

The Port Phillip Bay Ecosystem Model

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Abstract Port Phillip Bay has been the subject of a major integrated study. One result of this study has been the development of ecosystem models. In this paper I will discuss some simple modelling, which demonstrates the role of internal processes (specifically denitrification) in the maintenance of the water quality in Port Phillip Bay. I will then summarise a detailed model which has been developed to describe the Port Phillip Bay ecosystem. The modelled ecosystem components are discussed under functional groups and then the model processes and their formulations are discussed. The performance of this model with respect to observations is discussed in another paper (Parslow and Murray 1997), here we will very briefly discuss the overall response of the model to increased nutrient loading and compare this response to that of the simple models.

1. INTRODUCTION

Port Phillip Bay is a large (1950 km²) semi-enclosed bay in the state of Victoria, south-east Australia. As the site of the city of Melbourne this bay is a major asset for transport, fisheries, recreation, conservation and sewage disposal. An integrated CSIRO managed study was commissioned by Melbourne Water in order to aid the management of these potentially conflicting activities (Harris et al. 1996). A major aspect of this study was the development of models of various processes in the bay and its catchment. In this paper I will discuss the ecosystem models developed for the Port Phillip Bay project (task G8/9). Results from the model, and their relationship with observations, are discussed here by Parslow and Murray (1997), and, elsewhere, by Murray and Parslow (1997).

2. SIMPLE MODELS

Simple models have proven to be very powerful tools in the investigation of ecosystem behaviour and useful in describing behaviours observed in more detailed model formulations.

The simplest model used to investigate Port Phillip Bay is the steady state budget. Using observed bay-wide nutrient concentration, the

concentration in oceanic Bass Strait waters and the estimated time for water to exchange with Bass Strait (1 year), we can obtain an estimate of export:

$$\text{Export} = (C_{\text{PPB}} - C_{\text{BS}}) \cdot \text{turnover_rate} \cdot \text{bay volume}$$

Using this relationship we estimate export of P and Si to be close to input loads. However N export is only about 1000 out of 7000 tonnes p.a. input, most of the export is in the form of dissolved organic nitrogen. This proves that a major loss of N is occurring in Port Phillip Bay. Although we cannot rule out some burial, high observed efficiencies of denitrification show that the major part of this loss is to denitrification.

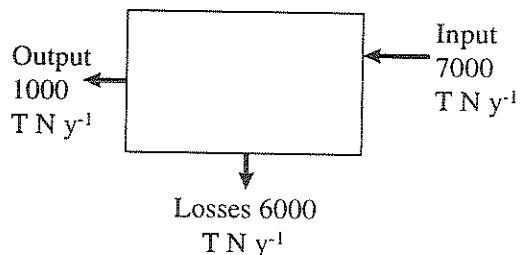


Figure 1. Overall nitrogen budget of Port Phillip Bay

Since there is very little accumulation of dissolved inorganic nitrogen (DIN) in the water-

column of Port Phillip Bay it follows that DIN is taken up shortly after it is produced, hence primary production must be close to DIN production. Primary production is equal to the external input (I) divided by the proportion of primary production that falls out of the water-column (f_w) and is denitrified (f_d):

$$PP = I / f_w \cdot f_d$$

Input is about 7000 tonnes y^{-1} , and primary production about 30000 tonnes y^{-1} , $f_w \cdot f_d$ therefore is 0.23. About half of primary production is recycled in the water-column ($f_w = 0.5$) so 46% of the material that falls out is denitrified.

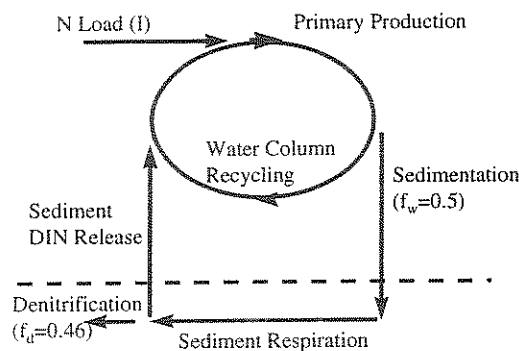


Figure 2. Fluxes of N determining total primary production.

