Bubbles

The Nutrient, Phytoplankton, Zooplankton and Fish Recruitment (NPZ-F) Numerical Model

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From The Englishman Thomas Anderson, 2005

“Biogeochemical cycling in marine systems is intimately linked to the activity of specific plankton functional types (PFTs) such as diatoms, coccolithophores and nitrogen fixers, thereby providing a focus for contemporary modelling studies. Incorporating extra complexity beyond simple nutrient-phytoplankton-zooplankton-detritus (NPZD) models is, however, fraught with difficulties: poorly understood ecology; lack of data; aggregating diversity within functional groups into meaningful state variables and constants; sensitivity of output to the parameterizations in question and their physical and chemical environment. Although regional models addressing the seasonal succession of plankton types have achieved some degree of success, predicted distributions of PFTs in global biogeochemical models have thus far been less than convincing. While the continued articulation of detail in ecosystem models is surely the way forward, I argue that this can only be so with due care and attention to the formulations employed and a healthy dose of scepticism regarding model outcomes. Future directions should emphasize building up complexity gradually, objective assessment of the resulting parameterizations, and variety in approach such as the use of empirical alternatives to the fully dynamic representation of PFTs in models”.

“… there’s no harm in trying” Kerry Black, 2015

Cover photo

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Citation

Executive Summary

Nutrient dynamics in Port Phillip Bay

The input of nutrients to Port Phillip Bay (PPB) is fundamental to the bay’s productivity, for example by supporting economically and socially important fisheries through the pelagic food chain. Nutrients entering the bay are rapidly taken up by phytoplankton, which are in turn grazed by zooplankton that is the critical food for young fish. Fish recruitment has been shown to depend on the type of zooplankton food available to larvae that is in turn likely to be related to levels nutrient inputs and the consequent composition of the phytoplankton. Ungrazed phytoplankton and zooplankton faeces sink to the bottom where excess nutrients are taken up by denitrifying bacteria that subsequently release Nitrogen gas back to the atmosphere.

Thus, when nutrient levels coming from the catchment and sewage treatment are low, ecological processes such as fish productivity may be inhibited, or conversely, if high, there exists the possibility of eutrophication resulting in excessive algal growth leading to negative consequences for ecological processes such as nutrient cycling and biological production. Most sewage discharge of nutrients into PPB is through the Western Treatment Plant (WTP). So far, regulators of nutrient inputs to the bay have focussed on the potential negative consequences of too many nutrients entering the bay, and, apart from modifying WTP discharge locations to support migratory waders within the intertidal zone, have largely ignored the negative impacts of too few nutrients inhibiting productivity in the broader bay. There is a need to look at the ecological benefits of nutrient discharge beyond the intertidal to a consideration of the broader bay and provide for a more optimal balance with regards to environmental management.

New modelling Platform

The transformation of nutrients through phytoplankton to zooplankton and finally to fish is a complex ecological pathway that requires sophisticated modelling techniques to understand and allow for simulations and predictions. Hydrodynamic models of Port Phillip Bay simulating complex 3-dimensional current patterns, as well as dispersal of material such as nutrients, toxicants, and sediments have been established, verified and applied in PPB over 30 years. However, modelling the ecological process of nutrient take up by biota is more complex and has only recently been addressed. Traditionally, this type of modelling has been based on a Nutrient-Phytoplankton-Zooplankton (NPZ) approach where the NPZ components are each treated as a single homogeneous group, with the modelling driven by underlying equations that have parameters that are largely set by trial and error in the calibration process. This approach means that while these models may adequately describe specific data sets retrospectively, they can’t otherwise be more universally applied, or applied independently based on site specific data sets to make predictions. Traditional NPZ models are relatively crude in their description of the intrinsic biological characteristics of the ecosystem. This report presents a new modelling platform to simulate this type of data that is much more general and informative on multiple phytoplankton and zooplankton types that exist in the studied environment, and gives a more precise specification of the movement of material (nutrients, phytoplankton, zooplankton) through space and time.
Bubbles modelling and benefits

This report presents the description of the single particle model called “Bubble” and the full spatial model called “Bubbles”. Here, the methods, equations and coefficients which underpin the models are presented and tested against data and are based on biological characteristics of phytoplankton and zooplankton.

These models are coupled to the comprehensive 3-dimensional hydrodynamic models that have been calibrated and applied over decades. A major innovation was that rather than the simulation occurring on a fixed grid where materials are transferred between adjacent modelling “cells”, in “Bubbles” the complex transformations (nutrients, phytoplankton etc) occur in packages (bubbles) that are moved through space based on the advection due to currents (coming from a full-3D ocean/atmosphere hydrodynamic model which has been calibrated for PPB) and which now incorporates novel treatment of the utilisation, mixing and recycling of nutrients, phytoplankton and zooplankton. This Lagrangian methodology gives better positional control and higher resolution than traditional Eulerian (grid-based) methods, with fewer numerical errors and much higher resolution.

A further innovation in the modelling was the use of plankton functional types (PFTs) that allow the model to simulate multiple phytoplankton types (e.g. diatoms, flagellates, dinoflagellate species) primarily on the basis of cell volume. This is because the life cycle processes are mostly based on volume, i.e. growth, half saturation coefficient, fall velocity, nitrogen content, cells per litre etc. For the zooplankton, methods were developed to allow more realistic representation of daily growth, nitrogen uptake and egg production. Thus, the modelling was much more realistic, incorporating significant biological complexity, compared with traditional NPZ type models. There is an opportunity to further fine-tune the model predictions by systematically considering interactions between multiple critical functional groups.

Finally, the model was developed with minimal coefficients that rely on unknown empirical coefficients that are not related to measured biological responses. This was achieved using the PFT approach where the trial and error setting of coefficients by the operator was largely eliminated. This means that the model will run with minimal “trial and error” setting of the coefficients during calibration, and greatly reduces the non-unique nature of the solutions, that are short-comings of traditional models. Overall, this greatly increases confidence that results are not just simply driven subjectively by the model operator.

The model has the potential to be extended beyond the pelagic ecosystem to include benthic processes such as cover and growth of seagrass habitat. Major processes controlling seagrass cover and growth can be simulated in the model, including wave exposure, light (as a function of sediment movement and associated turbidity) and nutrient input. Results of comprehensive field studies on seagrass interactions with nutrients that have been recently carried out in Port Phillip Bay could be used to inform model development.

Comparison of the new model with data

Testing the model against existing field data showed a high degree of accuracy in representing the basic processes linking nutrients to phytoplankton, zooplankton and fish. Comparison of the model output of phytoplankton concentration against fluorescence data (an index of chlorophyll a pigment
that is in turn proportional to phytoplankton concentration) showed a very good representation of
the mean levels and longer term fluctuations in the field data at three sites, Hobsons Bay, Long Reef
and Central Bay. Some short-term variability at the scale of a few days in the field data was not
represented in the model output. This may be an issue related to collection of the field data (i.e the
peaks may be anomalous) or the model may need further refinement to represent these very short-
term fluctuations.

The model prediction of zooplankton was based on the characteristics of the most common species,
the copepod *Paracalanus*. The model predicted the field concentrations of *Paracalanus* for the
north-eastern area of the bay over 5 years extremely well, with 94% of the variation in *Paracalanus*
abundance amongst years explained. The predicted abundance of *Paracalanus* was found to be
sensitive to the ratio of flagellate to diatom phytoplankton that was in turn sensitive to levels of
nutrients.

The zooplankton *Paracalanus* is the preferred food of larval snapper, the most important
commercial and recreational fish species in the bay. The abundance of young snapper over 7 years
was predicted based on the modelled *Paracalanus* concentrations. In this case, 90% of the variation
in recruitment of young snapper based on a fishery independent survey was explained by modelled
zooplankton concentrations.

**Conclusions from modelling and benefits**

The modelling indicated that snapper recruitment (and therefore numbers of fish entering the
population) increased with increasing nutrient levels, but there was a threshold at very high flows
and nutrient input where diatoms dominated the phytoplankton (high diatom/flagellate ratio)
reducing the survival of *Paracalanus* and consequently affecting snapper recruitment. Thus, except
at high levels, increased inputs of nutrients are likely to be beneficial to fish production in Port Phillip
Bay. Diatoms require silicate to form their external structure, but flagellates do not. The potential for
diatoms to dominate the phytoplankton may be greater in the north-east of the bay because silicate
levels are higher and less likely to limit diatom growth. Further field data on diatom/flagellate ratios
and silicate limitation would be useful for verifying and improving the accuracy of the model.

Overall, the model is potentially a very powerful tool for testing the effect of different levels of
nutrient input on the phytoplankton and zooplankton communities, and also on fish recruitment and
productivity. The model could be further extended to include other ecological components such as
seagrass and provide for more integration of impacts and benefits. Seagrass distribution could be
modelled in relation to wave exposure, light climate and nutrient availability mediated by
phytoplankton dispersal.
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Chapter 1  
Introduction

A Nutrient, Phytoplankton and Zooplankton model is described. The model was developed to examine fish recruitment in response to primary production, and to determine if discharged nutrients can be more beneficially used in bays, estuaries and lakes. With the focus here on Port Phillip Bay (south-eastern Australia), the general model is carefully crafted to be representative of the processes and species found there.

Firstly we describe the “single cell” model called “Bubble”, which neglects diffusion and advection. The model treats nutrients, phytoplankton, zooplankton and considers aspects of fish recruitment (NPZ-F). We then describe the translation of “Bubble” to the full spatial model called “Bubbles”, which includes diffusion and advection over the entire Bay.

1.1  NPZ Modelling

Computer models help us to understand complex processes when the simulation’s “evolutionary genetics” blend the best current knowledge. The modeller writing the code undertakes numerous comparisons with data, which may lead to extinction of some options and re-selection of other equations, coefficients etc. to get the best match. As such, the model code becomes an interesting hypothesis-testing “organism”, which is subject to evolution during testing. And the modeller may gain insights which may not arise from field testing of single hypotheses.

However, Nutrient Phytoplankton Zooplankton (NPZ) models have a troublesome history because there are many unknown empirical coefficients which must be adjusted to fit the calibration data. Historically, there has been a relatively consistent use of similar equations and coefficients in the various models, albeit within a coefficient range that some might assume is more mathematical than biological. Indeed, in complex models with many empirical coefficients, adjustments of these input coefficients can lead to frustration and a deep belief that the model is simply reproducing the whims of the modeller. Examples include adjustments outside the normal range of the Michaelis-Menten half saturation and growth constants for phytoplankton, but then compensating for the offsets by calibrating the mortality coefficients or the growth rates of grazing zooplankton.

Algal blooms always involve multiple species or species that may thrive best in high nutrient conditions while others fail. There are challenges with phytoplankton and zooplankton “edibility”, rafting, sinking, mucus excretion, nutrient uptake, growth, egg production, N:C and Chl:C ratios and other chemical issues that thread through the scientific literature. And the interactions are often assumed to be site specific, varying from bay to bay and varying also within any bay from low nitrogen open water sites to the high nitrogen entrances of major discharges. Such modelling is difficult as there may be no unique answer. Accordingly, those who believe that eco-systems are complex, interactive and essentially difficult to predict will have the same belief about computer models of eco-systems and primary production.
Black’s NPZ modelling started with a classical system of equations to examine impacts of mussel farms (Longdill et al. 2006), water quality in Port Phillip Bay (Lee and Black 2008) and several other cases. While good calibrations were obtained, the numerous uncertainties (unlike the more mathematical modelling of waves, currents etc.) were troublesome, and the Black sought to develop a model that had fewer unknowns. As a mathematical physicist, he has a belief that better use of the existing empirical and theoretical knowledge should lead to a self-determining model, rather than a helpful tool (Franks 2002).

Thus, one key goal for the model presented here was to minimise the unknowns, i.e. the model should simply run by itself with very few adjustable coefficients, thereby overcoming (1) the reliance on “trial and error” setting of the coefficients during calibration and (2) the non-unique nature of the solutions.

Another common problem confronted by the numerical modeller is the treatment of advection and diffusion in the numerical schemes. The historical dispersal models have generally utilised fixed grid (“Eulerian”) hydrodynamic models of currents (to determine the advection pathways) with linked Eulerian advection/diffusion modelling of passive tracers. Since the mid-1980s the Black has favoured the alternative Lagrangian approach, which bases the transport scheme on the dynamics of numerous “particles” (Black et al. 1993). Each particle is similar to a small volume of fluid (or “Bubble”) which follows flow streamlines. However for large grids, a Lagrangian particle solution requires considerable computer power. We overcome this by utilising the modern Graphics Processor Units (GPUs) which are now common for complex gaming programmes. The Tesla™ GPUs can have over 400 processors, allowing the model to function with numerous species simultaneously.

1.2 Diatoms and flagellates

Silicon is one of the most abundant elements as a majority of the igneous and sedimentary rocks are made of silicate minerals. Silicon is essential for the growth of diatoms which account for about three quarters of the primary production in coastal and nutrient replete areas of the world’s oceans. There is a close coupling of silicon and carbon in global biogeochemical cycling, with diatoms primarily absorbing silicic acid from the sea (Si(OH))₄. Thus, efforts to understand the marine carbon cycle must also consider the silicon nutrient cycle.

The diatoms are common in areas that are important for fisheries production such as bays, estuaries and upwelling zones (Uye et al. 1999, Reynolds 2006, Litchman et al. 2007). However, measures of primary production may not be reliable predictors of fisheries production and dynamics (Friedland et al. 2012). Numerous studies have now shown that high ingestion rates of diatoms can inhibit copepod egg viability, survival of nauplii and overall reproductive success (Poulet et al. 1994, 2007, Ianora et al. 1996, 2003, Lee et al. 1999, Miralto et al. 1999, 2003, Paffenhöfer 2002, Paffenhöfer et al. 2005, Vargas et al. 2006, Diekmann et al. 2009, Ianora and Miralto 2010, Lauritano et al. 2012). Moreover, flagellates have been suggested to play a key nutritional role for copepods (Kleppel et al. 1991, Ianora and Poulet 1993, Nejshtgaard et al. 2001, Bollens and Penry 2003, Miralto et al. 2003). Therefore, the abundance of flagellates relative to diatoms (i.e. the diatom:flagellate ratio \( R_d \)) is
likely to be a critical factor in explaining the variable relationship between nutrient enrichment, nutrient transfer across trophic levels and ‘bottom-up’ effects in pelagic food webs and fishery recruitment (Murphy et al. 2013).

In Port Phillip Bay (southern Australia), there are periods when diatoms may constitute as much as 95% of the algae present in the water column. Moreover, there are variations in the ratio $R_d$ at time scales of a few weeks to months.

Thus, in developing the code presented here, the model must have capability to simulate the special conditions when flagellates can prosper ahead of diatoms and so questions arise about what distinguishing characteristics lead to observed variations in the relative concentrations of algal species. Flagellates are thought to have a competitive advantage over diatoms in conditions of lower macro-nutrient (i.e. nitrate, phosphate, silicate) concentrations because they are non-chain forming, sometimes of smaller size, and better adapted to growth under low nutrient conditions (Eppley et al. 1969, Aksnes and Egge 1991). The advantage of smaller cell size at lower nutrient levels is, in part, because the half-saturation constant for nitrate uptake decreases with decreasing mean cell diameter (bigger cells have a higher $k_s$ and thus a lower nitrate uptake rate) (Aksnes and Egge 1991, Litchman et al. 2007). Consequently, larger phytoplankton species such as many diatoms do poorly when nitrate is limiting but may dominate under higher nutrient conditions. In addition, the flagellates have a higher carbon and nitrogen content than diatoms of the same volume (due to the Si in diatoms) (Strathman, 1967). This may influence the nitrogen uptake rates to give diatoms an advantage.

On the contrary, flagellates consist of a mixture of autotrophic, heterotrophic and mixotrophic taxa, and therefore do not rely solely on photosynthesis and nutrient absorption for growth and reproduction (Reynolds 2006). In addition, diatoms require silicon, which becomes limited when concentrations are below approximately 2 $\mu$M (Egge and Aksnes 1992, Diekmann et al. 2009). Thus, the growth isolines may lead to resource/nutrient ratios that favour diatoms and flagellates under different concentrations of silicate and nitrate. Finally, diatoms do not possess flagella to keep them up in the water column and the cells can be sticky or they can exude sticky transparent exopolymer particles (TEP) which can lead to mass flocculation of diatoms and rapid sinking out of the euphotic zone during blooms (Passow et al. 1994, Sarthou et al. 2005). Other processes such as microturbulence, turbidity/sheltering influences on light availability, differential temperature effects on growth, and selective grazing by zooplankton may also influence the diatom:flagellate ratio (Levasseur et al. 1984, Bell 2002, Duarte et al. 2003).

Given the multiple factors that can influence the competitive ability of flagellates relative to diatoms, predicting the diatom:flagellate ratio of phytoplankton assemblages is challenging and requires development of sufficiently complex models that can deal with multiple phytoplankton types that have different eco-physiological traits and responses to environmental variability (Litchman et al. 2007). Models that do not consider multiple types of phytoplankton with different roles in nutrient transfer to higher trophic levels will likely perform poorly in predicting mesozooplankton production. The use of “plankton functional types” (PFT’s), which cluster species based on size or other biologically/eco-physiologically important traits can facilitate modelling efforts by allowing biological complexity to be added using more general empirical relationships.
describing relevant physiological and life-history parameters (Anderson 2005). Plankton volume is shown below to be a primary distinguishing characteristic (Maranon et al. 2013).

1.3 Secondary Production

Port Phillip Bay in south-east Australia is a large, semi-enclosed, temperate, marine-dominated bay that supports important commercial and recreational fisheries and shellfish aquaculture (Harris and Crossland 1999). Understanding the processes influencing larval survival within Port Phillip Bay is clearly critical to understanding and predicting the dynamics of the fishery. Snapper (Chrysophrys auratus) is one of the valuable recreational and commercial fish (Coutin et al. 2003) and the Bay is a primary spawning and nursery habitat for snapper stock with a range that extends in coastal waters at least 1000 km from the entrance of the Bay (Hamer et al. 2011).

Annual surveys within the bay show considerable inter-annual variation in the success of recruiting fish (i.e. 0-age) which is closely correlated with the abundance of larval stages sampled several months prior (Murphy et al. 2013). This high recruitment variation, stemming from processes influencing larval survival, is a primary driver of fishery production dynamics. Recent studies of snapper larval feeding, growth and recruitment patterns suggest that food availability, which varies both inter-annually and spatially in the bay, plays a key role in influencing recruitment variation (Murphy et al. 2012). While snapper larvae can eat a variety of zooplankton taxa in Port Phillip Bay, their preferred prey are calanoid nauplii (Paracalanus spp. and Acartia spp.), and calanoid copepodites (Paracalanus spp., Gladioferens inermis, Bestiola similis) (Murphy et al. 2012). Field surveys conducted at the time when snapper larvae are prevalent in the bay (late November-January) have indicated significant inter-annual variation in abundance of Paracalanus spp. (Murphy et al. 2012). The causes of the variations in zooplankton abundance were not considered by Murphy et al. (2012). However, Murphy et al. (2012) showed that low zooplankton densities corresponded with generalist diet and lower snapper larval abundance years. Snapper survival and juvenile recruitment strength was shown to be linked to changes in larval diet that, in turn, related to prey abundance and composition. Studies of snapper larval dynamics in other large bays, i.e. Hauraki Gulf, New Zealand, have also led to the hypothesis that physical-chemical processes influencing zooplankton prey availability are the key drivers of recruitment variation (Zeldis et al. 2005).


Much of Port Phillip Bay’s shoreline is surrounded by the greater metropolitan area of the city of Melbourne (> 4 million people) and its associated industries. The major river flow/nutrient inputs to the Bay are the Yarra River and Melbourne’s Sewage Treatment Plant, the Western Treatment Plant
Variations in the relative responses and competitive advantages of diatoms and flagellates to different levels of nutrient inputs, in turn result in a complex non-linear relationship between river and sewage discharges, and production of copepods. To understand the fish recruitment, the model must go beyond NPZ to include fish dependence on zooplankton.

