phase PL and EP are limited, at times, by both phosphorus and their maximum growth rate. Seagrass, which is able to source nutrients from the sediment, is limited by either nitrogen or light during both the open and closed phases.

3.3. Model sensitivity

The model is relatively insensitive to most parameters. The sensitivity of the parameters is investigated using a normalised sensitivity that is derived from a power law relationship (Section 2.8). The relationship of PS and PL with their respective cell sizes (r_{PS} and r_{PL}) is approximately linear, as is the relationship of ζ_{EP} with EP (Table 5). The mortality and feeding

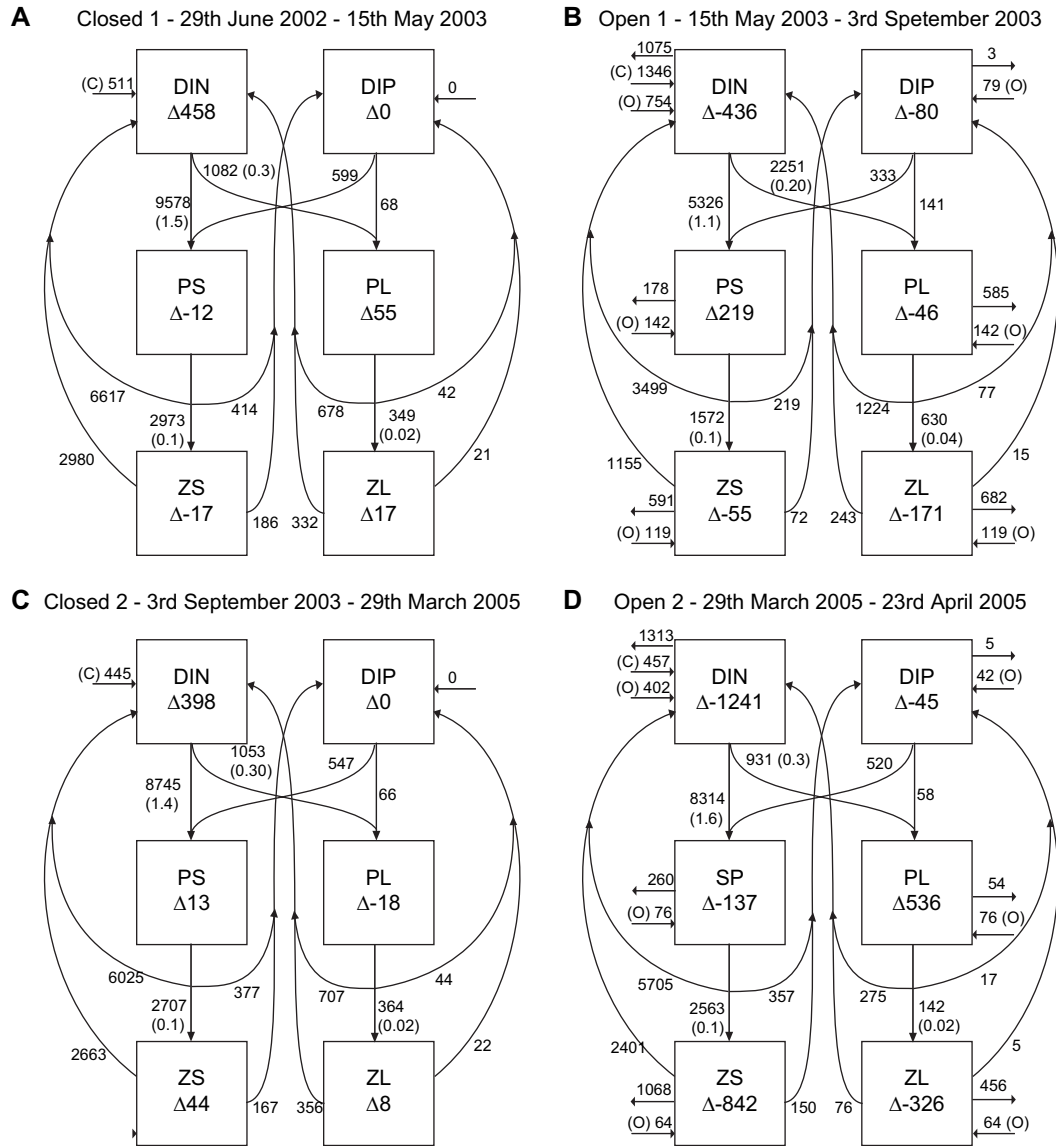


Fig. 5. Biogeochemical budget for water column properties of Smiths Lake. Each open/closed phase of the lake is shown individually. Arrows between boxes represent fluxes between state variables for the entire lake ($\text{mol N d}^{-1} \text{lake}^{-1}$ or $\text{mol P d}^{-1} \text{lake}^{-1}$). Input from the ocean (O)/catchment (C) and export to the ocean are represented by arrows out of, or into, the box. The values in brackets represent growth rate (d^{-1}). The delta values represent the sum of the water column processes for a particular state variable.