Denitrification requires the existence of oxic and anoxic zones within the sediment in which nitrification and denitrification respectively can occur. As sediment respiration increases the oxic zones disappear and without nitrification denitrification cannot occur. A simple model of this is to make f_d a function of sediment respiration rate R such that

$$f_d = \max[D_{\max} (1 - R/R_0), 0]$$

where R_0 is the loading at which nitrification is completely suppressed and D_{\max} is the maximum denitrification efficiency. This decline in denitrification efficiency means that increased inputs lead to a disproportionate increase in production. Total denitrification is:

$$\text{total denitrification} = f_d \cdot R \cdot A$$

(where A is the area of the bay bed). The maximum amount of denitrification is obtained at $R = 0.5 R_0$, thus maximum denitrification is equal to $0.25 D_{\max} \cdot A \cdot R_0$. Once external load significantly exceeds the denitrification capacity, nitrogen accumulates in the bay until it reaches a state in which export to Bass Strait replaces denitrification as the major loss term and production is massively increased (Fig. 3). Since production is greatly increased per unit input, the

restoration of denitrification capacity requires a disproportionate decrease in loads.

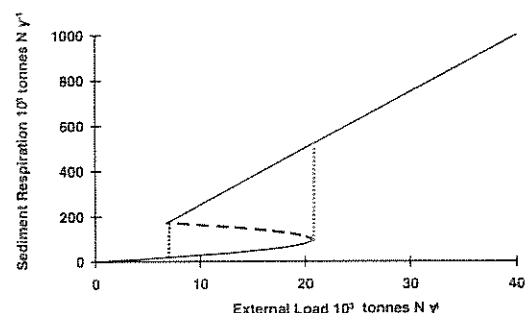


Figure 3. Responses of sediment respiration to changing external loads.

3. THE INTEGRATED MODEL STRUCTURE

Processes in Port Phillip Bay vary on a spatial basis. The model is therefore subdivided into 59 boxes. These 59 boxes are split into water-column, sediment and epibenthic components. Potentially the water-column and sediment layers could be vertically subdivided, but in most cases a single layer is used. Epibenthic components, macroalgae, seagrasses and filter-feeders, exist at the boundary between the water and the sediment. Interaction between these layers are handled by the P8 physical transport model (Walker and Sherwood 1997), with the exception of biologically mediated vertical exchanges, such as grazing by benthic filter-feeders on plankton.

External inputs of nutrients to the bay are also handled by the P8 model via runoff, atmospheric deposition and exchanges at the Bass Strait Boundary. The principal freshwater inputs modelled were the Western Treatment Plant (WTP) at Werribee and the Yarra River and Patterson River-Mordialloc Creek inputs (Sokolov 1996).

Model variables are mostly defined in terms of $mg N m^{-3}$ or $mg N m^{-2}$, nitrogen being the limiting nutrient over most of Port Phillip Bay. The model also explicitly includes Si in inorganic and detrital forms, DIP and O_2 . Si limits productivity in certain areas of the bay and its inclusion is necessary in order to obtain a match between model output and observations. P and O_2 were included as tracers of the model's

dynamics. Si in diatoms and P and C in all organic matter are also included implicitly at fixed Redfield ratio.

4. MODEL VARIABLES

The Port Phillip Bay model contains 16 state variables which are catalogued by functional groups below.

4.1 Primary Producers

The model contains five (or 6) categories of primary producers. The phytoplankton consist of two groups: small phytoplankton and large phytoplankton, the latter may be subdivided into diatoms and dinoflagellates but are by default considered as diatoms. Small phytoplankton require no Si and only low DIN concentrations but are generally controlled at low biomass by grazers. Large phytoplankton require higher nutrient concentrations, including Si, but are capable of escaping their grazers to form blooms. Benthic primary producers include microphytobenthic diatoms within the sediment, and seagrasses and macroalgae between the sediment and water (epibenthos). Seagrasses extract nutrients from the sediment, macroalgae adsorb nutrients from the water column.

Different primary producers predominate in different regions. Small phytoplankton are at their most important in offshore and southern regions of the bay, while large phytoplankton are commonest in northern parts of the bay, particularly in the vicinity of major input sources. In these regions they form moderately large blooms. Phytobenthos are restricted to the shallower parts of the bay, although microphytobenthos can grow throughout the bay in summer. Macroalgae are restricted to northern areas of the bay, where nutrient concentrations are high. Maximum biomasses are often at mid-depth (8 m), reflecting mechanical removal in shallow areas. Locally they contribute a large proportion of primary production and may be instrumental in keeping nutrients in coastal areas. Seagrasses are restricted to the southern bay and parts of Corio Bay. Locally they may contribute a significant proportion of the very low primary production in these areas.