1.4 Beneficial Use of Nutrients

Nutrients can have both positive and negative effects on marine systems. They underpin all primary production and thereby underpin life in the sea. But excess nutrients can lead to eutrophication and harmful algal blooms (including toxic algae). Such blooms can lead to ecosystem changes through shading and de-oxygenation leading to effects on biota as well as nutrient cycling processes. Thus, governments have introduced legislation and tight controls to limit the total nutrient discharges from rivers and other discharges like sewage farms. For example, the WTP discharges to Port Phillip Bay and large studies have been undertaken to set nutrient (nitrogen) discharge limits (Harris et al. 1996). WTP currently discharges at the shoreline which is listed under the Ramsar convention in part because many birds benefit from the rich benthic food source that grows with nitrogen enhancement. Indeed, bird conservationists oppose any reduction in nutrient discharges, while government agencies are reluctant to allow any increases without scientific evidence of benefits outweighing disadvantages.

In contrast to this, land farmers have been adding nutrients such as phosphate to improve productivity for many years. Studies in PPB have shown that internal nutrient concentrations are highly variable spatially with low concentrations in the central Bay and around the ocean entrance. Noting that nutrients underpin the commercial fisheries from the bottom-up, one goal of the modelling is to assess whether the level and timing of WTP discharges could be modified to enhance fish stocks in the Bay.

1.5 General goals

The broad aims of the present study are:

- to refine existing NPZ models by developing a PFT-based numerical model of plankton dynamics in relation to nutrient input and grazing, with minimal “unknown” coefficients;
- to evaluate the influence of nutrients on phytoplankton production and variations in the diatom to flagellate ratio;
- to predict how changes in nutrient inputs delivered by the Bay’s major river and sewage discharge affects the dynamics and composition of phytoplankton prey for developing copepods and snapper recruits, by incorporating a coupled fish recruitment module into the model; and
• to form the basis of further studies to enable better utilisation of the nutrient inputs to the Bay for fish population enhancement while re-examining previous studies that set limits of acceptable nitrogen inputs to the Bay from the WTP.

Chapters 2-5 present the description of the Primary Production particle model called “Bubble”. Here, the methods, equations and coefficients which underpin the model are presented and tested against data. The model is a comprehensive test platform for equation and coefficient selection. While the specific goal of these chapters is to present the modelling methods, the fast model Bubble also provides insights into NPZ dynamics in general and within PPB. Chapter 6 then presents the translation of this model the model “Bubbles” that includes fine-scale advection and diffusion throughout Port Phillip Bay.
Chapter 2  Description of the Model

2.1 Overview

Some 10 years ago, the primary production coupled modelling system known as 3DDLife (Longdill et al. 2006) was coded and developed by Black using Eulerian gridded solutions for the advection/diffusion. Next, the Model “Bubbles” was developed to utilise a more sophisticated Lagrangian particle solution which unified more recent plankton/fish research in the code. Finally, the simpler model Bubble was introduced to allow more rapid tests of the methods adopted within the critical NPZ-F sections of the computer code. Bubble was then found to provide many insights and was transformed from a background testing platform to a working model. The improvements in Bubble are regularly transferred back to the spatial model Bubbles.

Like most planktonic production models, “Bubbles” and “3DDLife” are coupled to other simulations, including the 3-dimensional hydrodynamic Model 3DD (Black et al. 1993, Black 1995, Jenkins et al. 1997, 2000, Harrison et al. 2007 a,b,c). In full 3-dimensional mode, Model 3DD provides sea levels and currents (for the advection and diffusion of matter) and salinity and temperature variations (for determination of plankton life variables such as growth rates, mortality etc. as a function of depth below the sea surface). These coupled models come from Black’s commercial “3DD Suite of Marine Physical Process Models” which can also provide several other inputs, e.g. horizontal circulation due to waves, wave-induced sea surface turbulence, sediment transport resuspending toxins, nutrients or muds/sands etc.. The linked models are separately operated and calibrated, while their output is written to binary computer files to be utilised by the other coupled models in the Suite.

The simpler model “Bubble” contains all the NPZ-F functions of Bubbles but neglects the advection and diffusion terms. In Bubble, discharges enter a single cell, where all matter entering the cell is instantaneously well mixed throughout the cell, both horizontally and vertically. Such matter can be freshwater, nutrients, algae, zooplankton or any other material of interest. The model calculates the temporal variation of all matter within the cell, with the known inputs/outputs from the cell determining the boundary conditions. Inputs could be a river discharge and outputs could be N₂ losses to the atmosphere, for example.

The primary state variables are nitrogen (nitrite, nitrate and ammonium), silicon (silicate) and phosphorus (phosphate). In the model, chemical mass is transferred between the water column, seabed, phytoplankton and zooplankton. As the model proceeds, Bubble monitors total chemical mass within the model domain by checking that all chemicals are conserved, after accounting for new inputs and losses from the cell.

The model equations come from laboratory and field investigations, and some are newly-developed here. The model uses empirical functions for many coefficients which virtually eliminates the need for “trial and error” calibration. For example, zooplankton egg production, zooplankton and phytoplankton growth, half saturation coefficient for nutrient uptake etc. are determined using empirical relationships developed in this report from published field and laboratory studies.
However, as noted by Anderson (2005):

“Incorporating extra complexity beyond simple nutrient-phytoplankton-zooplankton-detritus (NPZD) models is fraught with difficulties: poorly understood ecology; lack of data; aggregating diversity within functional groups into meaningful state variables and constants; sensitivity of output to the parameterizations in question and their physical and chemical environment.”

While the model Bubble treats numerous processes, some approximations are made. The model distributes total N for re-cycling by phytoplankton and zooplankton. Of course, there are other species recycling nutrients and so care must be taken with missing species; an example may be jellyfish or mussels which can uptake substantial plankton when their numbers are large (Longdill et al. 2006). Notably, the N within higher trophic levels in PPB is much less than the total N in the water column and seabed (dissolved and detrital) and held within the primary producers (Harris et al. 1996; Longmore and Nicholson 2012).

As well as the phytoplankton, there are myriad bacteria associated with dissolved organic carbon (DOC), and these are consumed by micro-zooplankton, sometimes referred to as the microbial loop (Azam et al. 1983, Fenchel 2008). The bacteria assimilate N and then become a food source which is incorporated into the model through growth of the phytoplankton and zooplankton. By back-calculating the N requirements, the N is conserved in the model, and the actual food production mechanisms may be neglected, although future studies may argue for a more specific treatment.

At the seabed, the model reduces the complexity to two coefficients (fraction of nutrients returned to the water column and fraction to the atmosphere), rather than dealing with factors such as bioturbation, mineralisation rates and denitrification as a function of seabed type and benthic biota. This may need further refinement when better data becomes available.

In Black’s original model (3DDLife), several of the processes are dealt with more specifically than in Bubble, including excretion, detritus and oxygen. Here, the excretion and detritus are calculated as fixed fractions of the number and size of the phytoplankton and zooplankton. Oxygen limitations in the Bay are rare because of re-aeration by waves and currents in the Bay, although strong blooms may lead to significant oxygen reduction (Longmore and Nicholson 2012) and additional data may indicate a need to re-incorporate oxygen use into the simpler model.

### 2.2 The functional types

Phytoplankton is highly diverse, and different species have different attributes and characteristics. Models which attempt to treat specific species have struggled when field observations may show that before, during and after a bloom numerous different species may occur or take precedence. Thus, it’s beneficial to attempt to categorise the various phytoplankton into groups with similar attributes, specifically “Plankton Functional Types”. But even then, the number of variations can be daunting.

A recent publication by Maranon et al. (2013) showed very strong correlations between cell volume and other characteristics including growth rate, CO$_2$ fixation and maximum N uptake rate. Their data
included different species of phytoplankton with sizes across 6 orders of magnitude, thereby greatly extending similar findings by other researchers (e.g. Eppley 1972). Here, the Maranon et al. (2013) results are incorporated into the model Bubble by using volume as the primary descriptive input variable for the phytoplankton.

The phytoplankton is then classified into Functional Types. For the modelling presented below, we adopted two Functional Types called: (1) “Diatom”; and (2) “Flagellate”.

The discriminating attributes of “Diatom” include:

- Silicon absorption
- Lower C, N and Chl-a content per unit volume than flagellate
- Inability to adjust vertical position, and therefore subject to a fall velocity that removes a percentage from the water column to the seabed each day
- Temperature function power of 1.5 (see below)

The attributes of “Flagellate” include:

- Ability to retain a position in the water column and therefore fall velocity is set to zero
- Temperature function power of 2.0 (see below)

The selection of functional types with attributes is critically important. Thus, the model has capability for inclusion of additional types and attributes, such as *Emiliania huxleyi* with its hard calcium carbonate shell.

The Functional Type selection raises many basic questions including what attributes might allow diatoms to bloom in greater concentrations than flagellates, as observed in Port Phillip Bay (Magro et al. 1996). The model provides the platform for testing (and potentially keeping or eliminating) attributes that succeed or fail to produce the observed outcomes. Notably, growth is taken as a function of volume only, and so the cell volume is not treated as an intrinsic attribute that discriminates diatoms from flagellates. Cell volume is an input parameter for both types.

### 2.3 Phytoplankton model equations

#### 2.3.1 Growth of Phytoplankton

The Michaelis-Menten formulation modified by temperature and light dependence is adopted for growth of phytoplankton (Raillard and Menesguen 1994; Chapelle et al. 2000):

\[ G_P = \mu_{max} f_P f_L \left( \frac{N}{N + N_H} \right) \left( \frac{S}{S + S_H} \right) \]  

(2.1a)

where \( N \) and \( S \) are the nitrogen and silicon concentrations in the water column while \( N_H \) and \( S_H \) are the half saturation coefficients. For flagellates the \( S \) dependence is neglected. The model adopts the
total mass of N in the water column from NO$_3$ and NH$_4$. There is no term in the current version of the model which describes phytoplankton preference for nitrate over nitrite or ammonium, partly because of the uncertain empirical nature of this term.

The phytoplankton growth may be limited by several factors, including light ($f_{PL}$), temperature ($f_{PT}$) and nutrients. Normally, the light and temperature limits are considered to be multiplicative, i.e.

$$\mu = u_{\text{max}} f_{PT} f_{PL} \quad (2.1b)$$

However, the influence of nutrients has been treated in several different ways, including:

- **Multiplicative:**
  $$\mu = u_{\text{max}} f_{PT} f_{PL} (f_N f_P f_Si) \quad (2.1c)$$

- **Largest limit:**
  $$\mu = u_{\text{max}} f_{PT} f_{PL} \text{MIN}(f_N, f_P, f_Si) \quad (2.1dc)$$

- **Arithmetic average:**
  $$\mu = u_{\text{max}} f_{PT} f_{PL} (f_N + f_P + f_Si)/3 \quad (2.1e)$$

where $f_N$, $f_P$ and $f_Si$ are the growth equations of Michaelis Menten form for N, P and Si respectively.

The “harmonic mean” is also adopted at times (O’Neil et al. 1989, DHI 2004) which allows for luxury uptake of nutrients, whereby a shortage of one nutrient can be offset by abundant quantities of others. The formulation is not valid if nutrient shortages are persistent. Using Black’s Model 3DLife, best agreement with measurements was obtained using the harmonic mean when simulating the oceanic Bay of Plenty in New Zealand (Longdill et al. 2006).

However, when modelling diatoms, both the Si and N are needed for growth and a limit in either will slow development, irrespective of which is the dominant limit. This implies that the multiplicative scheme is likely to be more representative and so multiplication is adopted in the model here (eqn. 2.1c).

### 2.3.2 Maximum growth rate of phytoplankton

From Maranon et al. (2013), the maximum growth rate versus cell volume ($V_{cell}$) peaks around 100 µm$^3$ (Figure 2.1a). Their empirical equations are:

For species with $V_{cell} < 300$ µm$^3$

$$\log_{10}(\mu_{\text{max}}) = 0.19 \log_{10}(V_{cell}) - 0.43 \quad (2.2a)$$

For species with $V_{cell} > 40$ µm$^3$

$$\log_{10}(\mu_{\text{max}}) = -0.15 \log_{10}(V_{cell}) + 0.22 \quad (2.2b)$$

Figure 2.1a shows that their log-log equations are discontinuous near the peak, which is the most important zone for growth rates. Thus, new third-order polynomial equations were fitted to obtain the empirical curves shown in Figure 2.1b.

The polynomial equation for species with $V_{cell} \leq 100$ µm$^3$ is,

$$\mu_{\text{max}} = 0.0336x^3 + 0.0399x^2 + 0.0999x + 0.3553 \quad (2.3a)$$
And for species with $V_{cell} > 100 \, \mu m^3$,

$$
\mu_{max} = -0.0146 x^3 + 0.2430 x^2 - 1.3793 x + 2.9432 \quad (2.3b)
$$

where $x=\log_{10}(V_{cell})$ and the equations have $r^2$ of 0.95 and 0.93 respectively, which is higher than the values presented by Maranon et al. (2013) of 0.94 and 0.86. The polynomial equations are adopted in the model. Note for growth rate comparisons,

$$
\mu_{max} = 0.69D \quad (2.4)
$$

where D is Doublings per day.

Figure 2.1a Growth versus cell volume showing the data and equations from Maranon et al. (2013).
Figure 2.1b. The Maranon et al. (2013) data with best-fit third-order polynomials.
2.3.3 Growth dependence on light
The light function is,

\[ f_{PL} = \frac{l_z}{l_{opt}} e^{(1 - l_z/l_{opt})} \]  \hspace{1cm} (2.5)

where \( l_z \) is light (watts.m\(^{-2}\)) at depth \( z \) (m) below the water surface and \( l_{opt} \) is the optimal light for growth (watts.m\(^{-2}\)). The light is attenuated with depth below the surface \( z \) according to Beer’s Law (e.g. Duarte et al. 2003) as follows,

\[ l_z = l_o e^{-K_L z} \]  \hspace{1cm} (2.6)

where \( l_o \) (watts.m\(^{-2}\)) is the light at the surface and \( K_L \) is the exponential decay coefficient.

2.3.4 Growth dependence on temperature
A widely-used function for the exponential growth phase of phytoplankton is based on the Arrhenius equation (Eppl ey 1972),

\[ f_{PT} = E_T (T_W - T_o) \]  \hspace{1cm} (2.7a)

where \( E_T \) is the Eppl ey coefficient (1.06), \( T_w \) is the water temperature and \( T_o \) is optimal temperature for growth. However, data from Montagnes and Franklin (2001) suggests that the temperature dependence might be better described by a different function. Using extracted values from Montagnes and Franklin (2001), a new function shape was obtained which is similar to the light function (Figure 2.2) and is,

\[ T_p = (T_W/T_o)^m \]

\[ f_{PT} = T_p e^{(1 - T_p)} \]  \hspace{1cm} (2.7b)

Notably, the power of \( m=1.5 \) was adopted for diatoms, but the flagellate example fits better with the power set to \( m=2.0 \) (Figure 2.2).

2.3.5 Half saturation coefficient for nitrogen
The half saturation coefficient determines the shape of the nitrogen uptake curve. For example, low values lead to more rapid uptake at low concentrations. This is a difficult factor to set in the model and so an empirical relationship was developed here. Re-examining the data of Eppl ey (1972), the half saturation coefficient for uptake of nitrogen was found to be a function of cell size (Figure 2.3).

One of Eppl ey’s outlier data points has not been included, but otherwise the data has Michaelis-Menten form with limited scatter. The equation is,

\[ N_H = \frac{0.25 R_{cell}}{(R_{cell} + 30)} \]  \hspace{1cm} (2.8)

where \( R_{cell} \) is the notional radius of the cell calculated as the cube root of the cell volume,

\[ R_{cell} = \left( \frac{0.75 V_{cell}}{\pi} \right)^{1/3} \]  \hspace{1cm} (2.9)
Figure 2.2 Response of growth to temperature. Measurements were taken from Montangnes and Franklin (2001), adjusted to pass through a maximum growth of 1.0 at the peak and then fitted to equation 2.7b. The first 3 panels are diatoms (power=1.5), while bottom right is a flagellate (power=2).
2.3.6 Half saturation coefficient for Silicon

The most common type of silicon is silicate ($\text{SiO}_4^{4-}$) but there are many different types, including silica quartz ($\text{SiO}_2$) which is the special case with no negative charge and no need for counter-ions. In the sea, the chemical forms of Si available to marine diatoms are undissociated silicic acid $\text{Si(OH)}_4$ which comprises about 97% of the dissolved silicon in seawater, while $\text{Si(OH)}_3$ accounts for most of the remaining 3%. Most diatom species transport undissociated silicic acid (Martin-Jezequel et al. 2000).

Egge and Aksnes (1992) described a sudden drop in diatom growth once the silicate concentration fell below 2 $\mu$M (Figure 2.4). This is equivalent to a silicon concentration of 0.056 g m$^{-3}$ (Appendix 1). Corresponding half saturation coefficients for Si limited growth are in the range 0.1 to 1 $\mu$M, according to Paasche (1980). A value of 0.04 g m$^{-3}$ is adopted for the Si half saturation coefficient. No empirical formula was developed in this report and so the Si half saturation is a user-selected variable in the model.

Figure 2.3 Half saturation coefficient $k_s$ versus cell diameter for NO$_3$ uptake. (Data from Table 2 of Eppley et al. (1972), not including one outlier data point.)
2.3.7 Phytoplankton fall velocity

The fall velocity of diatoms induces losses to the seabed each model time step. Fall velocity is found using a refinement of Stokes’ Law as,

\[ F_1 = 3 \times Visc \]
\[ F_2 = F_1^2 + gR^2 \rho_w (\rho_P - \rho_w) (0.015476 + 0.19841R) \]
\[ F_3 = \rho_w (0.011607 + 0.14881R) \]
\[ \text{Fall}_V = \left( \frac{F_1 + F_2^{1/2}}{F_3} \right) \]

where \( Visc \) is the water viscosity (\( 1.14 \times 10^{-3} \) kg m\(^{-1}\) s\(^{-1}\)), \( R \) is the radius of the phytoplankton (m), \( g \) is gravitational acceleration (9.81 ms\(^{-1}\)), \( \rho_w \) and \( \rho_P \) are the density of the seawater and phytoplankton respectively. The density of the seawater is taken as 1025 kg m\(^{-3}\).

The fall velocity calculation is sensitive to phytoplankton density and water properties, and so the formula was compared to measurements of sinking rate presented by Seip and Reynolds (1995). Their Table 1 provides the data shown in Figure 2.5. The best-fit power curve to their data is found here to be,

\[ \text{Fall}_V = 0.0112V_{cell}^{0.482} \]

with \( r^2 = 0.36 \).

The unknown diatom density needed in the Stokes equations was obtained by calculating fall velocities for a range of phytoplankton volumes using Stokes and comparing the results with the Seip and Reynolds (1995) data. After systematic variation in density, the best results were found with phytoplankton density set to 1070 kg m\(^{-3}\) (Figure 2.5). There is a very strong overall with Stokes (Figure 2.5), and so the modified Stokes equation is adopted in the model with diatom density of 1070 kg m\(^{-3}\).
The density of water is obtained from the salinity ($S_W$) and temperature ($T_W$) using a simplified equation of state as,

$$\rho_W = 1000(1 - 3.7 \times 10^{-6} T_W^2 + 7.5 \times 10^{-4} S_W) \quad (2.12)$$

The equation predicts density of 1026 kgm$^{-3}$ at 15°C with salinity of 35 ppt (Figure 2.6). The phytoplankton will settle faster in fresher and warmer water, although temperature has a relatively minor effect.

The fractional losses to the seabed each time step $\Delta t$ are

$$\Delta Chla = (\text{Fall}_V \Delta t / D). Chla \quad (2.13)$$

where $D$ is the water depth in metres. The $\Delta$Chl-$a$ reaching the seabed is converted to a mass of N, Si and added into the seabed mass repository.

![Figure 2.5](image1.png)

**Figure 2.5.** Fall velocity (m.d$^{-1}$) versus diatom cell volume ($\mu$m$^3$) showing data points of Seip and Reynolds (1995) (blue), the regression power curve to their data (black) and the modified Stokes equation (eqn 2.10) (green).