Table 4
Fraction of time during the open and closed phases that the growth of autotrophs is limited by nutrient uptake, light absorption or physiological processes

		N-limited	P-limited	Light limited	Maximum
Closed	PS	0	0.95	0	0.05
	PL	0	1	0	0
	EP	0	1	0	0
	SG	0.82	0	0.18	0
Open	PS	0	0.84	0	0.16
	PL	0	0.98	0	0.02
	EP	0	1.0	0	0
	SG	0.82	0	0.18	0

Table 5
Results of the sensitivity analysis where each parameter was varied by $\pm 10\%$. The results indicate the normalised sensitivity of the state variable to a change to the corresponding parameter. Only the most sensitive parameters to PS, PL, ZS, ZL, EP and SG are shown

	PS	PL	ZS	ZL	EP	SG
r_{PS}	-1.03	-0.82	0.86	-1.08	-0.55	0
r_{PL}	-0.92	1.03	-0.78	1.10	-0.38	0
ζ_{ZS}	1.64	-0.65	0.22	-0.83	-0.44	0
ζ_{ZL}	-0.81	1.53	-0.58	0.34	-0.19	0
ζ_{EP}	0.01	0.01	0.01	0.01	-1.02	0
ζ_{SG}	0	0	0	0	0	0.43
β_{ZS}	-1.66	0.45	-0.13	0.85	0.53	0
β_{ZL}	0.70	-1.55	0.51	-0.17	0.27	0