4.2 Secondary Producers

The model contains two size classes of zooplankton, which graze on the corresponding size classes of phytoplankton, and epibenthic filter-feeders, which graze all forms of plankton (except large zooplankton) and on suspended labile detritus. Higher trophic levels are not included in the model, except implicitly as part of the zooplankton (or filter-feeder) mortality. Zooplankton are spatially associated with their prey phytoplankton, filter-feeders are commonest in shallow productive waters of the northern bay. High filter-feeder biomass may strip phytoplankton from the water-column of these regions.

4.3 Detrital Matter

The model contains three classes of non-living organic matter, labile detritus, refractory detritus and dissolved organic matter. The labile detrital pool consists of the organic matter which is used within the first few weeks of its production. Refractory organic matter is the component turning over in the course of about a year, this is important in seasonal and interannual dynamics. In Port Phillip Bay sediments a large amount of organic matter appears to persist over periods of at least decades; this material is not modelled since it has little effect on short to medium term dynamics, its importance at very long time scales is uncertain. The dynamics of dissolved organic matter (DOM) are unknown, but export represents a significant loss for N from Port Phillip Bay. We model a moderately refractory (seasonal) pool. The model does not explicitly include labile (rapidly remineralised) DOM, although this may be important to nutrient budgets. Instead such labile dissolved assumed to instantly remineralise to DIN.

4.4 Inorganic Nutrients and Oxygen

The model contains four inorganic nutrients and oxygen. The inorganic nutrients are ammonia, nitrate, silicate and phosphate. DIN usually limits phytoplankton production and so must be modelled. It is split into ammonia and nitrate because there are extensive data on concentration and inputs of both and because they have different dynamics and so can reveal aspects of

model behaviour. Silicate was modelled since its supply can limit diatom production particularly near the WTP. Phosphate was modelled, despite not being a limiting nutrient, the large amount of observation data meant that modelling phosphate was a useful diagnostic of model behaviour. Oxygen was also modelled to provide insight into model dynamics and did not directly change behaviour of other modelled pools (although the potential to include such effects, particularly in multilayer version of the model, is available).

Nutrients tend to be most concentrated in the northern bay close to the major inputs. This particularly applies to nitrate and to ammonia. Phosphate and silica are conservative so their decline towards the south is more gradual and reflects export patterns. Silicate also shows substantial temporal variation as does nitrate in the vicinity of sources.

5. MODEL PROCESSES

The model variables summarised in the previous section interact in ways defined by the model's equations. All rates are temperature sensitive and a Q_{10} of 2 is assumed.

5.1 Primary Production

Small amounts of organic matter are imported, and comparable amounts exported, but the vast majority of organic matter in Port Phillip Bay is locally produced and consumed. Primary production is constrained by the product of maximum growth rate, nutrient uptake, light, (in some cases) space, and biomass. For example macroalgal production is:

$$MA_{\text{growth}} = \mu_{MA} \cdot hN \cdot hI \cdot hS \cdot MA$$

Nutrient uptake is in the form:

$$hN = N / (K + N)$$

where N refers to nutrient concentration (ammonia + nitrate or silicate) and K is a half-saturation constant. Competition between DIN limitation and Si limitation (for diatoms) is in accordance with Liebig's law of the minimum:

$$hN = \min \left[\frac{DIN}{(K_{DIN} + DIN)}, \frac{Si}{(K_{Si} + Si)} \right]$$

Ammonia is taken up in preference to nitrate (see 5.4)

Light limitation is calculated as a rectilinear function of light (either water-column average for plankton or bottom light for other producers)

$$hI = \min [I/K_I, 1]$$

Light is determined at depth z by attenuation by the water itself and by chlorophyll, suspended detritus and DON in that water.