![Figure 2.6](image2.png)

**Figure 2.6.** Density versus salinity for water at 15°C. The temperature has a relatively minor effect on density.
2.3.8 Phytoplankton cell carbon, nitrogen and Chl-a content

The content of carbon in a phytoplankton cell per unit volume was shown by Strathman (1967) and Maranon et al. (2013) to be dependent on cell volume, but Strathman found differences between flagellate and diatom (Figure 2.7a). The diatom has some of the volume occupied by silicon and so reduced carbon content per unit volume in diatoms may be anticipated. Their results are compared in Figure 2.7 and there is general overall agreement.

The equations are:

\[
\log_{10}(C_{\text{cell}}) = 0.88 \log_{10}(V_{\text{cell}}) - 0.69 \quad \text{Maranon all species (2.14)}
\]
\[
\log_{10}(C_{\text{cell}}) = 0.76 \log_{10}(V_{\text{cell}}) - 0.42 \quad \text{Strathman diatom (2.15)}
\]
\[
\log_{10}(C_{\text{cell}}) = 0.87 \log_{10}(V_{\text{cell}}) - 0.46 \quad \text{Strathman flagellate (2.16)}
\]

In the model, the two Strathman equations are adopted because they discriminate between flagellate and diatom.

For the ratios of carbon to other chemicals in phytoplankton, many modellers use the Redfield ratio of (41:7:1) which describes the mass proportioning of C:N:P. However, Maranon et al. (2013) shows the C:N ratio ranging from 4-12 rather than a constant value of 6, with the largest ratios occurring for \( V_{\text{cell}} > 10 \mu m^3 \). In addition, field data for C:Chl-a is highly scattered and dependent on factors such as quality of food, sunshine hours, stage of the bloom, colour of the algae, depth below the sea surface, shading etc. Furthermore, the diatoms may store dissolved Si which alters the chemical ratios and the dissolved Si can return to the water column more easily than the silicified shells.

Rios et al. (1998) measured the chemical ratio of multiple species divided into categories which included diatom and “other autotrophs”; the latter consisting mostly of dinoflagellates and flagellates. They warned that the fraction of the total mass in the category “other autotrophs” was small and less reliable. Their results are presented in Table 2.1 which shows that the ratios are different between diatoms and other autotrophs although they both approximately follow the Redfield ratio. When converted from units of atoms to weight using the elemental mass, the N fraction is 0.17 for diatoms and 0.21 for other autotrophs, which is a 23% change.

In relation to silicon, Brzezinski (1985) obtained a higher molar ratio for C:Si (of 106:17) than Rios et al. (1998), which changes the ratio by weight from 0.14 (Rios) to 0.374 (Brzezinski). The measurements of Paasche (1980) show that the Si:C weight ratio in diatoms varies with temperature and light (notwithstanding other research showing a dependence on Si limitation during growth). The Paasche results (Figure 2.7b) indicate that the Rios data are at the lower end of the range, but the Brzezinski results are at the upper end of the range. Four of the 5 species considered by Paasche have ratios lower than that reported by Brzezinski. Only Cerataulina pelagica spans the Brzezinski results, with Chaetoceros affinis having the second highest ratio (between 0.25 and 0.3). The ratio for S. costatum which is common in PPB varies between 0.14 and 0.27.

A similar variation occurs in the Chl-a proportion. The ratio C:Chl-a is often assumed to be around 40:1 which was obtained by Rios et al. (1998) for diatoms. However, the other autotrophs exhibit a much smaller fraction of Chl-a. Table 6 in Rios et al. (1998) summarises measurements of other
authors and the ratio (C:Chl-α) by weight varies around 50-100. We have adopted a ratio of C:Chl-α of 70:1 for flagellates. In summary, the weight factors adopted in the model are given in Table 2.1.

Notably, carbon is not tracked in the model, but the ratio is needed to convert from Chl-α content in the phytoplankton to nitrogen in grams. In keeping with common practice, the units of Chl-α are adopted in the model as mg.m⁻³ and the conversion factor to convert 1 mg.m⁻³ to total grams of N is:

For diatoms: \[ N = 6.8 \times 10^{-3} \text{Chl-α} \]  
(2.17a)

For flagellates: \[ N = 14.7 \times 10^{-3} \text{Chl-α} \]  
(2.17b)

The number of phytoplankton cells per m³, can be obtained from the Chl-α concentration as:

\[ N_{\text{cells}} = \left( \frac{1}{M_{\text{Chl-α}}} \right) 10^6 \]  
(2.18)

where \( M_{\text{Chl-α}} \) is the mass of Chl-α in picograms obtained from the cell volume converted to mass of carbon (eqns 2.15, 2.16) and then to the mass of Chl-α (eqns 2.17).

---

Table 2.1. The chemical proportions in diatoms and flagellates from Rios et al. (1998) and Brzezinski (1985).

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>N</th>
<th>P</th>
<th>Si</th>
<th>Chl-α</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elemental mass</td>
<td>12.0</td>
<td>14</td>
<td>31</td>
<td>28.1</td>
<td></td>
</tr>
<tr>
<td><strong>Diatoms</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ratio (atoms) (Rios)</td>
<td>106</td>
<td>15.7</td>
<td>1.17</td>
<td>6.20</td>
<td></td>
</tr>
<tr>
<td>Ratio by weight (Rios)</td>
<td>1.00</td>
<td>0.17</td>
<td>0.03</td>
<td>0.14</td>
<td>0.0250 (40:1)</td>
</tr>
<tr>
<td>Ratio (atoms) (Brzezinski)</td>
<td>106</td>
<td>16</td>
<td>1</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td>Ratio by weight (Brzezinski)</td>
<td>1.00</td>
<td>0.176</td>
<td>0.024</td>
<td>0.374</td>
<td></td>
</tr>
<tr>
<td><strong>Other autotrophs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ratio (atoms)</td>
<td>106</td>
<td>19.3</td>
<td>2.0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ratio by weight</td>
<td>1.00</td>
<td>0.21</td>
<td>0.05</td>
<td>0</td>
<td>0.0143 (70:1)</td>
</tr>
</tbody>
</table>
Figure 2.7a  Carbon content (pg C cell$^{-1}$) versus cell volume according to Maranon et al. (2013) for all species and Strathman (1967) for diatom and flagellate.

Figure 2.7b  Ratio of silicon to carbon by weight in 5 species of diatom (from Paasche, 1980). The species are Skeletonema costatum; Thalassiosira pseudonana; Chaetoceros affinis; Rhizosolenia fragilissima; Cerataulina pelagica.
2.4 Zooplankton model equations

2.4.1 Treatment of zooplankton
Commonly in NPZ models, the zooplankton is treated in the same fashion as phytoplankton, with a single variable that represents the count/number of total zooplankton (e.g. Duarte et al. 2003; Longdill et al. 2006). Indeed, this single variable of abundance is an inadequate surrogate for an accurate representation of the zooplankton life cycle (Neuheimer et al. 2010). These equations do not allow tracking of the ages of the zooplankton within the total population. Here, we wished to discriminate for age, as future investigations may consider fish recruits which feed preferentially on certain zooplankton size classes. Also, we wished to represent the life cycle of the zooplankton more realistically and with fewer unknown coefficients. Thus, a more sophisticated approach was needed.

Our procedure, once developed and proven, was most similar to the methods of Neuheimer et al. (2010).

In Model Bubble, the distribution of ages is known. The number and size of zooplankton is stored in a transfer array, in daily increments from birth to adulthood. This array is updated daily and each cohort is transferred to the next day increment, after size and number are updated respectively using the growth and mortality equations for that day. On reaching adulthood, they produce eggs which determine the number of newborn zooplankton that is entered into the first day array position. After a selected period of maturity and egg laying, the adults finally die.

Throughout the life cycle of a zooplankton cohort, the conditions experienced, such as salinity, water temperature and phytoplankton abundance, will change. As such, this method in Bubble allows the zooplankton to be more realistically subject to a variety of conditions during their growth, with appropriate time delays for zooplankton to mature before producing eggs.

Model Bubble can simultaneously treat multiple species of zooplankton. However, for the present study the focus was on a key food source for juvenile snapper, Paracalanus sp. This is a dominant zooplankter in PPB (Kimmerer and McKinnon 1985) and a preferred prey of snapper larvae (Murphy et al. 2012). Paracalanus typically represent 28-53% of the zooplankton in the Bay. Here, the model adopts the lifecycle of Paracalanus to represent all zooplankton in the Bay. This assumption is acceptable when the other zooplankton have similar life spans, growth curves and egg production.

2.4.2 Zooplankton growth and mortality
The Michaelis-Menten growth formula modified by a temperature factor is adopted to determine the zooplankton growth rates.

\[ G_Z = \mu_{Z_{max}} f_{T} \left( \frac{Chla}{Chla+Chla_{H}} \right) \] (2.19)

where Chl-\( \alpha \) represents the total concentration of phytoplankton in units of mg.m\(^{-3} \) and Chl-\( \alpha_{H} \) is the half saturation coefficient. The total Chl-\( \alpha \) in the model is obtained by summing the Chl-\( \alpha \) associated with each phytoplankton functional type that is being simulated.

The size of the zooplankton in each cohort is updated daily as:

\[ Z_{\text{new}} = (G_z + 1) Z_s \] (2.20)
where $Z_{new}$ is the new size after one day of growth and $Z_s$ is the size prior to the update. Growth doesn’t occur when the total Chl-$a$ value is less than a minimum threshold and then $G=0$.

The temperature function for *Paracalanus sp.* (Hirst and Bunker 2003) is:

$$f_{zT} = 1 + e^{(-3.751 + 0.0463T_w)} \quad (2.21)$$

where $T_w$ is the water temperature ($^\circ$C). With these equations at temperatures found in Port Phillip Bay of 11-21$^\circ$C, the time to maturity varies from around 13-25 days, depending on food supply. This duration agrees with measurements (Hirst and Bunker 2003, Campbell et al. 2001).

*Paracalanus* are subject to mortality, particularly at high temperature and low salinity. The maximum temperature tolerance for *Paracalanus* is 25$^\circ$C (Mauchline 1998). However, temperatures seldom reach this level and mortality for $T_w < 25^\circ$C is treated as:

$$Z_{dead} = Z_MZ_{scal}Z \quad (2.22a)$$

$$Z_{scal} = \min(1, Z/3000) \quad (2.22b)$$

where $Z_{dead}$ is the number of zooplankton subject to mortality from each cohort at the daily update and $Z_M$ is a mortality coefficient chosen by the modeller. The model in its present form allows mortality to be a function of age and size, but setting the coefficients is difficult and so this option was not used.

The scale factor $Z_{scal}$ allows for lower mortality when the density of zooplankton is low. This factor was added after model testing showed that zooplankton was being totally lost in periods of low food supply. This is contrary to field observations which exhibit some zooplankton at all times. At these times zooplankton feeding may be sustained through the microbial loop rather than phytoplankton (Azam et al. 1983, Fenchel 2008), with copepods feeding on protozoans such as ciliates that are common in PPB (Jenkins 1988). As such, the mortality drops with reduced density of the zooplankton.

Mortality due to salinity $S$ is obtained from an empirical relationship developed here using data taken from Youn and Choi (2008). The equation is:

$$M_s = 1.685 - 0.0502 S \quad (2.23)$$

where $0<M_s<1$. For salinities exceeding 34.2 ppt, there is no mortality, while total mortality occurs at salinities below 24 ppt.

### 2.4.3 Zooplankton egg production

Mature zooplankton egg production is:

$$E_P = E_{PR} \cdot E_s E_{ratio}(0.5Z_A) \quad (2.24)$$

where $Z_A$ is the number of egg-producing adults in the population while the factor 0.5 represents the fraction of females in the population. Notably, some studies have found that the ratio of females is often greater than half (Campbell et al. 2001). The factor $E_{PR}$ is the egg production rate per adult,
$E_{ratio}$ is described in the next section, while $E_s$ is an egg and naupliar survival factor dependent on diatom concentration (Vargas et al., 2006) which is described in the next section.

The measurements of Uye and Shibuno (1992) are reproduced in Table 2.2 and Figure 2.8 shows the Egg Production Rate ($E_{pr}$) versus water temperature, Chl-$\alpha$ and prosome length. Egg numbers were not found to be very sensitive to water temperature (Figure 2.8). However, low egg numbers occur when Chl-$\alpha$ is less than 2 mg m$^{-3}$, which occurs frequently over parts of Port Phillip Bay, including the large Central region. The egg numbers are also low when the prosome length of the adult is below average. However, the small adult zooplankton size may simply arise from the poor food supply. Campbell et al. (2001) found that condition measurements were not affected by temperature, but were positively related to food concentration. Growth rates increased with increasing temperature and increased asymptotically with increasing food concentration.

An equation of Michaelis-Menten form has been plotted against the Chl-$\alpha$ data in Figure 2.8. The equation is,

$$E_{PR} = \frac{75(\text{Chla}-0.5)}{\text{Chla}+2}$$  \hspace{1cm} (2.25)

With this equation, egg production rate is zero when Chl-$\alpha$$<0.5$ mg m$^{-3}$, although the data suggests that small numbers of eggs (approx. 5) may still occur. This equation is adopted in the model with a minimum egg number of 5. The number of days that mature females produce eggs was set to 3 (Uye and Shibuno, 1992).

Table 2.2 Minimum and maximum water temperature ($T^\circ C$), Chl-$\alpha$ ($mg.m^{-3}$), Prosome length (Length, $\mu m$), and egg production rate ($EPR$, eggs per female per day) for Paracalanus from the experiments of Uye and Shibuno (1992).

<table>
<thead>
<tr>
<th>Min T</th>
<th>Max T</th>
<th>Min Chl-a</th>
<th>Max Chl-a</th>
<th>Min Length</th>
<th>Max Length</th>
<th>Min EPR</th>
<th>Max EPR</th>
</tr>
</thead>
<tbody>
<tr>
<td>16.5</td>
<td>17</td>
<td>1.56</td>
<td>20.4</td>
<td>649</td>
<td>830</td>
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<td>63</td>
</tr>
<tr>
<td>21</td>
<td>22.4</td>
<td>0.26</td>
<td>2.07</td>
<td>620</td>
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<td>535</td>
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<td>3.52</td>
<td>644</td>
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<td>8</td>
<td>57</td>
</tr>
<tr>
<td>15.5</td>
<td>18</td>
<td>1.6</td>
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Figure 2.8 Minimum and maximum egg production rate versus water temperature (upper), Chl-$\alpha$ (middle) and prosome length (lower) for *Paracalanus* (Data from Uye and Shibuno, 1992).
2.4.4 Influence of diatoms

Vargas et al. (2006) considered the effect of diet and presented a linear relationship which showed that fewer nauplii survived with increased ingestion by breeding adults of diatoms > 20 µm. In Figure 2.9a, we re-plot their data and find a relationship between survival of nauplii and the amount of diatom ingested. For completeness, we also show the equation of Michaelis-Menten form with half saturation of 0.04 which predicts the percentage mortality (Figure 2.9b).

Lee et al. (1999) demonstrated that diatoms smaller than 20 µm also caused a reduction in egg hatching and naupliar survival (Figure 2.10). They tested the effects of Chaetoceros gracilis (diameter = 7.3 µm, height 4.9 µm and volume= 200 µm³) which has a similar size to abundant diatoms in Port Phillip Bay. The effect of diatom in the diet was substantial with hatching success and clutch size dropping to zero at Clutch sequence 5 (Figure 2.10). The larger diatom Phaeodactylum tricornutum (length=34 µm and width=10 µm) showed similar effects. In mixed diets of diatom and flagellate the effect was less dramatic, although the hatching success was still impacted (Figure 3 of Lee et al. 1999). Many additional studies referred to in the Introduction of this report show similar results.

To provide a function for the effect of diatom, we have developed a relationship dependent on the ratio of diatom to total phytoplankton which has a shape similar to the data of Vargas et al. (2006) (Figure 2.9a). The equation is:

\[ E_{\text{ratio}} = \left(1 - \frac{P_D}{P}\right)^3 \]  

where \( P_D \) is the concentration of diatom and \( P \) is the total concentration of all phytoplankton species being simulated. The shape of this curve is shown in Figure 2.11.

Notably, while the mortality induced by a diatom diet is evident in the various studies, uncertainties remain with respect to the functional form in mixed diets. Moreover, egg hatching success appears to be also affected by absolute diatom concentration, as well as the percent concentration. Further refinement of this relationship is warranted.

Figure 2.9 (a) Left panel: Percent survival of zooplankton nauplii versus the amount of diatom ingested (> 20 µm) by the female adult. (b) Right panel: Percent mortality with the Michaelis-Menten equation having half saturation of 0.04. (Data taken from Vargas et al. 2006).
Figure 2.10 Effects of four algal diets, the diatoms *Chaetoceros gracilis* (CHA) and *Phaeodactylum tricornutum* (PHA) and non-diatoms *Pavlova* sp. (PAV) and *Heterocapsa triquetra* (HET) on the clutch size (A) and hatching success (B) in *Pseudocalanus newmani*. Asterisks indicate significant differences at p<0.05 *; p<0.01 **; p<0.001 *** with one-way ANOVA (From Lee et al. 1999).

Figure 2.11 Percent egg survival ($E_{ratio}$) as a fraction of diatom in the water column.
With mixed diets, Vargas et al. (2006) found that naupliar survival also dropped as the clutch size increased (Figure 2.12). Their equation is,

\[ N_S = -1.3E_{PP} + 92.5 \]  

(2.27)

Interestingly, by combining equation (2.25) (the empirical curve obtained from the data of Uye and Shibuno (1992) for egg production) with equation 2.27 (the relationship for naupliar survival of Vargas et al. (2006)), we obtain an overall survival curve as a function of Chl-a concentration with a peak in egg numbers around Chl-a = 4 mg.m\(^{-3}\) (Figure 2.13). However, due to empirical uncertainties, the relationship in Figure 2.13 was not adopted in the model and \( E_S \) is set to \( E_S = 1 \) in equation (2.24). The effect of \( E_S \) is thus incorporated within the diatom ratio \( E_{ratio} \) and the mortality coefficient.

Figure 2.12 Relationship between naupliar survival and egg production in mixed diets of diatom and flagellates (over 4 seasons at Dichato Bay, central Chile). Black, grey and white symbols correspond to *Acartia tonsa*, *Paracalanus parvus* and *Centropages brachiatus* respectively (from Vargas et al., 2006).

Figure 2.13 Overall zooplankton egg survival rate \( E_S \) versus Chl-a for mixed diets containing diatom.
2.5 Nutrient cycles

The model tracks total mass of N, P and Si. However, because phosphorus is not considered to be limiting in Port Phillip Bay, the focus in the model was on N and Si.

2.5.1 Boundary conditions
The various relevant nutrients containing dissolved N (e.g. NO$_2$, NO$_3$ and NH$_4$ and Detritus) are combined to produce time series of total mass of N (g m$^{-3}$) for the input boundary condition. The same method is used for other nutrients.

2.5.2 Phytoplankton growth and mortality
N is utilised for phytoplankton growth and returned by phytoplankton mortality. The change in water column nitrogen ($\Delta N_W$) per model time step ($\Delta t$) is,

$$\Delta N_W = (-F_{CN}\Delta Chl_a + F_{CN}RP_{dead})\Delta t \quad (2.28)$$

where the conversion factor $F_{CN}$ is presented in Table 2.1.

R is the fraction immediately re-mineralised to the water column (for example through the microbial loop), with the remainder going to the seabed. $P_{dead}$ is the Chl-$a$ lost due to mortality. The same methods are adopted for Si in the diatom fraction of the phytoplankton. Notably, the losses of phytoplankton due to zooplankton grazing are treated independently of phytoplankton mortality.

2.5.3 Zooplankton grazing on phytoplankton and excretion
The phytoplankton losses due to zooplankton grazing are obtained as follows. The mass of nitrogen ($W_Z$ g) in each zooplankton (Figure 2.14) is,

$$W_Z = \exp(2.78 \ln(L_Z) - 16.52) \cdot 10^{-6} \quad (2.29)$$

where $L_z$ is the zooplankton prosome length (µm) (Webber and Roff 1995). The mass of N in Paracalanus is 11% of the total weight (Ara 2001).