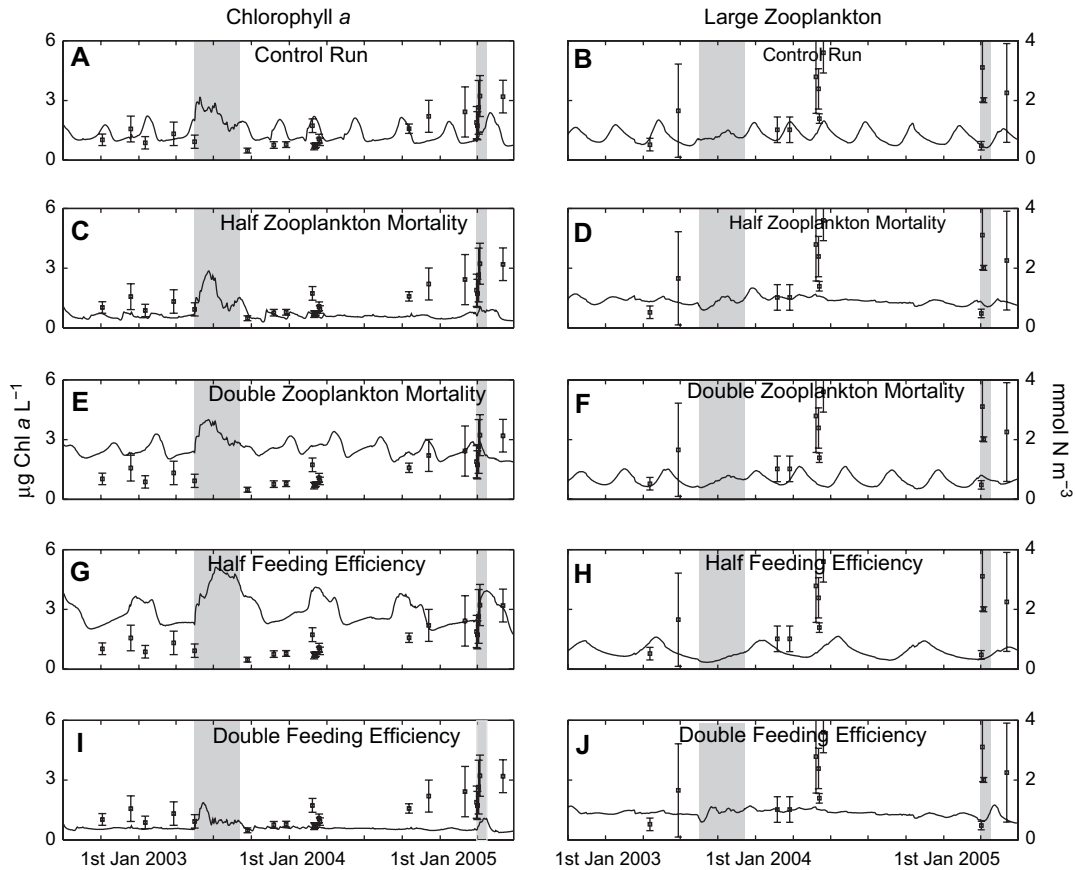


Fig. 6. Comparison of the effect of large (halving and doubling) changes in the most sensitive parameters. The left column is the volume-weighted spatial mean of chlorophyll *a* ($\mu\text{g chl } a \text{ L}^{-1}$) and the right column is the volume-weighted mean of large zooplankton (mmol N m^{-3}). The grey symbols are field data described in Fig. 5. Panels A and B represent the control runs, C–F represent changes in zooplankton mortality and G–J represent changes in zooplankton feeding efficiency.

efficiency of ZS and ZL are the most sensitive parameters with nearer to a quadratic relationship with the biomass of PS and PL, respectively.

The impact of varying the four most sensitive parameters (ζ_{ZS} , ζ_{ZL} , β_{ZS} and β_{ZL}) was investigated by halving and doubling the parameter value and observing the effect on the corresponding state variables (Fig. 6). No significant change occurs in the mean biomass of ZL, with a change in the four parameters resulting in varying changes in the amplitude of the ZL oscillation. The biomass of ZL remains within the range predicted by the field data. A much larger change occurs in chlorophyll *a*. When the mortality of zooplankton is halved (Fig. 6C), it results in a halving of the average chlorophyll *a* biomass. A doubling of the mortality (Fig. 6E) results in a doubling of the average biomass. A halving of the feeding efficiency (Fig. 6G) results in an increase in the biomass of chlorophyll *a*. A doubling of the feeding efficiency (Fig. 6I) lowered the average biomass and decreased the size of the oscillations.

4. Discussion

The model performed well when compared against field data. The model output is within the range of the field data for the majority of the simulation and shows a strong response

to the opening. Contrary to initial expectations, the model reaches a long-term quasi steady-state soon after closing. Immediately prior to the opening, there is an increase in DIN (first opening) and chlorophyll *a* (both openings), before a decline in concentration over the course of the open phase as they are flushed with lower concentration oceanic water. Benthic processes are able to assimilate the small loads entering the lake, resulting in Smiths Lake having low chlorophyll *a* throughout the open/closed cycle.

The model fails to capture the increased DIN and chlorophyll *a* at high lake levels (Fig. 4B,D). Increased DIN may be released at high lake levels from sediments not previously submerged, a process not captured in the model configuration. The results for DIN also show the difficulty in accurately capturing the non-limiting nutrient. The chlorophyll:nitrogen ratio within the model is fixed based upon phytoplankton cell size. Natural variations in the actual ratio or changes in phytoplankton cell size may account for some of the difference between the measured and modelled chlorophyll *a*. At high lake levels, as with DIN, nutrient release from the sediment may have allowed further growth in phytoplankton which was not captured by the model. Measured DIP is below the quantification limits of the nutrient autoanalyser for a large proportion of the time series. The values portrayed in Fig. 4 which are below the quantification limits

(marked with an *) could conceivably be lower, and hence, closer to the simulated values for DIP. Regardless, the values of DIP for both the observed and simulated data can be considered low.

4.1. Model budget

Comparing the first closed phase with the first open phase, there is an increase in the lake-wide primary production of PL from 1082 to 2251 mol N d⁻¹. The primary production of PS decreases from 9578 to 5326 mol N d⁻¹, a change of 44% (Fig. 5). Between the second closed and open phase, a decrease in primary production of PS occurs again (5%), along with a decrease in PL production (12%). The magnitude of the change in production is reduced as the second opening was only 3 weeks long with the salinity reaching just 24. Due to the shorter open phase, the ocean conditions do not exert such a strong influence on the lake properties, and tidal exchange is reduced (Fig. 2). Between the first closed and open phases, there is only a small change in the growth rate of phyto- and zooplankton (Fig. 5 – in brackets). The change in productivity is a result of the changing biomass of PS and PL. There is an increase in the productivity of phytoplankton and zooplankton during the open phase. This increased productivity is exported out of the lagoon with a net nitrogen export from water column variables of 489 and 2012 mol N d⁻¹ during the two studied openings (the sum of all outgoing and incoming nitrogen in Fig. 5B,D, respectively).