Finally space (and resultant self-shading) limit the maximum biomass of macroalgae and seagrasses to:

$$hS = 1 - MA/MA_{\text{max}}$$

or

$$1 - SG/SG_{\text{max}}$$

5.2 Secondary Production

Grazers capture prey organisms (or detritus) and turn ingested material into production. The grazing function used is based on a Holling type II response (rectangular hyperbola). For example grazing by small zooplankton on small phytoplankton is defined as:

$$ZS_{\text{grazePS}} = ZS \cdot PS \cdot C_{ZS} / (1 + PS \cdot C_{ZS} \cdot E_{ZS} / \text{mum}_{ZS})$$

where C_{ZS} is filtration rate, E_{ZS} is assimilation efficiency and mum_{ZS} is maximum growth rate. Grazing by large zooplankton and filter-feeders is complicated by the existence of several potential prey types, ingestion in these cases is in proportion to relative prey concentrations. Grazer growth is then found by multiplying the ingestion by growth efficiency, filter-feeders have a lower growth efficiency when feeding on detritus.

5.3 Mortality

Losses of water-column phytoplankton are explicitly defined by zooplankton or filter-feeder grazing. All other losses of biomass are defined implicitly by mortality functions. There are two main mortality functional description - linear and quadratic - and two special mortality function which apply to macroalgae and seagrasses.

Mortality can be a linear function of biomass, X , ($m \cdot X$) or it can be a quadratic function of biomass ($m \cdot X^2$). Quadratic mortality reflects rising mortality at higher biomass owing to increased populations of predators of X . In the case of zooplankton the choice of mortality function is (surprisingly) perhaps the single most important decision in model construction. Under

linear mortality, zooplankton biomass rises with phytoplankton production, allowing them to control the phytoplankton's population at a constant level regardless of nutrient inputs. Under quadratic mortality, zooplankton biomass rises with the square root of loading and so cannot keep pace with phytoplankton production, allowing phytoplankton biomass to rise. The quadratic form has been strongly recommended by Steele and Henderson (1981).

Due to the unrealistic effect on phytoplankton biomass of linear zooplankton mortality we have adopted the quadratic form for both forms of zooplankton and for benthic filter-feeders. We have also adopted this form for microphyto-benthos mortality to reflect increased predation at higher biomass. However, we do use linear mortality in some cases. Firstly when phytoplankton fall from the water-column to the sediment (large phytoplankton only) we allow them to die off at a constant rate. This mortality is due to environmental stress and so its rate is not dependent on biomass. Secondly, macroalgae and seagrasses have a linear mortality function. The quadratic mortality model would imply dense beds of these plants were heavily grazed which does not seem to be consistent with observations. Model stability problems are avoided by the maximum biomass limit for macrophytes discussed in 5.1.

Two special mortality terms are included in the model. Macroalgae are subjected to a loss rate proportional to bottom stress. There is also a loss rate proportional to water-column DIN concentration which causes mortality on seagrasses. This function represents the choking of seagrasses by epiphytes. These processes produce realistic distribution of macrophytes.

5.4 Detritus production and remineralisation

By far the largest proportion of primary production in Port Phillip Bay is supported by recycled nutrients. Modelling the underlying processes (including losses) is a critical part of the Port Phillip Bay model.

A constant fraction of unassimilated grazing and of zooplankton or filter-feeder mortality is turned into detritus (the remainder being released as inorganic nutrients). All non-grazing mortality on primary producers is released as detritus. All

detrital production is assumed to be labile detritus. Labile detritus breaks down at a fixed rate producing nutrients, refractory detritus and DOM. Refractory detritus breaks down to DOM and nutrients. DOM breaks down to form inorganic nutrients only.

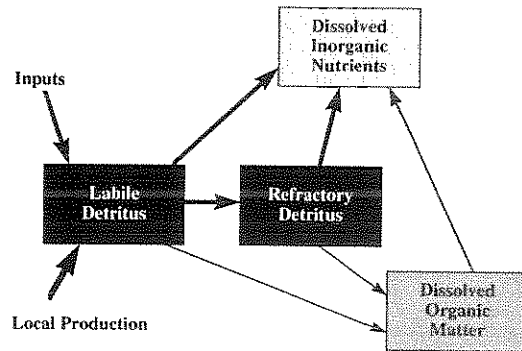


Figure 4. Breakdown pathways for detritus

In the water-column the inorganic nitrogen released from organic matter breakdown is in the form of ammonia. In the sediment inorganic nitrogen can be released as ammonia, nitrate, or it can be denitrified to N₂ gas. As discussed earlier denitrification efficiency depends on loading. In the model there are two processes, nitrification and denitrification.