With eqn (2.29), the total mass of N within the zooplankton population can be obtained by summing across all daily cohorts, knowing the zooplankton length and the number of zooplankton in each cohort. The N required for growth and egg production is calculated for each cohort and summed.

The total N is then back-calculated to an equivalent amount of Chl-$a$ and the phytoplankton concentrations are adjusted downwards accordingly. With multiple phytoplankton species, it is assumed that grazing is not selective, and so the total Chl-$a$ required for zooplankton growth is allocated against each species, using a weighting based on the abundance of each species multiplied by the fraction of N in each species present.
The N being transferred from phytoplankton to the water column by zooplankton excretion is calculated as being a fixed fraction of the zooplankton size and multiplied by the number of zooplankton in the cohort. As such, the total Chl-a required for zooplankton growth and excretion is directly back-calculated with no unknown coefficients.

2.5.4 Zooplankton mortality
The mass of N returned to the water column due to zooplankton mortality is obtained in the same way as growth. Knowing the size of each zooplankter and the number of dead per day in each cohort, the total N associated with mortality is calculated. The corresponding mass of N is then released by partitioning it between the seabed and water column.

2.6 Seabed
In marine sediments, the organic nitrogen, derived mainly from phytoplankton, is first converted to ammonium (Longmore 2006) (Figure 2.15). Nitrification involves the microbial conversion of ammonium to nitrate in the presence of oxygen. Denitrification involves the conversion, by a different suite of microbes, of nitrate to N₂ gas. These processes are important because they result in the conversion of nitrogen from forms readily available for plant growth (ammonium, nitrate), to a form that is lost to the atmosphere (N₂).

Efficient coupling depends on the existence of oxic and anoxic zones in the sediment, and an effective means of transporting nutrients between the zones. Sediment that is uniformly anoxic cannot nitrify, while sediment that is uniformly oxic cannot denitrify. The oxygen regime in the sediment is therefore a strong determinant of denitrification, as are the rates of supply of oxygen from the atmosphere and organic matter from primary producers. Processes that enhance advection in the sediment (bioturbation and bio-irrigation by infauna) are also important. Fauna, and possibly
microphytobenthos, play a role in the distribution of oxic and anoxic zones and in transporting nutrients between the zones.

In Port Phillip Bay, Nicholson and Longmore (1999) found a strong correlation between phytoplankton production in the water column and carbon respiration rate in the sediment (Figure 2.15b). That is, the amount of Carbon coming back to the water column is proportional to the total amount stored in the seabed, which in turn relates to the intensity of water-column primary productivity at the site. The DIN flux was found by them to be linearly proportional to CO$_2$ release (Figure 2.15c). This means that sites such as Hobsons Bay return more seabed C (and N) than sites where primary productivity in the water column is lower. This important finding is adopted in the model by treating the seabed as a repository for chemicals arising from excretion and primary production mortality. For example, the amount of N returned to the water column is a fixed fraction per day, and is thereby proportional to the accumulated inputs entering the seabed, albeit delayed by the time taken for denitrification and nitrification to occur within the sediments.

Notably, limited experimental evidence (Berelson et al. 1998) indicates that increasing nutrient loads lead to a decline in denitrification efficiency (the relative proportion of N lost as N$_2$, compared to ammonium and nitrate). Further investigation of this important matter is needed, particularly the association with seabed sediment type and the presence of bioturbators.

In the model, N, P and Si enter the seabed from several sources: phytoplankton mortality, zooplankton mortality, and zooplankton excretion. Losses of N from the seabed occur when a user-selected fraction of the nutrients are released each model time step to the water column as dissolved N (nitrification), and lost to the atmosphere as N$_2$ (denitrification). The silicon is lost by burial at the seabed and fractionally returned to the water column over time as the diatom shells slowly dissolve.
2.15a. Conceptual model of nutrient cycling (from Longmore, 2006).

Figure 2.15b Relationship between sediment CO$_2$ flux and primary productivity of the water column.
Figure 2.15c. Correlation of DIN benthic flux with carbon flux.

2.7 Model Coefficient Selection
As discussed above, most coefficients are set in the model using equations from the scientific literature and/or developed in the sections above. The remaining “unknown” coefficients in the model are listed in Table 2.3. Sensitivity testing was undertaken to define ranges for these and the most sensitive were the mortality coefficients.

2.7.1 Light/temperature
Chlorophyll is most efficient in capturing red and blue light, particularly Photosynthetically Active Radiation (PAR) in the spectral range of 400-700 nanometres. The value 45% was adopted in the model for the fraction of PAR in the measured Global Solar Radiation (Escobedoa 2010).

For the light penetration into the water, Kuwahara et al. (2000) provides an exponential decay coefficient for PAR of 0.12. Longmore et al. (1996) recorded 0.4-0.5 in the more turbid Yarra plume, while Black et al. (1994) measured the attenuation coefficient to be 0.38 for PAR over seagrass beds in Port Phillip Bay. A decay coefficient of \( k_L = 0.4 \) was chosen to represent overall water clarity. Optimal light for phytoplankton growth in PPB was taken as 68 W.m\(^{-2}\) at 2 m depth below the surface.

Time series measurements of water temperature from the permanent monitoring station at Hobsons Bay had gaps in the dataset, so we adopted temperatures from the numerical hydrodynamic 3-dimensional model of Port Phillip Bay (Harrison et al. 2007a,b,c) which was calibrated against the station time series and satellite sea surface temperature observations. Optimal temperature for growth of phytoplankton was taken as 20°C. Some refinement could be achieved by further considering temperature dependence of observed species in Port Phillip Bay.
2.7.2 Nitrogen and Silicon

Modelled inputs of N from the atmosphere each year are small compared with the river discharges (Harris et al. 1996). Nutrients are lost from the Bubble as N\textsubscript{2} to the atmosphere, while Si is buried at the seabed. N returns to the water column by nitrification, while Si in the diatom shell is slowly dissolved. Typically, seabed nitrogen is released back to the water column over a period of days to weeks, depending on sediment type and ambient conditions (Longmore 2006). The seabed thereby “smooths” out the nitrogen flow through the N-cycle, while also acting as a repository for sustaining low concentrations of algae during lean times with minimal river discharges.

We considered the studies of Longmore and Nicholson (2012) and Yoon and Benner (1992) which measured fluxes of nitrogen with cores and domes. The results of Longmore and Nicholson (2012) suggest a very efficient denitrification rate in PPB.

In the model, the fraction per day of N lost to the atmosphere was set to 0.04, i.e. a 25 day turnover. The fraction returned to the water column is smaller by a factor of 1.16 (Yoon and Benner 1992). PPB studies showed about 52% of primary production remineralised at the sediment is ultimately lost to denitrification (Heggie et al. 1999, Murray and Parslow, 1999). After some testing, the model was calibrated with 0.04 of seabed N being returned to the water column per day. The total fraction of seabed N moving from the seabed to the water column and atmosphere was therefore 8% per day.

For silicon, the recycling is much slower and a value of 0.01 was adopted for the fraction returned to the water column from the seabed. In addition, Si is lost by burial in the sediments, through bioturbation and sedimentation. With diatom falling to the sea bed, mortality of phytoplankton and the excretion of Si by zooplankton all occurring simultaneously, the inputs to the bed are large and burial losses are also substantial. In addition, much of the Si falls to the seabed in water where the waves are unable to resuspend it. Thus, the loss by burial also includes a loss due to deposition which remains at the seabed. The loss by burial was taken as 15% per day. Further refinement of this coefficient is needed. If burial is too slow, the Si builds up in the water column to levels much greater than those measured in the Bay. Factors which remove Si from the system need to be further considered.

The fraction of N immediately re-mineralised in the water column after mortality of phytoplankton and zooplankton (for example by phytoplankton uptake, zooplankton feeding or through the microbial loop) was set to 0.5. The fraction of Si re-mineralised was taken as 0.1, which mostly represents the fraction of dissolved Si contained in the diatom pool (Martin-Jezequel et al., 2000).

The model was found to be relatively insensitive to these values around the river entrance where new inputs of dissolved N and Si are occurring regularly. However, cases with nutrient limitations are sensitive to the recycling coefficients. “Trial and error” sensitivity testing was guided by successful prediction of averaged concentrations of the nutrients and the Chl-a in the water column. The nitrification, denitrification, dissolving rate and burial coefficients are catch-bags containing all the individual processes which can lead to N and Si turn-over in the seabed.

2.7.3 Phytoplankton

The mortality of phytoplankton proved to be a highly sensitive variable. We chose 10% d\textsuperscript{−1} after numerous sensitivity tests. Notably, mortality occurs in addition to zooplankton grazing in the
model. The minimum N concentration for plankton growth was not a sensitive parameter and a value 0.0001 g m\(^{-3}\) was adopted.

### 2.7.4 Zooplankton

For *Paracalanus*, Hirst and Bunker (2003) found limiting maximum growth rates of 0.303 and half saturation coefficient of 0.85 (mg.m\(^{-3}\) of Chl-\(\alpha\)). The half saturation coefficient is low compared to many other copepod genera and may explain the predominance of *Paracalanus* in PPB where the nutrient and Chl-\(\alpha\) concentrations are often low. After calibration of the model and testing this sensitive mortality coefficient, we found best agreement with a value of 15%.

In relation to temperature and salinity effects, surface water temperature in PPB rarely exceeds 24°C (Lee *et al*. 2012), which is within the tolerance of *Paracalanus* (Mauchline 1998). Salinity is mostly greater than 34 ppt, except in the surface waters near the Yarra river discharge and during extreme flow events, where it can drop below 30 ppt. Above salinities of 34.2 ppt, there is no salinity influence on mortality, while salinities below 24 ppt induce total mortality of *Paracalanus* (Youn and Choi 2008).

From the data of Uye and Shibuno (1992), the minimum and maximum adult prosome lengths average 631 and 789 µm (Table 2.2), with overall average of 710 µm (Uye and Shibuno, 1992). More recent data of Webber and Roff (1995) suggests the prosome length of the adult may be slightly bigger and so 750 µm was adopted in the model. The juvenile size was taken as 40 µm (Webber and Roff, 1995). The prosome length \(L_p\) is linearly related to total length \(L_T\) (Figure 2.16) with best-fit equation,

\[
L_p = 0.784L_T - 27.945 \quad (2.30)
\]

### 2.7.5 Phytoplankton size

Previous studies (e.g. Ansotegui *et al*. 2003) have defined 4 size divisions of phytoplankton: microplankton (>20 µm); large nanoplankton (8–20 µm); small nanoplankton (1–8 µm), and picoplankton (<1 µm). However, Bubble allows a continuum of cell sizes (volumes), selected by the user.
Figure 2.16  Prosome length versus total length for *Paracalanus* (Data from Nichols and Thompson 1991, Liang and Uye 1996).
Table 2.3 Settings in the model. Those with a star "**" may be varied by the operator. Others are obtained from empirical or measured values.

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<th>Value</th>
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<td>Fraction of seabed N returned to water</td>
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<tr>
<td>$N_m$</td>
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<td>day$^{-1}$</td>
<td>Fraction of plankton remineralised to water. The remainder goes to the seabed. Both phyto and zoo.</td>
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<td>Fraction of plankton remineralised to water. The remainder goes to the seabed.</td>
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**Model set-up**

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Chapter 3  
Field data analysis

3.1 Introduction

The goal of this chapter is to examine the plankton dynamics in Port Phillip Bay, south eastern Australia, which is the focus for modelling. The Bay has been monitored and studied for decades providing essential data for model validation (Spooner et al. 2010) and is an ideal system to examine the links between dynamic nutrient inputs and phytoplankton production. The Bay has been studied in relation to its physical and chemical properties and circulation (Black et al. 1993, Harris et al. 2006, Lee et al. 2012). It has well-defined point source nutrient inputs, with major inputs from the Yarra River in the north, and Melbourne’s largest waste water treatment plant which discharges secondary to tertiary treated waste water in the west (Figure 3.1). The Yarra River is the most significant nutrient input relevant to this study, which is focussed on the northern and eastern region of the Bay (i.e. the ‘Yarra plume’ region) (Figure 3.2), where the most important snapper spawning and nursery grounds occur (Hamer et al. 2011).

A multi-faceted study of Bay circulation, nutrients and primary production conducted by CSIRO in 1990-96 (Harris et al. 1996) concluded that nitrogen in Port Phillip Bay was primarily lost to the atmosphere, rather than through the entrance to Bass Strait. Their study set limits for nutrient discharges from the WTP which still stand today, even though urban growth has been substantial and river nutrient loads are different. Moreover, the knowledge of the Bay and primary production has greatly improved over the last 25 years.

South-eastern Australia had been suffering drought conditions for around a decade until it finally broke in in 2010. The Bay in 2009 was hypersaline and nutrient levels were relatively low (Lee et al., 2012). With substantial rainfall in 2010, the high salinity of the upper Bay of nearly 39 ppt began to return to normal values averaging around 35-36 ppt (Lee et al., 2012). In this chapter, we present data from 2004 to 2011, with a focus on the period 2008-2011 when phytoplankton identification data were available during the transition from drought conditions. The “years” presented here start on July 1 (to June 30) because the model is started in July 1 of each year when the Bay is most dormant.

3.2 Methods

3.2.1 Description of Port Phillip Bay

Port Phillip Bay (PPB) has a surface area of 1930 km², volume of $2.63 \times 10^{10}$ m³, an average depth of 14 m, and a maximum depth in the central basin of 24 m (Figures 3.1 and 3.2). The narrow entrance to PPB and a large area of shallow channelized sand banks (The Great Sands) essentially isolate the ocean from the inner bay basin resulting in long residence times of around 12 - 16 months (Harris et al. 1996). Thus bottom-up effects are largely driven by the dynamics of catchment inputs, particularly the Yarra River, and the rate of seabed denitrification, which varies throughout PPB, depending on sediment type and proximity to discharges (Longmore and Nicholson 2012). Medium-
sized sand dominates over the large sand banks near the entrance, while soft muds predominate in the 18-24 m deep central region. Mixed sand/muds occur in the north and in waters less than about 10 m deep around the margins of the bay (Greilach et al. 1997). Water temperature varies from approximately 11°C in winter up to 23°C in summer. Salinity is typically around ocean values of 35-36, but cycles at decadal time scales from hyposaline to hypersaline due to slow shifts in the evaporation and rainfall balance (Lee et al. 2012).

### 3.2.2 Yarra River flow.

Hourly measurements of Yarra River flow volume were obtained from the Chandler Highway gauge (gauge No. 229143) approximately 25 km upstream from the discharge point into Hobsons Bay. The hourly values were combined to provide a measure of total daily flow volume and then adjusted for inputs below the gauging station (ML day⁻¹) using a multiplying factor.

### 3.2.3 Physico-chemical water quality data for PPB

Measurements of a range of physico-chemical water parameters have been conducted at a bay-wide scale at monthly intervals since 1986 (EPA 2011, 2012) and other information is available from periodic studies (Figure 3.3). For this study, in situ continuous measurements of salinity, temperature, dissolved oxygen and Chl-α fluorescence (calibrated against actual water samples and laboratory determination of Chl-α) were obtained from permanent loggers two depths below the surface situated in the Yarra plume (i.e. Hobsons Bay 3 and 10 m), Central Bay (3 and 18 m) and near the WTP (Long Reef, 3 and 5 m)) (Figure 3.1).

Historical measurements in the river entrances indicate concentrations of NOₓ and silicate (SiO₄) which are substantially higher on the north and east of the Bay than in the west (Table 3.1). There are no big rivers in the south near the ocean entrance. The silicon concentrations in the rivers are much higher than NOₓ (Table 3.1).

We assume that dissolved and detrital forms of N (NH₄, NO₂, NO₃, detrital N) all become available for phytoplankton growth, albeit via different biochemical routes, and so the model tracks N rather than the individual compounds (Chapter 2). The Yarra River Inorganic N load at Hobsons Bay is dominated by NOₓ (EPA 2011, 2012), and is known to have the largest impact on the bay in the zone under consideration. Phosphorus, carbon and oxygen were assumed to be not limiting at the river entrance, which is consistent with previous studies of the Bay (Harris et al. 1996).

### 3.2.4 Snapshot measurements of the whole Bay

Snapshots of chemical parameters over the whole bay had not been done since the PPBES studies in 1992-95 (Longmore et al., 1996). Thus, we conducted surveys of key parameters across the full Bay over a two-day period (November 22-23, 2010). The timing of the survey coincided with snapper spawning.

These data have been used for calibration of the full spatial model Bubbles (Chapter 6). Here, we consider the salinity, NOₓ, Si and Chl-α results.
Figure 3.1. a) Port Phillip Bay showing the open ocean entrance to Bass Strait (Port Phillip Heads - PPH), the ‘Great Sands’ region and the discharge location of the Yarra River. The + indicates sites where water physico-chemical parameters, Chl-α measurements and/or phytoplankton community composition and abundance data were collected: with the main field sampling sites within the Yarra plume: Hobsons Bay and Carrum; b) Areal image of Port Phillip Bay showing the Yarra plume model domain region after a flow event.

Figure 3.2 Numerical 3-dimensional modelling of Port Phillip Bay using Model 3DD from the “3DD Suite” (Black, 1995), showing the Yarra and Patterson River plume during flood flows (relative salinity is shown where: red is seawater; blue is fresh).
Table 3.1 NO\textsubscript{X} and silicate in river discharges at the north, east and west of Port Phillip Bay

<table>
<thead>
<tr>
<th>Discharge</th>
<th>NO\textsubscript{X} (g.m\textsuperscript{-3})</th>
<th>Silicate (g.m\textsuperscript{-3})</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yarra</td>
<td>1</td>
<td>8</td>
<td>North</td>
</tr>
<tr>
<td>Mordialloc</td>
<td>0.9</td>
<td>12</td>
<td>East</td>
</tr>
<tr>
<td>Patterson</td>
<td>1.1</td>
<td>9</td>
<td>East</td>
</tr>
<tr>
<td>Werribee</td>
<td>0.1</td>
<td>5</td>
<td>West</td>
</tr>
<tr>
<td>Kororoit</td>
<td>0.6</td>
<td>4</td>
<td>West</td>
</tr>
</tbody>
</table>

Figure 3.3 Measurement sites around Port Phillip Bay.
3.2.5 Phytoplankton composition.

The phytoplankton community composition and abundance data presented in this study were obtained from 3 sites within the Yarra plume; Hobson Bay and Carrum (Site 939 on Figure 3.3), and at the remote Central Bay site (Figure 3.3). The data were collected at approximately monthly intervals over the period from February 2008 until December 2011. At each site, three 1L integrated water-column samples (0-10 m) were collected using a 10m hose-pipe sampler (Hötzel and Croome 1998). Immediately after collection of each water-column sample, a corresponding phytoplankton net-tow sample (qualitative sample) was collected via a 10 m vertical tow of a 20 µm mesh phytoplankton net. All phytoplankton samples were preserved with Lugol’s Iodine Solution and placed on ice in a dark, insulated storage container. Water-column samples were concentrated 100x prior to enumeration of phytoplankton species, and cell counts were undertaken in a Sedgwick-Rafter counting chamber. Cell counts were undertaken using Zeiss Axiolab and Zeiss Standard microscopes equipped with bright field and phase contrast optics.

For this study, aimed at modelling plankton functional types, we combined the field phytoplankton data into three groups: diatoms, dinoflagellates and other flagellates. We were primarily interested in modelling the relative proportions of diatoms and flagellates so we calculated the ratio of diatom cells to the sum of dinoflagellates and other flagellates to create the diatom to flagellate ratio.

To further explore the relationship between nutrient enrichment and the diatom to total phytoplankton ratio we obtained additional data on phytoplankton community composition (same methods as above) and NO₃ levels (Longmore and Nicholson 2012) measured at four additional sites outside of our modelling domain plus the Hobsons Bay and Carrum sites (see Figure 3.3). Data were obtained for the period 2008-2011 and were pooled across the monthly sampling intervals to provide the mean relationship between the diatom to total phytoplankton ratio and NO₃ levels across the six sites.