4.2. Growth limitation

Autotrophic growth is primarily limited by phosphorus and, to a lesser extent, the maximum growth rate (Table 4). Phosphorus availability is the dominant growth limiting factor in the model for phytoplankton and epiphytes. This is due not only to the less than Redfield water column nutrient ratios, but also to the different rates of diffusion for nitrogen and phosphorus. Mass transfer becomes important in determining nutrient uptake and growth in nutrient limited systems such as Smiths Lake. In more eutrophic systems, where nutrients are not limiting, molecular diffusion becomes less important (Sanford and Crawford, 2000). The use of physical limits to key ecological processes such as nutrient uptake and light capture seems justified in this application, with autotrophs spending the majority of their time at the physical limits of nutrient and light uptake, rather than the maximum growth rate.

4.3. Model sensitivity

The model is relatively insensitive to most parameters as evidenced by only four parameters having a normalised sensitivity of greater than 1.5. These parameters were the feeding efficiency (β_{ZS} and β_{ZL}) and the quadratic mortality (ζ_{ZS} and ζ_{ZL}) of small and large zooplankton, respectively. The closure term of an ecological model can significantly affect its dynamics, hence, in this model it is important to correctly capture zooplankton mortality (Edwards and Yool, 2000).

The choice of parameter values for mortality and feeding efficiency of zooplankton in the model is reasonable. A doubling and halving of each parameter gives model values that are on either side of the measured field values for chlorophyll *a* (Fig. 6). No significant change occurs in the model values for ZL. A halving of the feeding efficiency results in a large increase in the chlorophyll *a* biomass due to an increase in the nutrients which are released directly back into the water column. A doubling of the efficiency does not elicit such a large response in chlorophyll *a*, however, it does shorten the length of the predator–prey oscillations substantially (not shown) because ZL reaches its maximum biomass more quickly. There is a relatively large degree of uncertainty surrounding the parameter values for feeding efficiency, however, the values chosen in this study were extracted from a compilation of 27 field studies on 33 different species (Hansen et al., 1997).

4.4. Biomechanical descriptions

The ecological model is similar to Baird et al. (2003), however, some key changes were made, primarily related to the benthic component of the model. A seagrass-specific C:N:P ratio of 474:21:1 (Duarte, 1990) was used for seagrass as opposed to a more generalised one for macroalgae 550:30:1 (Atkinson and Smith, 1983) which has been used in ecological models (Murray and Parslow, 1999; Baird et al., 2003). This has the effect of the seagrass requiring less nitrogen and more phosphorus per mole of carbon. Seagrass are also able to extract nutrients from both the water column and the sediment, which further enhances their growth ability. An effect of this seagrass-specific ratio is that seagrass require more light per mole of nitrogen, than the more generalised macroalgae ratio. Light limitation has only a small effect on the present simulations (Table 4) due to the low water column concentration of TSS and shallow depth of Smiths Lake. This, however, may become more important in scenarios with increased sediment loads from the catchment or with lake levels increased above the current maximum of 2.1 m. Another difference is that epiphytes are modelled as individual cells on top of the seagrass rather than a layer. While they absorb their nutrients through the same effective boundary layer as the seagrass, their cellular shape means they absorb light the same way phytoplankton cells do, as a function of their cell shape, pigment concentration and the average available light.

In conclusion, the model captures the important ecological dynamics of Smiths Lake with a fit of simulated data to the field data classified as good to very good (Moll, 2000). There is an increase in primary productivity during the open phase of the lake which is exported to the ocean. The increase in productivity is a result of a larger average biomass when the lake was open to the ocean. Phosphorus is the dominant limiting nutrient for phytoplankton and epiphytes. Nitrogen is the limiting nutrient for seagrass due to their ability to source nutrients from both the water column and sediment. Future work will involve manipulating forcings, such as maximum lake height, rate of lake level rise, opening times and

catchment loads to further assess parameter sensitivity and to consider the ecological impact of different opening regimes which may be imposed on ICOLLS by their managing authorities.

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