$$\text{Nit_eff} = D_{\text{max}} (1 - R_{\text{net}} \cdot \Delta z / R_0)^+$$

$$\text{Den_eff} = \min(R_{\text{net}} \cdot \Delta z / R_D, 1)$$

$$\text{Nitrification} = R_{\text{net}} \cdot \text{Nit_eff}$$

$$\text{Denitrification} = \text{Nitrification} \cdot \text{Den_eff}$$

R_{net} is net remineralisation (ammonia production - MPB uptake) and Δz is model sediment layer thickness since R₀ and R_D are defined per unit area. The release of N₂ equals denitrification, ammonia release equals R_{net} - Nitrif and nitrate release Nitrification - Denitrification.

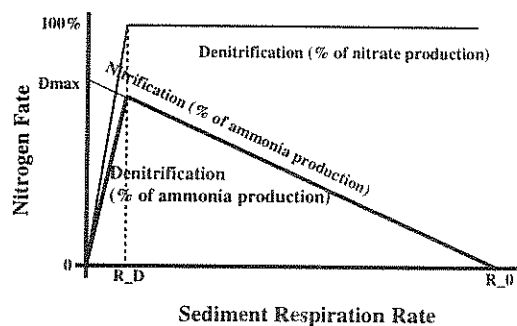


Figure 5. The denitrification model

Nutrient uptake is determined by primary production. Limiting nutrients determine growth rate, non-limiting nutrients (including P) are

taken up according to the Redfield Ratio. Uptake of ammonia and nitrate uptake interact and are respectively determined from total DIN uptake multiplied by:

$$\frac{NH}{(K+NH)} \cdot \frac{(K+DIN)}{DIN}$$

$$\frac{NO}{DIN} \cdot \frac{K}{(K+NH)}$$

This competition formula is based on one by Parker (1993).

6 MODEL RESULTS

The performance of the model with respect to observations is discussed in more detail by Parslow and Murray (1997). I will however briefly compare the response of the model to changes in loads with that of the simplified model discussed earlier.

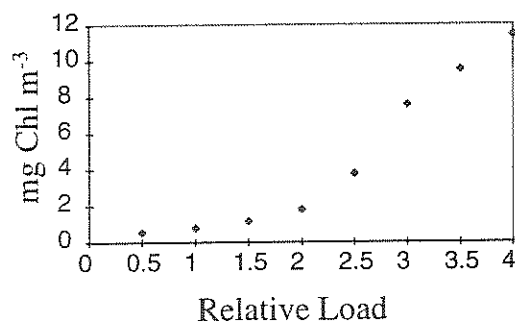


Figure 6. Mean chlorophyll concentrations at given nutrient input loads relative to current load.

The response of chlorophyll to changed loads has been investigated by multiplying the four principle nutrient sources (WTP, Yarra, Patterson and Mordialloc) by factors of from 0.5 to 4. For loadings of less than 2 times the current load increase in chlorophyll with load is slow and chlorophyll concentrations are low. However, for loads between 2 and 3 times current levels there is a rapid increase in chlorophyll as the bay's denitrification capacity is reached.

The response differs from the simple model in that, although deterioration is rapid, it is not instantaneous, and denitrification continues to occur in less productive areas, particularly in the southern bay. These regions of effective denitrification will expand if loading is reduced, thus the bay can recover in time; the simple model allows for no such recovery. Due to the destruction of benthic communities in the anoxia associate with high loadings it is probable that recovery would be slow. More seriously, the model denitrification capacity is exhausted at a

significantly lower level than simple modelling predicted (15000 as opposed to 22000 tonnes N y⁻¹). This is because denitrification capacity in the bay centre is exhausted while capacity remains in other regions, particularly the Sands, So A is less than the total bay area.

These results demonstrate the complimentary roles of simple and detailed modelling. The simple model demonstrates clearly the mechanism underlying the predicted response of Port Phillip Bay to increased loading, while the detailed model shows the important role of spatial variation in modifying the overall response of the system. The detailed model also allows investigation of spatial variation and of temporal responses to perturbation events, but time does not allow any exploration of these issues here.

ACKNOWLEDGEMENTS

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