3.3 Results

3.3.1 River flow and Chl-α.

The annual time series of Yarra River flow showed major variation in flow volumes across the three years 2008-11, with relatively low flow years in 2008/09 and 2009/10 (associated with the end of the prolonged drought period) and high flows during 2010/11 (associated with the first wet year post drought) (Lee et al. 2012) (Figure 3.4). The flow dynamics were also highly variable among years with no clear seasonality in flow volumes, although in the wet year 2010/11 highest flows occurred from November to March, due to a series of intense short-period rainfall events (Figure 3.4).

The Chl-α levels measured at Hobsons Bay peaked at daily averages of approximately 10 mg.m⁻³ in the high flow year of 2010-2011 compared to approximately 3-5 mg.m⁻³ in the low flow years (2008-2009, 2009-2010) (Figure 3.4). In all years, Chl-α was lowest in July-August (winter). Transient peaks in Chl-α often (but not always) occurred shortly after transient flow peaks, and there were Chl-α peaks between September and December in all years (i.e. spring), with a gradual increase to maximum levels between January and April in each year (Figure 3.4).

At the Central site which is remote from the river entrances, Figure 3.5 shows the Chl-α data over 4 years from July 1, 2004 to June 30, 2008. Strong inter-annual similarity is evident with lowest Chl-α in September/October (Day 100) and highest values around February-April (Days 210-300). Chl-α in
winter is as low as 0.1 mg.m\(^{-3}\) and ranges to 0.8 mg.m\(^{-3}\), while summer values are typically 1.0-1.5 mg.m\(^{-3}\) (Figure 3.5). The lowest values in winter appear to be less than the threshold for successful production and survival of zooplankton eggs (Figure 2.8).

There is no evidence of a spring bloom in October. Full modelling of the Bay shows that the rare peaks at the Central site arise from advected plumes associated with the river discharges along the north-eastern side of the Bay (see Figure 3.2, for example).

Figure 3.4 Comparison of Yarra River flow and Chl-\(\alpha\) dynamics at the Hobsons Bay permanent logger site across three years. Top and bottom fluorescence sensors have been averaged together and then daily averaged.
3.3.2 Nutrient concentrations

The average nutrient concentrations in the Yarra River are presented in Table 3.2. Nitrogen and silicon are sufficient for diatom growth.

At sites away from the Yarra River, the annual variation in NOx is consistent between the years, with highest levels in winter (May to September) and lowest in summer (from October to April) (Figure 3.6). Common concentrations are <0.005 g m$^{-3}$ but the peak values are around 0.04 g m$^{-3}$.

The pattern of highest concentrations in winter may be caused by reduced phytoplankton growth leading to the return of nutrients to the water column and seabed, thereby raising dissolved nutrient levels in winter. Longmore et al. (1996) saw the same seasonal peak at coastal sites throughout the Bay. However, the pattern is strongest at Clifton Springs, which receives advected water from the ocean more readily than Corio Bay and the same pattern was observed at sites near the open entrance of the Bay (EPA, 2012), which may suggest that the higher N concentrations are coming from Bass Strait in winter (EPA, 2012).

Table 3.2. Average nutrient concentrations in the Yarra River (g.m$^{-3}$)

<table>
<thead>
<tr>
<th>Nitrogen</th>
<th>Phosphorus</th>
<th>Silicon</th>
<th>Detrital N</th>
<th>Detrital P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>0.04</td>
<td>8.2</td>
<td>0.07</td>
<td>0.05</td>
</tr>
</tbody>
</table>

3.3.3 Snapshots

The baywide surveys (November 22-23, 2010) show salinity being lowest around the Yarra plume, which extends from the entrance down the north-east coast (Figure 3.7a). Salinities are generally lower over the entire north and east segments of the Bay, relative to the Geelong Arm and entrance regions.
The Chl-α is also highest along the north and east shoreline, presumably in response to nutrient discharge from the Yarra River (Figure 3.7b). Maximum values of around 3 mg m⁻³ are less than those recorded at the same time at the Hobsons Bay fixed site which shows Chl-α > 7 mg m⁻³ (Figure 3.4), suggesting that the plume and Chl-α is not spatially uniform.

It was noted that several peaks in Yarra River flow do not produce a Chl-α peak, and some of the Chl-α peaks do not have prior flow. At times, the Yarra plume hugs the north-east shoreline and misses the fixed station. Figure 3.7b shows the low salinity plume heading down the north-east shoreline, although in this example the plume also passes through the Hobsons monitoring site and a corresponding Chl-α peak can be seen in Figure 3.4.

The NOx is highest around the WTP, although there is little evidence of elevated Chl-α (Figure 3.7b and c). In the Yarra plume, the NOx is low along the north-east coast, suggesting that much has been used for algal growth. Typical concentrations of NOx are around 0.01 g m⁻³ (Figure 3.7c).

![Figure 3.6](image)

**Figure 3.6** Measured yearly cycles in dissolved NOx concentration at sites away from the Yarra River inputs (from EPA, 2012). Clifton Springs is on the south shore of the Geelong Arm, while Corio Bay is at the western extremity of the Geelong Arm (Figure 3.1). PPBES is data collected for the Port Phillip Bay Environmental Study (Longmore et al 1996).

The ammonia increases to the south in the Yarra plume, arising as a by-product from mortality and decay of the Chl-α bloom that came from the river entrance, but concentrations are <0.01 g m⁻³ (Figure 3.7d).

The Si concentrations (Figure 3.7e) are of great interest as the dominant species were diatoms around this time (see next section). The Si concentration for unlimited growth of diatom must exceed 0.056 g m⁻³, according to Egge and Aksnes (1992) (see Appendix 1 for units conversion).

In the snapshot sampling there were several locations around the Bay where Si concentrations were less than this, suggesting that Si was limiting in some areas of the Bay. Limiting concentrations occurred at 20 of 63 measurement sites, i.e. in Corio Bay, Central Bay, Yarra entrance, ocean entrance and in the Geelong Arm. Non-limiting concentrations were evident around the eastern Bay and central bay. Baywide modelling is needed to determine if the low values relate to utilisation by
diatoms. These observations support previous studies showing Si limitation in the Geelong Arm (Murray and Parslow 1999)

More focus on Si is needed, including discharges, utilisation by diatoms and the losses (e.g. burial). Measurements of SiO₂ at WTP show concentrations of 5-15 g m⁻³ in the discharge, with an average from 2004-2014 of 11.7 g m⁻³.
Figure 3.7 (a) Salinity (ppt) and (b) Chl-a (mg m⁻³) measured during November 22-23, 2010 in Port Phillip Bay.
Figure 3.7 (c) NOx (g m\(^{-3}\)) and (d) ammonia (g m\(^{-3}\)) measured during November 22-23, 2010 in Port Phillip Bay

Figure 3.7e Silicon concentrations (g m\(^{-3}\)) measured during November 22-23, 2010 in Port Phillip Bay
3.3.4 Phytoplankton composition and abundance.
The identification of microalgal cells indicated that the most frequently occurring phytoplankton were the diatoms, notably Skeletonema and Chaetoceros species, and the cryptophyte flagellates, Plagioselmis prolonga and Hemiselmis sp. (Table 3.3).

Beardall et al. (1997) noted that up to 30% of Chl-a in PPB is attributed to phytoplankton which is too small to count or identify. However, around the Yarra River, the high counts of the diatom and flagellate species make the background percentage relatively smaller.

At the Hobsons site, the diatom counts were often an order of magnitude higher than the flagellates and dinoflagellates (Figure 3.8). The diatoms are particularly dominant in the bloom events, and while all of the three phytoplankton groups are typically lowest in late winter and start to grow again around August, the winter phytoplankton community has a greater proportion of non-diatom phytoplankton (Figure 3.8). Dinoflagellates exhibit a signal that is primarily seasonal, while the flagellates are more variable and influenced by the competition for nutrients. In all cases, the counts increase slowly over the period from August to May, followed by a more sudden decay around May-August (Figure 3.8).

The largest peak with abundant diatoms in December 2009 is not correlated with the river flow or the measurements of Chl-a at Hobsons (compare Figures 3.4 and 3.8). Indeed, the correlation between counts (Figure 3.8) and the fluorescence measurements at the Hobsons site (Figure 3.4) is generally weak and not significant.

![Figure 3.8 Monthly time series of phytoplankton community composition measured at the Hobsons Bay site across three years.](image)

There is a suggestion of sequencing with the diatom leading the flagellates, but the monthly data resolution is inadequate to make confident inferences. In general, growth in all three groups tends...
to occur near simultaneously, with the exception of the bloom in 2009 when the flagellates substantially failed to grow (Figure 3.8). The shorter-duration peaks in the dinoflagellates mostly occur after a diatom peak. Both heterotrophic and autotrophic dinoflagellates are known to occur, and so this sequencing may relate to feeding on the diatom or the release of N back to the water column when the diatom bloom decays.

### 3.3.5 Diatom to flagellate ratio

The ratio of diatom over total phytoplankton cell concentration is highly correlated with total phytoplankton cell concentrations measured at the Hobsons Bay and Carrum sites (Figure 3.9). At both sites, the diatom/total phytoplankton cell ratio is highest during periods of high algal concentrations or "blooms" (i.e. diatoms dominate in blooms) while the flagellates generally make higher contributions during periods of low overall algal concentrations. The plotted data in Figure 3.8 has Michaelis-Menten shape which can be represented by a family of equations,

\[ R_{df} = \frac{C_d}{C_d + C_f} \]  

(3.1)

where \( R_{df} \) is the ratio of diatom to total phytoplankton, \( C_d \) is the concentration of diatom and \( C_f \) is the concentration of flagellates. Thus, the \( C_f \) factor acts in the same way as a half saturation coefficient and the curves on Figure 3.9 show examples of the effect of varying \( C_f \). The scatter in the data in Figure 3.9 can be explained by variations in the concentration of flagellates, with 100,000<\( C_f <700,000 \), while the diatoms range up to 10,000,000 cells L\(^{-1} \) (Fig. 3.9). The Patterson site (which scatters the least) appears to be the most dominated by diatom, in accordance with the higher Si measurements recorded there during the snapshot survey (Figure 3.7e).

### 3.3.6 Phytoplankton composition and nutrient enrichment.

In Figure 3.9, the long-term average of all measured NO\(_X\) concentrations is compared to the average of the diatom ratio (diatom counts/total phytoplankton counts) at the Hobsons Bay and Carrum sites, and four additional sites. There is a clear Michaelis-Menten type relationship between the relative diatom abundance and the average concentrations of NO\(_X\).

Guillaud and Menesguen (1998) found that silicon inputs regulated diatom production in the Seine River plume. The flagellate summer production in the plume was enhanced by high water temperature and high N/Si ratios, which occurred during dry years with low discharge regimes. The PPB results are compatible with their findings, noting the higher flagellate percentages in the dry years (Figure 3.8) and the high diatom counts when the plume discharges substantial N and Si in the wet years. In PPB, blooms are dominated by diatoms, rather than flagellates.

### 3.3.7 Measured and empirical growth rates

The measurements of Chl-\( a \) at the Hobsons site show daily growth rates that mostly vary around 0.25 to 1.0 mg m\(^{-3} \)d\(^{-1} \), with most being from 0.0 to 0.5 mg m\(^{-3} \)d\(^{-1} \) (Figure 3.10).

While the field data are affected by advection of mature blooms through the site which can exaggerate the apparent growth rates, the predominance of growth rates less than 1.0 (per day) is in agreement with Figure 2.1b showing the Maranon et al. (2013) growth measurements. For the two common species of Skeletonema costatum and Chaetoceros sp. observed in PPB, equation 2.3 predicts growth rates of around 0.6 and 1.0 respectively. These are compatible with the field
measurements of growth (Figure 3.11) and thereby further confirm the relevance of the adopted Maranon et al. (2013) equations.

Figure 3.9 Relationship between the proportion of diatom cells in the phytoplankton community and the total abundance of phytoplankton cells measured at monthly intervals across three years (2008-2011) at two sites; (upper) Hobsons Bay and (lower) Carrum in north-eastern Port Phillip Bay. The multiple curves are examples of equation (3.1)
Figure 3.10 Relationship between long-term average (1994-2011) NO\textsubscript{X} concentrations versus the average of the diatom to total phytoplankton cell ratio (R = diatom cell concentrations/total phytoplankton cell concentrations) for 6 sites (see figure 3.1) in Port Phillip Bay.

Figure 3.11 Frequency distribution of differences between consecutive daily mean Chl-a values measured at the Hobsons Bay permanent logger site.

3.3.8 Relationship of size to abundance

While other factors play a role (e.g. half saturation, Si availability, competition, temperature etc.), in general the fastest growing species should be the most common globally. The growth curve (eqn. 2.3) shows that species with volumes around 50 to 500 µm\textsuperscript{3} grow most quickly and so species with that volume should be common in nature. Indeed, several studies have found correlations between optimal size and abundance (Jacobsen et al. 2005, Chisholm 1992, Finkel 2008). The predominance of Skeletonema costatum, both globally and in PPB, may be explained by its volume of 242 µm\textsuperscript{3} which is close to the peak of the growth curve (Figure 2.1b).

In PPB, the most common phytoplankton species are listed in Table 3.3 with their sizes and counts. The two most common are Skeletonema costatum and Chaetoceros sp. which both have sizes in the
optimal range. Thus, there is a relationship in PPB between volume and species abundance, with the most common species having volumes between 27 and 560 µm$^3$. An exception is *Teleaulax acuta*, a cryptophyte with volume of 200 µm$^3$ but low abundances, even though this species was present in virtually every sample and the largest abundance in a single sample exceeded 100,000 counts. Olenina et al. (2006) confirm that the volume of *Teleaulax acuta* is in the range from 125-305 µm$^3$, and so it remains exceptional in the dataset.

Further study of the relationship between volume and abundance in PPB is recommended and better correlation may be obtained if:

- the sizes of the plankton were measured in the laboratory, rather than taken from other studies which can exhibit wide ranges for cell volume for the same species. For example, Olenina et al. (2006) quote volumes ranging widely from 13-393 µm$^3$ for *Skeletonema costatum*.
- the plankton identification analysis was undertaken with larger samples and more regular intervals
- the data was sub-divided into regions in PPB to reflect the different nutrient concentration zones

Table 3.3 Phytoplankton species with high abundance in PPB. The counts are averaged across all monthly sampling events for all sites in PPB, over the period from February 2008 to September 2011.

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>Volume (µm$^3$)</th>
<th>Mean counts</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Skeletonema costatum</em>;</td>
<td>Diatom</td>
<td>242</td>
<td>165431</td>
</tr>
<tr>
<td><em>japonicum/pseudocostatum</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Emiliania huxleyi</em></td>
<td>Coccolithophore</td>
<td>158</td>
<td>25359</td>
</tr>
<tr>
<td><em>Planktolyngbya sp. (Unident.)</em></td>
<td>Cyanobacteria</td>
<td>300</td>
<td>34000</td>
</tr>
<tr>
<td><em>Chaetoceros sp. (Unident.)</em></td>
<td>Diatom</td>
<td>110</td>
<td>131506</td>
</tr>
<tr>
<td><em>Leptocylindrus danicus</em></td>
<td>Diatom</td>
<td>500</td>
<td>20580</td>
</tr>
<tr>
<td><em>Cylindrotheca closterium</em></td>
<td>Diatom</td>
<td>180</td>
<td>18559</td>
</tr>
<tr>
<td><em>Pseudo-nitzschia delicatissima group</em></td>
<td>Diatom</td>
<td>150</td>
<td>12991</td>
</tr>
<tr>
<td><em>Plagioselmis prolonga</em></td>
<td>Cryptophyte</td>
<td>60</td>
<td>52535</td>
</tr>
<tr>
<td><em>Hemiselmis sp. (Unident.)</em></td>
<td>Cryptophyte</td>
<td>27</td>
<td>40889</td>
</tr>
<tr>
<td><em>Teleaulax acuta</em></td>
<td>Cryptophyte</td>
<td>200</td>
<td>8093</td>
</tr>
<tr>
<td><em>Chrysochromulina sp. (Unident.)</em></td>
<td>Haptophyte</td>
<td>60</td>
<td>17733</td>
</tr>
<tr>
<td>Pyramimonas sp. (Unident.)</td>
<td>Chlorophyte</td>
<td>560</td>
<td>16229</td>
</tr>
<tr>
<td>---------------------------</td>
<td>---------------</td>
<td>------</td>
<td>-------</td>
</tr>
</tbody>
</table>
Chapter 4  Model validation

4.1  Introduction

Three case studies are modelled to examine model behaviour and to gain insights into the systems being considered. The three cases were chosen to successively test different aspects of the model as follows:

- Seasonal – testing the temperature and light functions
- Silicon and nitrogen limits – testing the Si and N limited responses with full model, excluding zooplankton
- River plume – testing the full model in the Yarra river plume with zooplankton

4.2  Seasonal variations

4.2.1  Background
The Central Bay Chl-\(\alpha\) measurements were noted for interannual consistency, with lowest Chl-\(\alpha\) in winter and highest in late summer (Figure 3.5). Also, remote sites in the Bay show that the dissolved NO\(_x\) tends to behave opposite to the Chl-\(\alpha\) (Figure 3.6). In Chapter 3, it was suggested that the increase in NO\(_x\) in winter might relate to the release of nutrient to the seabed and water column when phytoplankton concentrations drop in the colder water. Optimal phytoplankton growth temperatures are around 20\(^\circ\)C (Figure 2.2) and the temperatures in winter are only 10-11\(^\circ\)C.

The model is applied here to determine if annual water temperature and sunshine cycles provide sufficient variation in NO\(_x\) and Chl-\(\alpha\) to explain the observations. At the same time, as the pattern appears to be seasonal, the model equations for temperature and sunlight modulation of growth can be tested for applicability to Port Phillip Bay. We hypothesise that the observations are primarily caused by seasonal changes in water temperature and sunlight.

4.1.2  Methods
The model settings are given in Table 2.3. Only the settings that are changed for the simulation are specified here.

To model the Central site, the Bubble was set to have no nett inputs or outputs, i.e. river inputs and losses of N to the atmosphere are equal. The assumption being made is that the observed variations at the remote Central site can be mostly explained by N recycling within the phytoplankton, zooplankton, seabed and water column. Of course, advection occurs at the site (Black et al. 1983), but we assume that surrounding waters are behaving the same, as the seasonal changes in Chl-\(\alpha\) have been observed baywide. The year 2005/06 was modelled as it had low rainfall and therefore less chance of substantial nutrient inputs to the Central site from the river plumes.
Two Plankton Functional types were adopted, i.e. a diatom with volume 242 µm$^3$, representative of *Skeletenoma costatum* and a flagellete with volume 50 µm$^3$, representative of *Plagioselmis prolonga*.

### 4.2.3 Results

The model exhibits a good correspondence to the observations (Figure 4.1). The Chl-$\alpha$ prediction (black line) is exhibiting the seasonal pattern and the correct magnitude variations over the year, compared to the data. In synchrony, the dissolved nitrogen in the water column rises in late winter and falls again in summer with a magnitude variation of about 0.015 g m$^{-3}$ and mean of 0.009 g m$^{-3}$, which is compatible with the observations shown in Figure 3.6. The nitrogen contained in the seabed lags the Chl-$\alpha$ time series by approximately 20 days. This lag is induced by the setting of 0.04/day for the fraction of N released back to the water column (Table 3.3), i.e. around 25-30 days for 100%.

The water temperature is mostly responsible for the observations, while sunshine plays a lesser role. Sensitivity tests were conducted on the temperature function and it was found that the Eppley equation (2.7a) gave better results than equation (2.7b), if the Eppley coefficient was changed from 1.06 to 1.10.

![Figure 4.1](image-url)

*Figure 4.1* Central Site in the year 2005/06. (Top panel) Green lines indicate measurements and black lines are model predictions of Chl-$\alpha$. (Bottom panel) Nitrogen in the water column (thick line) and seabed (thin line).
4.3 Nitrogen and Silicon limitations

4.3.1 Introduction
Egge and Aksnes (1992) conducted experiments in an estuary in Bergen Norway using enclosures to examine the growth of natural phytoplankton species with different doses of nutrients. We consider their results from Enclosure 1 which was 4 m deep with volume 11 m$^3$. In their experiment, the enclosure was filled with estuary water, initially dosed with nutrients and then left as batch cultures (without any inputs) for 7 days. Water was then pumped from 40 m depth into the enclosure to replace 30% of the volume per day. The average concentrations of nutrients in the inlet were 10.4, 1.0 and 8.6 µM of nitrate, phosphate and silicate respectively. In addition, they topped up the nutrient levels every second day to instantaneous final concentrations of 5.5, 1.5 and 6 µM of nitrate, phosphate and silicate respectively. They regularly measured Chl-a, nutrients and cells/litre in the enclosures. They identified an early dominance by Skeletonema costatum which was later succeeded by Phaeocystis sp. (possibly P. pouchetii) and small, unidentified flagellates which prospered at the end of the experiment (Figure 4.2). The water temperature varied from 8-14°C.

![Figure 4.2](image-url)
Egge and Aksnes didn’t identify or count the phytoplankton species or report on the daily concentrations of nutrients (only the averages) coming into the container from 40 m. Also, no sizes (volumes) of the phytoplankton in the container were recorded.

4.3.2 Methods
In the model, we duplicated their initial conditions, nutrient doses and experimental methods. The initial concentrations of nutrients were taken from for their Figure 2. Because of the uncertainties in light and temperature, their effects were eliminated by setting the model to optimal light for 12 hours per day while the optimal temperature for growth was set equal to the water temperature. The remaining unknowns were phytoplankton volumes and mortality in the enclosure.

Olenina (2006) suggest that the average size of Skeletonema costatum is around 162 µm³ (ranging from 13-393 µm³), while Maranon et al. (2013) found 242 µm³. For the P. pouchetii, Olenina et al. (2006) present two sizes, 268 and 65 µm³. Given the uncertainties about cell volumes, we modelled two combinations (a) with two large cells (242 and 268 µm³) and (b) with two small cells (162 and 65 µm³). The results were better with the larger sizes and so only these are shown here.

The flagellate which was not identified by Egge and Asknes could not be included in the model. The mortality was set to 5%/day during calibration. Other settings remained the same as in the previous simulations.

4.3.3 Results
There is evidence of agreement between the model and data (Figures 4.3). For example, the Si concentrations fall to nearly zero after about 5 days which halts the growth of the diatom around days 5-8 before pumping of new water into the container from 40 m depth. The N falls to near zero around day 10 in both the model and measurements. The diatom grows first and is eventually replaced by the P. pouchetii in both model and data, and the Nitrogen levels drop very low at the end of the simulation after day 17 when the P. pouchetii starts to dominate. The recurring small peaks in the N time series from the model after day 10 relate to dosing every second day, while Egge and Aksnes measurements were recorded prior to each dosing and so the peaks are not evident in their data.

There are discrepancies. Two temporary peaks in the phytoplankton data (around days 15 and 18) occur after the nitrate in the enclosure of Egge and Aksnes rises inexplicably around day 15, which is probably due to unmeasured higher nutrient concentrations from the inlet. Also, the Si asymptotically approaches the external concentration of 8.6 µM in the model, and is higher than the data. Possibly, another species might be present which is absorbing the Si or the mean value of Si over the full experiment is not well representing Si inputs from the pumping during the later stages of the experiment. On the contrary, the N is well predicted by the model at that time. The prediction of Chl-a by the model is lower than the values measured by Egge and Aksnes.

This simulation raised several issues. The cell volume is a critical and sensitive input. Thus, best results should be obtained when cell volume is measured directly. Also, there are wide variations in size reported in the literature, which can be caused by variations in food abundance, competition between species, temperature, light etc.
The low prediction of Chl-a implies an error in (a) the assumed ratio of C:Chl-a (eqn 2.17); (b) the weight of C per cell (eqn 2.15 and 2.16); (c) the assumed cell sizes; or (d) the fluorescence measurements/counds of Egge and Aksnes. Notably, changing the C:Chl-a ratio in the model (eqn 2.17) gives better agreement between model and data but we were reluctant to make a permanent change to the model in the absence of further confirmation.

The Rios et al. (1998) C:Si ratio for diatom of 0.14 (Table 2.1) was adopted. The Brzezinski ratio by weight of 0.374 caused the available Si to be used up too quickly and the diatom failed to grow to measured levels.

The growth rates from equation (2.3) had to be multiplied by 1.3 for the case with larger phytoplankton (Figure 4.3). The growth rates needed no change when the smaller cell sizes were adopted (not presented here) and so the growth rate discrepancy may relate to uncertainty in cell size.

The lowered setting of the remineralisation coefficient 0.3 (reduced from 0.5) led to the correct abundances of *P. pouchetii* in the model. Other settings caused the prediction to be too low or high. Unfortunately, Egge and Aksnes didn’t report measurements of ammonia levels and no comments were made about detritus in the enclosure.

The measurements in PPB showed that flagellates grow relatively better than diatoms in low N conditions (Figures 3.9 and 3.10). This is compatible with flagellates having a lower half saturation coefficient. However, from the limited dataset of Eppley, the flagellates, on the contrary, appear to have a higher ks for a given cell size (Figure 4.4) while Maranon et al. (2013) found no apparent discrimination between flagellates and diatoms. Similarly, we didn’t have to adjust the ks value obtained from equation (2.8), which is a function of size only, not taxa.

Larsen et al. (2004) suggested that virioplankton are important elements of the total microbial diversity and that they possibly act as an internal driving force in spring bloom successions. However, the virioplankton are unlikely to explain the results here, given the 30% flushing of the enclosure volume per day.

The model was sensitive to the initial phytoplankton concentrations. The *S. costatum* was more abundant initially and grew to outbreak levels first. After the bloom abated and the *P. pouchetii* abundances had increased, it simply took over, starving the *S. costatum* of nitrogen. In relation to discriminating factors, the *S. costatum* had a slightly faster maximum growth rate (being closer to the peak volume of 100 µm³), but the fall velocity of 0.11 m d⁻¹ (in the 4 m deep container) and the Si availability put the *S. costatum* at an overall disadvantage later in the simulation.

Notably, *Phaeocystis pouchetii* is prominent in the open waters of the Barents Sea and around Arctic waters where, as a general rule, outbreaks follow a diatom bloom in late spring (Rey and Loeng 1985). The same behaviour is being modelled here, i.e. the *P. pouchetii* dominates when the N is exhausted by the diatom bloom.
Figure 4.3 Simulations of the Enclosure 1 experiment of Egge and Aksnes (1992), using cell volumes of 242 and 268 µm$^3$ for *Skeletonema costatum* and *Phaeocystis pouchetii* respectively. Top panel: Nitrate (red) and Silicate (black) showing data (thin line) and model (thicker line). Centre panel: Chl-$a$ from the model. Black line is total Chl-$a$; red line is *S. costatum* and blue line is *P. pouchetii*. Bottom panel: Cells/litre for *S. costatum* (red) and *P. pouchetii* (blue). Model is thick line and data is thin line.

Figure 4.4 Data of Eppley (1972) showing nitrate half saturation coefficient versus geometric mean cell diameter for diatoms and flagellates.
4.4 River plume

4.4.1 Introduction
The major river discharge (Yarra River) into the north-eastern section of Port Phillip Bay is considered in this section, with the aim of examining competitive utilisation of nitrogen for the growth of two functional types of microalgae representing diatoms and flagellates. This full-model test uses measured variable boundary conditions in a complex environment around the river entrance, and includes zooplankton growth and grazing. The zone experiences the full effects of the discharging river which flows southward into Hobsons Bay (Figure 4.5).

![Figure 4.5 Northern Port Phillip Bay showing the Yarra River, Hobsons Bay. The Chl-α permanent monitoring site (red dot) is shown within the 4x4 km region of the single “Bubble”.

4.4.2 Methods
The model was tested by comparing the predicted values against:

- time series of Chl-α measured near the surface over an 7-year period from 2004-2011
- the diatom ratio (Diatom: Total Phytoplankton) which was available for the Hobsons Bay site for 3 years from mid 2008 to mid 2011.
- Measurements of juvenile fish (snapper) recruitment over a 7-year period

As noted in the previous chapter, the plankton data were collected approximately monthly, while the Chl-α fluorescence data were daily averaged.
Zooplankton concentrations of dominant taxa have been measured in PPB during the snapper spawning/larval period; December -January, using towed plankton nets. Murphy et al. (2012, their Figure 2a) show typical densities of Paracalanus spp. zooplankton <5,000 individuals m$^{-3}$ (Table 4.1). The actual abundance is greater because the net mesh size of 80 µm would have under-sampled the smallest life stages. For compatibility, the number of zooplankton with prosome length greater than 80 um was extracted from the model for comparison with the data.

Table 4.1. Zooplankton counts (No. m$^{-3}$) from the north and eastern side of Port Phillip Bay. Prey includes Paracalanus nauplii, copepodites, and cladocerans. The “% Paracalanus” is the percentage of Total Zooplankton. Two surveys are conducted each year, the first near the end of November or start of December and the second near the end of December or early January. The values shown are the averages of the two surveys (Pooled data from Murphy et al., 2012). Net size was 80 µm.

<table>
<thead>
<tr>
<th>Year</th>
<th>Paracalanus</th>
<th>Total zooplankton</th>
<th>% Paracalanus</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006/07</td>
<td>21328</td>
<td>71312</td>
<td>29.9</td>
</tr>
<tr>
<td>2007/08</td>
<td>29893</td>
<td>72430</td>
<td>41.2</td>
</tr>
<tr>
<td>2008/09</td>
<td>41063</td>
<td>85711</td>
<td>47.9</td>
</tr>
<tr>
<td>2009/10</td>
<td>49048</td>
<td>106493</td>
<td>46.1</td>
</tr>
<tr>
<td>2010/11</td>
<td>17382</td>
<td>62045</td>
<td>28.0</td>
</tr>
</tbody>
</table>

The region of interest is focussed on Hobsons Bay which receives the full impact of the nutrient-loaded river discharges. A zone 4x4 km was defined as the area of the Bubble (Figure 4.5). The depth was taken as the depth of the halocline dividing the upper layer of fresher river water from the lower layer of salty Bay water. The monitoring station for Chl-a at 3 m depth is mostly recording phytoplankton growth within or just below the upper layer. Thus, the model was compared to the measurements from the upper sensor. The data were daily averaged.

The depths of the halocline for each year are a function of the rainfall intensity, but no attempt was made to vary the layer thickness ($D$) during the years. Instead, a value for the upper layer thickness was chosen for each year (Table 4.2) which was proportional to the mean annual river flow. The volume of the Bubble over the 16 km$^2$ region is therefore $1.6 \times 10^7 D$ m$^3$.

Boundary conditions to the model were time series of (a) daily river flows (interpolated to hourly) (m$^3$ s$^{-1}$) (b) hourly Global solar radiation recorded at the Melbourne Airport (watts m$^{-2}$), (c) average concentrations of N, P and Si in the Yarra River (g m$^{-3}$) and (d) water temperatures and salinities taken from calibrated simulations of the 3-dimensional hydrodynamic modelling of the Bay over the 7 years of interest (Harrison et al. 2007 a,b,c).
Two plankton functional types were simulated: diatoms and flagellates. Within the functional types, we adopted the most common species in the Bay from Table 3. For the diatoms, three species were simulated simultaneously:

- *Skeletonema costatum*
- *Chaetoceros sp. (Unident.)*
- *Cylindrotheca closterium*

with two flagellates:

- *Plagioselmis prolonga*
- *Hemiselmis sp. (Unident.)*

The coccolithophore *Emiliania huxleyi* (while globally important) was neglected because its calcium carbonate shells put it into a different phytoplankton functional group. It was also less prolific in the Bay than the other species.

The phytoplankton volumes are their defining characteristic and the values in Table 3.3 were adopted unchanged in the model. The only remaining unknowns were the mortality coefficients. For the phytoplankton we adopted 10% d\(^{-1}\), noting that much of the losses occur due to zooplankton grazing which is treated separately in the model. For the zooplankton, we adopted 15% d\(^{-1}\) after calibration simulations. All other coefficients remained unchanged (Table 2.3).

Equation 2.7b was adopted for the temperature influence on growth, with optimal temperature in the Bay of 20°C, in accordance with the findings in Chapter 2 (Figure 2.2). As found during the Egge and Aksnes (1992) simulations, the half saturation coefficient for Si was taken as 0.04 g m\(^{-3}\). However, Si proved to be not limiting around the river entrance where common concentrations of silicate in the discharge average 8 g m\(^{-3}\) and so no tests of this parameter were possible. Each model run of 1-year duration started on July 1 of each year when the Bay is relatively dormant and Chl-\(\alpha\) is typically lowest (Figure 4.1).

### 4.4.3 Results

**Phytoplankton**

The calibration of Chl-\(\alpha\) is presented in the top panel of Figures 4.6a-g for the 7 years of simulation. The diatom (red line) and flagellate (blue line) are shown against the measurements of Chl-\(\alpha\) at the Hobsons site (black line).

The measured variation in average levels between the years is being well predicted. Within each year, many of the measured peaks are being well simulated. For example, the substantially higher

<table>
<thead>
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</thead>
<tbody>
<tr>
<td>D</td>
<td>7</td>
<td>5</td>
<td>2.5</td>
<td>2.5</td>
<td>2.5</td>
<td>2.8</td>
<td>9</td>
</tr>
</tbody>
</table>
Chl-a levels in 2004 and 2010 are being simulated, together with the low levels of Chl-a in 2007. The peaks in 2004 are mostly reproduced, and they occur in the model after a spike in the Yarra River inputs (shown in the bottom panel).

The Chl-a measurements of 2009 show no substantial peaks, although floods occur in the Yarra River (Figure 4.6f). The model indicates that zooplankton grazing explains the observations.

There are deviations which occur during two conditions: (a) when measured Chl-a has not responded to a peak in river flow or (b) when a peak in Chl-a is not preceded by a river pulse. The model is unable to treat case (b). Case (a) appears to relate to Chl-a being held in check by zooplankton, although other factors such as plume advection due to variable winds, tides and stratification are not being simulated in Bubble.

Deviations occur rarely due to zooplankton grazing which partially eliminates a Chl-a peak in the model while the peak remains evident in the data.

The peaks of 2010 (Figure 4.6g) appear to be sometimes mistimed by the model, although the substantial increase in total phytoplankton compared to other years is evident in the model. Notably, total phytoplankton from the model is equal to the sum of the magnitudes of the diatom (red line) and flagellate (blue line) and so the model predicts totals similar to the measurements. Other settings provided better results for 2010, but we didn’t wish to start “trial and error calibration” of the coefficients, as this goes against the philosophy of the modelling task (see next Chapter).

Diatom ratios
The predicted diatom ratios for the 3 years when data were available are shown in Figure 4.7a-c. While some of the short-duration variations are not being predicted, the overall pattern is in good agreement with the data. Further discussion can be found in the next Chapter.

Larger Yarra River nitrogen inputs are mostly correlated with a rise in the diatom ratio, as anticipated (Figure 4.7). The largest exception occurs in 2010 from Days 150-230 where river flows are large but the fraction of diatom shows a long-term drop over this 80 day period. The model also shows a drop at this time, albeit much less pronounced than the field data. At the same time, the model shows a slow rise in zooplankton (Figure 4.6g).

Zooplankton
To obtain good calibration, the model must also make an effective prediction of the zooplankton numbers, which have a very substantial impact on phytoplankton abundance and vice versa. Zooplankton numbers were available for 5 years. In each year, two tow surveys were conducted in separate months (Murphy et al., 2012) and the averages are presented in Table 4.1. For the model, we extracted the zooplankton numbers from the same two months, averaged over the month.

The predicted and measured zooplankton best-fit equation has $r^2=0.94$ (n=5) indicating most of the measured variation is predicted by the model (Figure 4.8). The gradient of the regression line is 2.16 which indicates that the model is predicting more than twice the measured numbers of Paracalanus. However, Paracalanus represent only a fraction of the total present in the measurements (Table 4.1). From Table 4.1, the average percent of Paracalanus is 38.6% over the five years. Thus, scaling the gradient by 0.386 gives a value of 0.85, which is closer to the expected value of 1.0.
Inspection of the calibration plots (Figures 4.6a-g) shows that the presence of diatom substantially alters the timing of the zooplankton peak. The peak shape and timing varies between the years due predominantly to the usual factor of rainfall inducing a large phytoplankton bloom which is succeeded by zooplankton. However, if the bloom is predominantly diatom, the zooplankton fails due to equation (2.26) which modulates egg production. The strong comparison between model and measurements indicates that the methodology in the model is highly important. Further implications are discussed in the next Chapter.

**Fish recruitment**

The recruitment of juvenile snapper has been recorded over 7 years (Figure 4.9). Spawning in snapper occurs in water temperatures ranging between 18 to 22 °C (P. Hamer pers. comm.). The trigger water temperature for spawning was taken as 19°C. Accordingly, we extracted the mean zooplankton numbers for the month following the first occurrence of the trigger temperature. This is a critical month for the juvenile fish, as they prosper best with *Paracalanus* in their diet in the early stage of their life (Murphy et al. 2012). Measured recruitment numbers (snapper larval density and 0+ recruits) are shown in Figure 4.9. The larval density and 0+ recruits are highly correlated (Murphy et al. 2013) indicating that the recruit numbers are primarily determined by the density of surviving larvae after spawning.

We hypothesise that inter-annual variations in larval survival depend on the presence of *Paracalanus* and so the zooplankton numbers from the model are compared with the snapper larval density. Once again, the correlation is strong (Figure 4.10). The best-fit curve has $r^2=0.89$ (n=7), which is significant at the p<0.05 level. The gradient of the curve in Figure 4.10 has little physical relevance.
Figure 4.6a  2004/05. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m$^3$ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6b 2005/06. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m$^3$ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6c  2006/07. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m$^3$ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6d  2007/08. Top panel: Calibration of Chl-$\alpha$ showing diatom (red line), flagellate (blue line), with the Chl-$\alpha$ fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m$^3$ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6e  2008/09. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m$^3$ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6f  2009/10. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m³ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.6g  2010/11. Top panel: Calibration of Chl-α showing diatom (red line), flagellate (blue line), with the Chl-α fluorescence measurements (thin black line) from 3 m depth at the Hobsons site. Second panel: Model-predicted zooplankton counts per m³ for sizes >80 µm. Third panel: Nitrogen dissolved in the water column (thick line) and nitrogen in the seabed repository (thin line). Bottom Panel: Inputs of N from the Yarra River.
Figure 4.7a-c  Predicted (thick black line) and measured (thin black line) diatom ratio (diatom/total phytoplankton) for the years (a) 2008/09, (b) 2009/10 and (c) 2010/11. The red lines are scaled Yarra River inputs of nitrogen.
Figure 4.8 Model predicted zooplankton versus measured *Paracalanus* zooplankton (Both No. m\(^{-3}\) for sizes > 80 µm). The best-fit linear equation has \(r^2 = 0.94\).

\[ y = 2.1913x - 18297 \]
\[ R^2 = 0.9366 \]

Figure 4.9 (a) Snapper larval abundance and (b) 0+ juvenile recruit abundance for the 7 years from the 2004/05 season. They are significantly correlated.
Figure 4.10  Model predicted zooplankton (No. m\(^3\) for sizes > 80 µm) versus the number of snapper recruits over the 7 years from 2004/05 to 2010/11. The best-fit linear equation has \( r^2 = 0.89 \).
Chapter 5  Discussion

5.1  Goals of the model development

The initial goal of the work, i.e. to develop an NPZ model that has very few unknown coefficients, has been achieved. Without the guidance of the internal model equations and settings, the number of variables is far too large to test and find a unique calibration result.

Slightly better calibration results may be obtained if the model coefficients were manually tuned. However, tests with the model have shown that the best overall results are produced without manual adjustments because of the numerous coefficient combinations.

5.2  Diatom ratio

The lack of shorter-duration peaks in the model prediction of diatom ratio (Figure 4.7a-c) suggests that the model may be under-estimating the sudden changes in abundance from flagellate to diatom and conversely. This brings us back to the fundamental question of factors which discriminate between phytoplankton functional types.

The two PFT’s in the simulation were diatom (3 species) and flagellate (2 species). The flagellates were smaller. However, they remained close to the growth peak (Figure 2.1b) and had maximum growth rates that were similar to the diatoms (Table 5.1). The smaller size however gave the flagellates a lower half saturation coefficient, which meant that they bloomed better in low N conditions, when their slower growth rate was compensated for by the small half saturation coefficient.

To accentuate the discriminating factors, tests with the model showed that if the half saturation coefficient and maximum growth rate for diatom were increased by 40%, without altering the values for flagellates, the short-term peaks in species abundance appeared in the model. This change accentuated the tendency for flagellates to favour the low nutrient conditions and diatoms to bloom in high nutrient loads (Figure 3.9). Accordingly, the variations in nutrients due to intermittent river flow were paralleled by faster and more numerous transitions from flagellate to diatom and conversely. Further assessment of half saturation coefficients which may discriminate between diatoms and flagellates is warranted.

The model indicated that zooplankton grazing plays a dominant role in controlling phytoplankton numbers, as anticipated. However, the higher egg mortality when diatoms are abundant reduces zooplankton numbers at these times. Notably, the measurements in Port Phillip Bay show that the total zooplankton numbers (i.e. Paracalanus plus other species) tend to be less variable than the Paracalanus (Table 4.1), but they remain correlated (Figure 5.1). This suggests that the diatom effect is felt at the total zooplankton level, rather just Paracalanus.
Table 5.1 Description of the phytoplankton in the Yarra River simulation.

<table>
<thead>
<tr>
<th>Number</th>
<th>Type</th>
<th>Volume (µm³)</th>
<th>$\mu_{\text{max}}$ (d⁻¹)</th>
<th>NO_x half saturation (g m⁻³)</th>
<th>$V_{\text{fall}}$ (m d⁻¹)</th>
<th>Cells L⁻¹ x10⁶</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Diatom</td>
<td>110</td>
<td>1.02</td>
<td>0.009</td>
<td>0.054</td>
<td>2.96</td>
</tr>
<tr>
<td>2</td>
<td>Diatom</td>
<td>180</td>
<td>0.90</td>
<td>0.011</td>
<td>0.076</td>
<td>2.03</td>
</tr>
<tr>
<td>3</td>
<td>Diatom</td>
<td>242</td>
<td>0.84</td>
<td>0.012</td>
<td>0.092</td>
<td>1.62</td>
</tr>
<tr>
<td>4</td>
<td>Flagellate</td>
<td>27</td>
<td>0.68</td>
<td>0.006</td>
<td>0</td>
<td>11.47</td>
</tr>
<tr>
<td>5</td>
<td>Flagellate</td>
<td>60</td>
<td>0.85</td>
<td>0.008</td>
<td>0</td>
<td>5.72</td>
</tr>
</tbody>
</table>

5.3 Fish (snapper) Recruitment

The model shows that the success of snapper recruitment is governed by the number of *Paracalanus* present after spawning. In turn, the number of *Paracalanus* depends substantially on parameters such as river flow, nutrient levels and phytoplankton abundance. However in addition, the model demonstrates that the diatom ratio plays a critical role which is being represented in the model through zooplankton egg mortality and survival, modulated by equation 2.26.

The number of zooplankton is less after a diatom bloom (due to low egg numbers) than after a flagellate bloom. As such, fish spawning after a large diatom bloom is more likely to fail. This explains
why 2010 had substantial rain, nutrient delivery and high phytoplankton abundances, and yet the fish recruitment was poor (Figure 4.9). The model shows this was due to failure of the zooplankton at the time of spawning because of higher diatom abundance.

5.4 Summary of model effectiveness

There are many biological, chemical and physical parameters embedded in the model, and these must operate collectively to produce the final outcomes and predictions. Thus, the model has effectively dealt with:

- the variety and complexity of boundary conditions and marine environments as confirmed in 3 different case studies
- the use of volume as a key descriptor for phytoplankton which enabled life cycle factors to be determined internally and allowed different phytoplankton to be simulated simultaneously across taxa
- more realistic exposure of the zooplankton to the environment throughout its life cycle and the methodology allowed daily growth to be tracked and utilised
- The effects of diatom on primary and secondary production
- Other factors and equations which have been automated, as described in Chapter 2

In general, we have adopted several novel combinations of equations, developed new empirical relationships from published data and blended these to create a model which is able to simulate primary and secondary productivity within a complex river discharge, and under conditions of multiple nutrient limitations over seasonal and inter-annual time scales.
Chapter 6  Bubbles

6.1  Introduction
A Nutrient, Phytoplankton and Zooplankton model acting within a single cell has been described above. This chapter presents the full multi-cell model “Bubbles”. The solution methods described in previous chapters for a single particle are applied to numerous individual particles to fill the spatial domain of Bubbles. The fundamental differences between the single and multi-cell models are:

- Treatment of multiple particles, rather than a single particle (while retaining the same methods for each particle).
- Allowance for advection of particles and for diffusion of the information that the particles carry
- Allowance for multiple boundary conditions (including Bass Strait, rivers and WTP)

In addition, a more specific treatment of ammonium cycling was incorporated into both models. While the model is general and suitable for a diversity of locations, the focus here remains on Port Phillip Bay and nearby Bass Strait.

6.2  Features specific to the spatial model

6.2.1  The need for coupling with other models
Bubbles is one of several models within the well-known “3DD Suite of Coupled Physical and Biological Process Models”, developed commercially by Black. The 3DD Suite contains modules to predict most marine and aquatic physical processes. The flagship model is 3DD, a three-dimensional hydrodynamic, salinity and temperature model with ocean/atmosphere interactions. Bubbles reads the calibrated files coming from 3DD to obtain currents for advection, temperatures for growth rates and salinities for mortality or growth modification.

6.2.2  Ammonium cycling
Ammonia is a by-product of mortality and excretion of phytoplankton and zooplankton. The ammonia is nitrified in the water column to NO\textsubscript{X} at a rate of approximately 3-5% per day (depending primarily on water temperature). In the model, the dead phytoplankton and zooplankton excretion is released as ammonia and then converted to NO\textsubscript{X} at a base rate of 3.5% per day. In the model, the phytoplankton can preferentially feed on either NO\textsubscript{X} or NH\textsubscript{4} or both. The preference ratio is set by the user.

6.2.3  Advection and Diffusion
Each particle in Bubbles is most easily understood as a volume of water where phytoplankton and zooplankton grow and die. Each particle contains the following state variables:

- XYZ coordinates describing the position of the particle in the model domain, both horizontally and vertically
Two additional processes need to be incorporated into the spatial model. For example, diffusion is a very important process in nature. In reality, any initial volume of water mixes through time, and the particle volumes are no exception. Such mixing leads to diffusion of the particle contents. Further diffusion occurs due to current shear (both horizontally and vertically), and due to short-term temporal variation of currents around the mean. The particles are also subject to advection when carried by currents.

Advection is calculated by 3-dimensional interpolation of the currents onto the particle XYZ position from the gridded (Eulerian) data of Model 3DD. This advection has a random walk (non-deterministic) component that associates with the mixing of whole particles in space. There is no transfer of information between the particles. The random walk is modelled as:

\[ \Delta X = R_n (6A_H dt)^{1/2} \]  

(6.1)

where \( R_n \) is a random number (-1<\( R_n \)<1), \( A_H \) is the horizontal eddy diffusivity (m²s⁻¹) and \( dt \) is the model time step (s). The model applies different eddy diffusivities along and across the flow direction.

In addition, diffusion of information between the particles occurs. This is modelled by interpolating all of the information held by the particles (e.g. zooplankton arrays, Nitrogen etc.) onto a regular grid. Then, new particles are created at equi-distant locations throughout the model domain by interpolating the gridded data. This double interpolation smooths the model domain while ensuring that particle contents are diffused with nearby particles. The diffusion step occurs at a user-selected interval which is less frequent than the model time step. For the modelling here, the diffusion occurs every 72 hrs and the model time step is 1 hr.

6.2.4 Treatment of the seabed

Sea bed treatment was the same as the single particle model, except that:

- The seabed was divided into cells, of the same size as the HD model.
- At each time step, the nitrogen and other chemicals released back to the water from each seabed cell was divided between all particles in the water column above that cell. Because the particles above that section of seabed have different volumes, a weighting based on
particle volume was applied when proportioning the chemicals released to particles from the seabed.

- At the seabed, some of the chemicals are released to the atmosphere, buried or taken up with a rate determined by the coefficients (%/day).
- The total mass of chemical arriving at the bed due to decay or mortality of phytoplankton and zooplankton (via deposition processes from the water column) is added to the total concentrations of each chemical stored in the seabed arrays on a cell-by-cell basis each time step. The cell is found knowing the horizontal position of the particle.

6.3 **Testing of the model**

The methods adopted in the single particle model were fully embedded within the Bubbles code. The computational overheads with particle solutions are large and so the code must be efficient. Also, every variable in a computer code is linked through the calculations and so the modeller must check all variables one-by-one to guarantee that any inconsistencies are eliminated.

Bubbles was then tested in 3 different ways:

1. The model was upgraded to enable simulations of a single particle, thereby fully duplicating the single particle model. This allowed all elements of the new code to be tested within the new model domain.
2. An idealised embayment which resembled Port Phillip Bay was modelled on a coarse grid.
3. Detailed PPB modelling for 3 years was calibrated against measurements of Chl-α at 3 sites.

6.3.1 **Single cell**

Using Bubbles, a single particle simulation was undertaken for the year 2004/05. The model was found to reproduce the single particle model results presented in earlier chapters.

6.3.2 **Idealised embayment**

The idealised embayment is shown in Figure 6.1. Model 3DD (in 3-dimensional, barotropic mode) simulated the hydrodynamics for the year 2004/05. Three vertical layers, each 2 m thick, allowed 3d circulation to occur. Measured time-varying winds and Yarra River flows (m$^3$s$^{-1}$) formed the boundary conditions. The river entered in the top right cell of the grid (Figure 6.1) and winds were taken as spatially uniform. The embayment is fully enclosed, except for the river inputs.

Examples of the hydrodynamics from Model 3DD are shown in Figure 6.2. A clockwise or anti-clockwise vortex is common in the Bay, with upwelling at the lee coast and downwelling at the windward coast (Figure 6.2).

For the Bubbles modelling, the same settings used in the single particle model were adopted. Five different phytoplankton and one zooplankton species were modelled simultaneously. All the growth, mortality, half saturation coefficients etc. were identical to those in Table 2.3.
The main goal is to show that the model is behaving as expected. Bay-wide measurements can be seen in Figures 3.7 for comparison with model results. The Yarra Plume dominates the system, with NOx, NH4 and Chl-a tracking the plume’s location. Typical measured values of 0.02 g.m^{-3} for NOx are evident in the model, and similarly the noticeably smaller typical values for NH4 of 0.01 g.m^{-3} are also being reproduced. The Si pattern is more variable bay-wide and less strongly associated with the plume in the model and measurements. Finally, the mean Si values of around 0.12 g.m^{-3} are being reproduced.

While this comparison is not a formal calibration, the magnitudes and patterns from the model are in good agreement with observations, which justifies proceeding to the fully calibrated model of PPB.

![Figure 6.1: Bathymetry (m) of the idealised embayment. The green colour is land. Maximum depth is 6 m. The river inputs occur in the top right hand cell (similar to the Yarra River position in Port Phillip Bay). The model is 3-dimensional with three 2 m layer thicknesses.](image)

![Figure 6.2: A clockwise vortex at the surface layer of the model associated with wind-driven circulation. Downwelling occurs at the windward coast of the idealised embayment. The circulation in layer 2 (right panel) is different to layer 1 (left panel).](image)
Figure 6.3a,b. N associated with NO$_x$ (left panel) and NH$_4$ (right panel) from the model shows highest levels around the river discharge. These dissipate to the west. The magnitudes are in agreement with typical Baywide measurements and the pattern is similar to the observed dynamics associated with the Yarra plume. While similar to NO$_x$ patterns, the NH$_4$ occurs in response to mortality and excretion and then nitrifies to NO$_x$ and so the patterns are different.

Figure 6.3c. Silicon associated with silicic acid from the model shows a very different pattern to the nitrogen due to silicon’s much slower release rate back to the water column from the seabed. Also, Si uptake and recycling is associated with diatom abundance, not total phytoplankton.
Figure 6.3d,e. Total Chl-α associated with three diatom and two flagellate phytoplankton. The magnitudes decay away from the river particularly to the west in the idealised Geelong Arm. The right panel shows advection carrying the main bloom to the south of the river entrance.

Figure 6.3f. Zooplankton (Paracalanus) distribution. In this example, most Paracalanus are found on the eastern side of the bay where the nutrients are sufficient for ample phytoplankton growth.
6.4 Port Phillip Bay Calibration

In this section, the model is calibrated against PPB measurements over a 3 year period. The years are:

- 2006/07 - low rainfall and low snapper recruitment
- 2008/09 - intermediate rainfall and high snapper recruitment
- 2010/11 – high rainfall with low snapper recruitment

A three-fold model coupling was required:

1. the dynamic Catchment model provided by the Environment Protection Authority of Victoria and Melbourne Water (defining freshwater and nutrient inputs),
2. the 3-dimensional salinity and temperature stratified Hydrodynamic Model 3DD (for tidal, wind and density-induced circulation),
3. Primary Production Model Bubbles (for nutrient uptake, phytoplankton, zooplankton and fish).

6.4.1 Hydrodynamic Model 3DD

Model 3DD uses a sophisticated set of boundary conditions, including satellite sea surface temperatures to eliminate temperature drift in the model over long (multi-year) simulations (e.g. Harrison et al. 2007a,b,c). The mathematical equations for heat gains and losses in the water column are based around hourly inputs of Global Solar Radiation, humidity and winds. The winds also drive circulation, along with the tides and low frequency oscillations coming from Bass Strait. River inputs are either recorded or from a catchment model when the river measurements are not available.

The modelling presented here covered Port Phillip Bay and northern Bass Strait. The hydrodynamic model was first established in the mid-1980’s (Black et al. 1993). Subsequent long-term studies using the same models have required detailed model calibration, for example:

- Low-frequency oscillations around the coasts of Victoria, Tasmania and NSW for the Australian Research Council (Middleton and Black, 1994)
- King George whiting recruitment for the Australian Research Council (Jenkins and Black 1994, Jenkins et al. 1997, 1999, 2000)
- Scallop investigations (Black and Parry 1999) for the Fisheries Research Development Corporation
- Better Bays and Water Ways (BBWW) programme at the request of the Environment Protection Authority of Victoria (EPA Victoria) and Melbourne Water
- Victoria’s Desalination Plant Environmental Assessments for the Government of Victoria
- Western Sewage Treatment Plant (WTP) for Melbourne Water

No further calibration of the hydrodynamics was required. For the present study, we used existing stratified hydrodynamic modelling of 3 different years (each starting on July 1 when the bay is most dormant). These HD simulations were originally developed for the King George whiting studies. The
adopted 800x800 m hydrodynamic model grid has been calibrated for currents, salinities and temperatures.

Measured flows were used for (1) the WTP outfalls, and (2) the combined Yarra and Maribyrnong Rivers. The Catchment Model provided flows for 6 other inputs:

- Little River
- Werribee River
- Skeleton Creek
- Kororoit Creek
- Mordialloc Main Catchment
- Patterson River

6.4.2 Boundary Conditions for Bubbles

For the WTP, measured chemical concentrations and flows provided by Melbourne Water were interpolated to daily time series.

For river sites, the mean chemical concentrations for the different years were obtained from Melbourne Water annual summaries of waterway water quality. Bass Strait data were inferred from measurements at the Heads during the PPBES (Longmore et al., 1996). Silicate data were obtained from historic measurements in the State Government Water DataWarehouse, but no silicate data were available for the modelling years. Given the importance placed on silicate in this model, accurate river silicate discharge data is a clear need.

Table 6.1. Nutrient boundary conditions: mean annual concentrations for the modelled years 2006/07, 2008/09 and 2010/11.

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>NH₄-N</th>
<th>NO₂-N</th>
<th>NO₃-N</th>
<th>PO₄-P</th>
<th>SiO₄-Si</th>
<th>DetN-N</th>
<th>DetP-P</th>
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</thead>
<tbody>
<tr>
<td>Yarra</td>
<td>2004/05</td>
<td>0.05</td>
<td>0.55</td>
<td>0.011</td>
<td>(8.05)</td>
<td>0.51</td>
<td>0.054</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2007/08</td>
<td>0.037</td>
<td>0.27</td>
<td>0.011</td>
<td>0.54</td>
<td>0.047</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>2008/09</td>
<td>0.044</td>
<td>0.45</td>
<td>0.008</td>
<td>0.54</td>
<td>0.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2010/11</td>
<td>0.048</td>
<td>0.61</td>
<td>0.01</td>
<td>0.81</td>
<td>0.08</td>
<td></td>
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</tr>
<tr>
<td>Maribyr</td>
<td>2004/05</td>
<td>0.03</td>
<td>0.18</td>
<td>0.012</td>
<td>(5.0)</td>
<td>0.9</td>
<td>0.046</td>
<td></td>
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<tr>
<td></td>
<td>2007/08</td>
<td>0.017</td>
<td>0.053</td>
<td>0.004</td>
<td>0.9</td>
<td>0.032</td>
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<tr>
<td></td>
<td>2008/09</td>
<td>0.022</td>
<td>0.078</td>
<td>0.002</td>
<td>0.98</td>
<td>0.058</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2010/11</td>
<td>0.031</td>
<td>0.38</td>
<td>0.008</td>
<td>1.05</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mordi</td>
<td>2004/05</td>
<td>0.09</td>
<td>0.75</td>
<td>0.1</td>
<td>(12.0)</td>
<td>1.02</td>
<td>0.14</td>
<td></td>
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<td></td>
<td>2007/08</td>
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<td>0.175</td>
<td>0.04</td>
<td>0.87</td>
<td>0.15</td>
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<tr>
<td></td>
<td>2008/09</td>
<td>0.062</td>
<td>0.29</td>
<td>0.042</td>
<td>0.74</td>
<td>0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2010/11</td>
<td>0.1</td>
<td>0.51</td>
<td>0.11</td>
<td>1.26</td>
<td>0.16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Patterson</td>
<td>2004/05</td>
<td>0.06</td>
<td>0.64</td>
<td>0.03</td>
<td>(8.9)</td>
<td>0.93</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2007/08</td>
<td>0.066</td>
<td>0.24</td>
<td>0.02</td>
<td>0.88</td>
<td>0.07</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>2008/09</td>
<td>0.05</td>
<td>0.59</td>
<td>0.011</td>
<td>0.75</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2010/11</td>
<td>0.05</td>
<td>0.65</td>
<td>0.025</td>
<td>1.05</td>
<td>0.09</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
### 6.4.3 Calibration

The third model assessment involved calibration of the predicted time series of Chl-α against the measurements at 3 sites in Port Phillip Bay (Figure 3.3), which were:

- Hobsons – near the entrance to the Yarra River
- Long Reef – offshore of the WTP
- Central - an isolated site near the centre of the Bay

Each of the three sites was compared to the 3 years of model simulation.

The results are shown in Figures 6.4a,c for years 2006/07, 2008/09 and 2010/11 respectively. The model is clearly finding the right levels for the different years, with low Chl-α in both 2006/07 and 2008/09 and high levels in the wet year 2010. Moreover, the differences between the 3 sites for each year are well reproduced.

For 2010, we have included both the upper and lower data sensors for Hobsons, and the model is mostly predicting levels between the two measurement sensors (Figure 6.4c). On one occasion during 2010 at Hobsons, the model predicts a peak not evident in the data around Day 160 (Figure 6.4c). There are periods when the upper and lower sensors at Hobsons do not correlate, probably due to the 3-dimensional circulation caused by northward intrusion of bottom water below the fresher surface layer flowing south from the river.

In 2010, the model fails to predict the small increases/peaks at the Central site which appear to be associated with advection of blooms from either WTP or Yarra. Further calibration of the model is needed to resolve the source.
In 2010 at Long Reef, the data around 60 days is anomalous. The model otherwise predicts the overall variations in the Long Reef measurements, but appears to miss some of the short-duration peaks.

Figure 6.4a  2006 calibration of the model against measured Chl-α at Hobsons, Central and Long Reef. The model time series is coloured black and the field data is green. Missing field data is presented as a straight segment (Note that the field data for Long Reef is not available).
Figure 6.4b  2008 calibration of the model against measured Chl-α at Hobsons, Central and Long Reef. The model time series is coloured black and the field data is green. Note that missing field data is presented as a straight segment.
6.4.4 Sensitivity testing

There seems to be more “noise” in the measurements and some sharper peaks than in the model. Sensitivity testing was undertaken to assess this, with a focus on phytoplankton growth rates, horizontal eddy diffusivity, and phyto/zoo mortality coefficients. The year 2010/2011 was adopted for its greater variation in measured Chl-α and rainfall.

The growth rates are set by the model from the phytoplankton volumes (eqns. 2.3). Thus, to undertake sensitivity testing, the computer code was modified internally to multiply the empirical growth rates by a factor of 5. At the same time, the phytoplankton mortality was increased by a factor of 5 from 5%/day to 25%/day. Figure 6.5 shows the comparison of Run 4 with normal growth rates and Run 2 with the same settings except for the 5-fold growth and mortality changes.

Enticingly, Run 2 shows more variation and appears to mimic the sharp rise in the peaks better than Run 4. However, while Run 4 underestimates the peaks, it produces a better agreement overall with the underlying variations over the year. Run 2 shows substantial deviation around Day 200 at Long Reef and over the second half of the year at the Central Site.
Growth rates of order 5/day are substantially greater than measured values (e.g. Furnas (1991), Maranon et al. (2013)). Our own analysis of growth rates in PPB showed that most were less than 1/day (Figure 3.11). Examination of the model output indicates that many of the peaks at Central Site and Long Reef are advected from the Yarra River, while some at Long Reef come from WTP. That is, the blooms are not growing locally and so the sharp rise in concentration is not due to local growth, but more simply reflects an advecting concentration gradient.

Thus, in the next sensitivity tests, we considered the influence of horizontal mixing which tends to diffuse sharp concentration gradients as they advect with the currents. Run 6 with horizontal eddy diffusivity of 4 m$^2$s$^{-1}$ is compared to Run 7 with diffusivity of 10 m$^2$s$^{-1}$ in Figure 6.6. Clearly the larger eddy diffusivity in Run 7 is damping out the peaks before the blooms are reaching the sensor sites from the key sources. The effect is most pronounced at Hobsons.

Further investigation of the growth and migration of blooms is warranted. This may be best approached with high-resolution measurements around the Yarra entrance (or WTP) over single blooms.

Figure 6.5 Comparison of Run 2 (left column) with Run 4 (right column). The empirical growth rates and phytoplankton mortality were 5 times greater in Run 2.
Figure 6.6  Comparison of Run 6 with Run 7, whereby the horizontal eddy diffusivity was increased from $4\, \text{m}^2\text{s}^{-1}$ to $10\, \text{m}^2\text{s}^{-1}$.
Chapter 7  Discussion

The purpose of the study was to develop, test and validate a powerful model of Primary Production which is general, but focussed on Port Phillip Bay. The requirements were (1) to find novel techniques that eliminated most of the “unknown coefficients”, which (2) allowed a much more general approach and (3) provided ways to treat PPB phytoplankton more effectively by classifying into Plankton Functional Types. This has been achieved with unprecedented accuracy, given that the model takes most of the control away from the operator by primarily using just species volume as the main input descriptor.

With this powerful tool, the next goal is to examine the impacts of nutrient discharges on PPB. Impacts may be felt on biomass, fish recruitment and the marine eco-system in general and can be either positive or negative.

It’s well accepted that nutrients are needed for the survival of Port Phillip Bay’s marine life and that different nutrient concentrations lead to different phytoplankton dominance. In PPB, the diatoms favour the higher nutrient loads coming from the Yarra River. For example, Figure 7.1 from December 2010 shows diatoms dominating near the Yarra plume and being most common on the east side of the Bay. The Geelong Arm and the plume from WTP had higher flagellate concentrations at this time.

However, while relative nutrient concentrations between Yarra and WTP play a role, the underlying cause of the reduced diatom prevalence in the west appears to be the Si influence. Figure 7.2 shows that the eastern Bay is above the 0.2 gm⁻³ level, while the western Bay experiences lower levels. The hydrodynamic modelling revealed a common net current which runs from the entrance past St Leonards and towards the WTP. In Figure 7.2, this current can be inferred from the zone of low Si coming from the ocean. Thus, lower Si in the west is not only associated with the discharges (WTP versus Yarra) but also relates to the advection of low Si ocean waters into this region by the dominant circulation.

In the lower Si concentrations of the western Bay, the zooplankton was most common in the Geelong Arm at this time (Figure 7.3), noting that the zooplankton are subject to better egg survival as the diatom concentration drops (eqn 2.26). Interestingly, the model prediction of zooplankton distribution is confirmed by field measurements in December 2010. Figure 7.4 shows the highest measured zooplankton abundance occurring in the Geelong Arm near Point Wilson, in agreement with the model. Moreover, the magnitudes of the predicted zooplankton numbers in the Geelong Arm, east side of the Bay and in the entrance are in good agreement with the measurements.

Over the full year 2010/11, the average phytoplankton concentrations exceed 2 µgL⁻¹ around the north, north-west and north-east of the Bay (Figure 7.5), i.e. along the dominant hydrodynamic pathways of nutrients discharged from WTP and Yarra River. However, with the spatial variation in the ratios of diatom to flagellate, the zooplankton pattern is similar to the phytoplankton overall, but there are differences with relatively more zooplankton in Corio Bay and Geelong Arm (Figure 7.6). Different patterns occur in other years in response to changed nutrient inputs and hydrodynamics under the variable weather conditions.
Notably in relation to snapper recruitment, the model shows the zooplankton growing after the snapper spawning period of November/December, which can explain the poor recruitment of snapper in 2010/11.
Figure 7.1  The relative proportion of diatoms and flagellates (where 0 is all flagellates, 0.5 is even and 1.0 is all diatoms) during December 2010. The diatoms are more dominant near the Yarra plume and are more common on the east side of the Bay. The Geelong Arm and the plume from WTP is flagellate dominated at this time.

Figure 7.2  Silica with threshold of 0.2 g.m$^{-3}$. The western side of Port Phillip Bay is more Si limited.
Figure 7.3  The modelled zooplankton abundance during December 2010. Most are found in the Geelong Arm near Point Wilson where the numbers are 40-60,000 m$^{-3}$. Numbers on the east side of the Bay are 10-25,000 m$^{-3}$ and the entrance is <10,000 m$^{-3}$.

Figure 7.4  Mean zooplankton numbers measured found in PPB in December 2010 (G. Jenkins and P. Hamer, unpublished data). Most were found in the Geelong Arm south of Point Wilson.
Figure 7.5 Integrated phytoplankton averaged over the year 2010/11. The zones around the north, north-west and north-east all experience average levels above 2 $\mu$g L$^{-1}$, but much of the Bay and near the entrance is lower.

Figure 7.6 Integrated zooplankton averaged over the year 2010/11. The Geelong Arm and Yarra plume have the highest average.
Let’s start with some very simple equations:

1. Not enough nutrients = dead or poor marine life
2. Too many nutrients = increased chance of algal blooms and possibly poor marine life
3. Wrong kind of nutrients = wrong kind of algae?
4. Perfect amount of nutrients = beautiful Bay with lots of fish to catch!

So what’s the perfect amount? This depends on many factors but the key ones are:

- **Volume of the Bay** which leads to dilution. The volume of the Bay is orders of magnitude larger than the volumes discharged per day from rivers and outfalls.
- **Strength of the currents** which leads to removal of nutrients by advection from around the river entrances. The strongest harmful blooms near the Yarra entrance appear to have occurred after rain in calm or southerly wind conditions (which hold the plume near the Yarra River entrance) and after the nutrient levels have been primed by prior rainfall events.
- **Dilution due to ocean entrance exchanges.** For a Bay volume of $2.63 \times 10^{10} \text{ m}^3$ and flushing time of 14 months, the net volume exchanged per second to flush the Bay is $700 \text{ m}^3 \text{s}^{-1}$. This is greater than the total river and WTP input volumes and so a considerable fraction of the nitrogen and other nutrients is being removed by entrance flushing, notwithstanding the need for nutrients to advect and mix from the rivers to the entrance.
- **Absorption by marine biota** and possible removal by human activities, e.g. fishing, seaweed harvesting, mussels, oysters etc. Current estimates suggest that only a small percent of the total N is contained within harvestable species in the Bay, i.e. most is held within the phytoplankton (Longmore and Nicholson, 2012).
- **Denitrification in the seabed** causing substantial losses of N$_2$ to the atmosphere. Murray and Parslow (1999) estimated a total annual loss of around 6,000 tonnes of N, which was 70% of the total inputs from rivers and outfalls.

Previous studies (e.g Harris et al. 1996) have focussed heavily on the denitrification capacity of the seabed to remove the inputs and decisions were taken with respect to establishing upper limits for nutrient inputs from WTP. However, our study has shown that other factors need to be considered. Moreover, the distribution of N in PPB is not uniform (Figure 3.7c). The Central regions have very low N concentrations, while Yarra and Geelong Arm is above the Baywide average.

Our view is that more nutrients are needed in many parts of the Bay to increase marine biomass. Currently, large areas throughout the Central Bay are unproductive, especially during the winter. No studies in the past have examined the benefits of the nutrients entering the Bay from rivers and WTP. No studies have been previously able to examine the downstream impacts of changing phytoplankton composition on the marine eco-system.
7.3 Next steps

Overall, the model is potentially a very powerful tool for testing the effect of different levels of nutrient input on the phytoplankton and zooplankton communities, and also on fish recruitment and productivity. The model could be further extended to include other ecological components such as seagrass and provide for more integration of impacts and benefits. Seagrass distribution could be modelled in relation to wave exposure, light climate and nutrient availability mediated by phytoplankton dispersal.

Proposed future Research needs and applications

The work to date leads to eight modules of potential future work:

1. Refining and further developing the model
2. Benthic nutrient exchange studies
3. Modelling to support target setting and operational insight
4. Modelling to support actions from EMP review
5. Pathways to Productivity project / ARC Linkage application
6. Bubbles modelling to incorporate seagrass dynamics
7. Bubbles modelling to incorporate drift algae dynamics
8. Bubbles modelling to incorporate shellfish reef dynamics

Module 1. Collection of field data to refine and further develop the model

Further refinement and development of the model would be valuable to increase confidence in the predictions and also allow for a greater range of ecological processes to be addressed. This would also increase confidence in using the model for future scenario planning, that is, further exploring opportunities to increase environmental benefits while at the same time, where possible, reducing costs. The current calibration of the model is based on continuously recorded fluorescence data that is proportional to Chlorophyll a pigments that are in turn proportional to phytoplankton concentration. Unfortunately these relationships are quite imprecise with wide variation in the Chl-a content of different phytoplankton species, and also significant variation in the relationship between fluorescence and Chl-a depending on species and environmental conditions. Fluorescence measurements can also be affected by fouling of meters and a number of other factors. This means that where there is deviation in the modelled phytoplankton concentration abundances with the field fluorescence measurements (as occurred in some cases at very short time scales); it is unknown whether this is an issue with the specification of the model or if it is related to anomalies in using fluorescence as a proxy for phytoplankton abundance. This issue could be resolved by taking high frequency (i.e. daily) phytoplankton samples in the same location as the fluorescence sensors for comparison with model predictions. Ideally this high-frequency sampling would be carried out over a period of variable flow (i.e. a flood event). Sampling will include physical measurements (temperature, salinity, turbidity), nutrients and chlorophyll a, as well as laboratory identification and enumeration of phytoplankton. The results will then be used for model calibration and adjustment.
Moreover, the current study has highlighted the possible important role of silicate limitation on diatom growth that is potentially beneficial to fish recruitment. Further information on silicate levels and diatom growth limitation would be valuable. This would include field surveys of silicate levels in relation to the diatom/flagellate ratio, as well as laboratory studies on diatom growth in different levels of silicate concentration. The results will lead to improvement in the model treatment of silicate, and therefore more accurate model predictions (N.B. This work would be covered in Module 4 if that were funded either by ARC or directly, and the cost may be reduced if EPA underway sampling can provide the field data on silicate concentrations).

Module 2. Benthic nutrient exchange studies

The specification of exchange of nutrients between the water column and the benthos (i.e. denitrification) could also be improved through some targeted field sampling. Information on these processes to date has come mainly for benthic chambers deployed in in a few selected locations; however, information is needed from a range of sites with varying sedimentary and environmental conditions. New methods currently being developed by Andy Longmore (funded by DELWP and Melbourne Water) based on genomics (measuring the expression of Nitrogen cycling genes) are expected to provide a cost effective means of examining denitrification at a range of sites, providing invaluable data for the development and calibration of the model. The sampling will provide valuable empirical data of interest to a range of stakeholders. The results will also form the basis of potential ongoing monitoring. The technique is currently under development and will be ready to apply in the 2016/17 financial year. The module also includes updating and refining the model based on the results.

Module 3. Modelling to support operational planning and insight

The model has the potential to support the setting of nutrient targets and also provide insights into potential operational changes that could make nutrient delivery more efficient. As well as exploring the effect of different nutrient levels on the pelagic community and fish productivity, the model can be used to evaluate different management strategies for the release of nutrients. For example, insights from modelling to date are that nutrient limitation of the productivity in the bay is greater in drought conditions, opening the possibility of time varying nutrient targets in response to climatic conditions. In addition to time varying targets on an annual scale, the modelling also indicates that there is potential to release more nutrients in winter than in other seasons because phytoplankton growth is limited by other factors. The modelling could also be used to investigate the relative impacts of nutrients from the catchment versus the Western Treatment Plant (WTP). Management may involve varying the mix of limits on nutrient input from these two major sources. Scenario modelling of the effects of nutrient inputs on bay productivity can potentially be linked to future management actions, such as the extent and timing of WTP upgrades. Modelling would investigate management scenarios that provide environmental benefits while at the same time minimising costs.

Module 4. Modelling to support actions from EMP review

The review of the Port Phillip Bay Environmental Management Plan (EMP) is utilising modelling scenarios to test review outcomes. This modelling will primarily be undertaken using the ELCOM-CAEDYM suites. The “bubbles” modelling, however, may prove useful for examining specific EMP
questions relating to pelagic productivity. Underlying equations and outputs from the “bubbles” model will be transferable to the ELCOM-CAEDYM modelling. An example of where Bubbles modelling could prove useful to the EMP review is in determining the potential economic benefit of nutrient inputs to Port Phillip in relation to fisheries and aquaculture, and also through habitat productivity (e.g. seagrass, shellfish reefs)

Module 5. Pathways to Productivity project (ARC Linkage Application)

An ARC Linkage application has been developed for submission in 2015 based on the “bubbles” modelling and was focussed around an extensive field calibration and verification program, including innovative methods for continuous measurement the flagellate/diatom ratio, as well as expanding the analysis from snapper to include a number of other important fish species (e.g. flathead, anchovy) and invertebrate species (e.g. aquaculture mussels, scallops). This work represents an expanded level of spatial and temporal sampling for model verification and development that would build on the minimum level of critical field verification represented by the work in Module 1.

Module 6. Bubbles modelling to incorporate seagrass dynamics

Seagrasses provide highly valued ecosystem services such as increasing secondary productivity, providing nursery and feeding habitat for fish, stabilising sediments and preventing erosion, and sequestering Carbon. Recent studies have suggested that seagrasses in the central and southern regions may be nutrient limited, and may be dependent on dispersal of phytoplankton from the north of the bay to obtain nutrients. Further development of the model could occur though the inclusion of seagrass cover and growth, where changes to cover would be predicted based on wave climate and light climate, together with sediment transport and inputs of nutrients from the catchment and sewage treatment. Seagrass can use dissolved nutrients directly, but may also remineralise nutrients from trapped phytoplankton, so there is a direct link to the pelagic component of the model. The model could then be used to investigate potential future management scenarios of nutrient input from catchment and sewage treatment, in terms of their effect on seagrass cover and growth. Module will include GIS mapping of seagrass distribution incorporated into model bathymetry, model coding and development, existing data collation and manipulation for model calibration and verification.

Module 7. Bubbles modelling to incorporate drift algae dynamics

Large areas of drift algae off the north-west coast of the bay could have a significant effect on nutrient and food chain dynamics (for example the interaction with urchin outbreaks). It is potentially possible to include of specification of drift algae in Bubbles, however, a significant field and laboratory program would be required to provide the necessary information for modelling. The field program would identify the species of algae and map the distribution and biomass. Laboratory studies will determine nutrient uptake rates and growth rates. Stable isotope analyses will be used to determine the dependence of drift algae on WTP outputs. Once obtained, this information would be used to incorporate this habitat into the model.
Module 8. Bubbles modelling to incorporate shellfish reef dynamics

There is a significant project underway funded by the Nature Conservancy and the Recreational Fishing Licence Grants to investigate the practicality of restoring shellfish reefs in Port Phillip Bay. Historically, beds of mussels and oysters occupied significant areas of the bay but were wiped out by destructive fishing practices. If significant areas of shellfish reef were to be restored, there could be significant effects on nutrient dynamics and uptake, potentially influencing nutrient management and target setting. The habitat could be incorporated into Bubbles to test scenarios of the relationship between the extent and placement of reefs and nutrient dynamics. There is considerable information on nutrient uptake and utilisation by shellfish reefs from overseas that could be used to inform the scenario modelling.
Acknowledgements

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References


Appendix 1

Molar Mass

The molar mass of atoms of an element is given by the atomic mass of the element multiplied by the molar mass constant (1 g mol⁻¹). Multiplying by the molar mass constant ensures that the calculation is dimensionally correct as atomic weights are dimensionless quantities (i.e., pure numbers) whereas molar masses have units (in this case, grams/mole).

As an example, the molar mass of water is approximately \( M(\text{H}_2\text{O}) \approx 18 \text{ g mol}^{-1} \).

Table A1 Atomic mass of certain elements

<table>
<thead>
<tr>
<th>Element</th>
<th>Mass (g/mol)</th>
</tr>
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<tbody>
<tr>
<td>Hydrogen</td>
<td>1.01</td>
</tr>
<tr>
<td>Oxygen</td>
<td>16.00</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>14.00</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>30.97</td>
</tr>
<tr>
<td>Silicon</td>
<td>28.09</td>
</tr>
</tbody>
</table>

In Egge and Aksnes (1992), they show a strong drop in diatom growth when silicate falls below 2 µM. The threshold concentrations can be obtained from the molecular weights. For example, for silica (SiO₂) which has molecular mass of 28.09+32=60.09 g mol⁻¹, the threshold concentration is,

\[
2 \times 60.09 \times 10^{-3} = 0.12 \text{ g m}^{-3} \quad (A1.1)
\]

The threshold concentration of Si is 0.056 g m⁻³, silicic acid (Si(OH)₄) is 0.192 kg m⁻³ and silicate (SiO₄) is 0.184 g.m⁻³.

Molar Unit

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>Concentration</th>
<th>Concentration (SI unit)</th>
</tr>
</thead>
<tbody>
<tr>
<td>millimolar</td>
<td>mM</td>
<td>(10^{-3} \text{ mol/dm}^{3})</td>
<td>(10^{0} \text{ mol/m}^{3})</td>
</tr>
<tr>
<td>micromolar</td>
<td>µM</td>
<td>(10^{-6} \text{ mol/dm}^{3})</td>
<td>(10^{-3} \text{ mol/m}^{3})</td>
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<tr>
<td>nanomolar</td>
<td>nM</td>
<td>(10^{-9} \text{ mol/dm}^{3})</td>
<td>(10^{-6} \text{ mol/m}^{3})</td>
</tr>
<tr>
<td>picomolar</td>
<td>pM</td>
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<td>(10^{-9} \text{ mol/m}^{3})</td>
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<td>aM</td>
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<td>(10^{-15} \text{ mol/m}^{3})</td>
</tr>
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<td>(10^{-18} \text{ mol/m}^{3})</td>
</tr>
<tr>
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<td>yM</td>
<td>(10^{-24} \text{ mol/dm}^{3})</td>
<td>(10^{-21} \text{ mol/m}^{3})</td>
</tr>
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</table>