

Modelling periphyton in New Zealand rivers

Part 2: A review and prospects for mechanistic modelling

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Executive summary

Periphyton is a complex mixture of algae, cyanobacteria, microbes, and detritus found on river beds and forming the base of the aquatic food web. Ecologically healthy river ecosystems depend on the presence of periphyton, but high periphyton abundance can have negative effects on habitat quality, water chemistry and biodiversity, and can reduce recreation and aesthetic values. The New Zealand Periphyton Guidelines recommend that maximum periphyton abundance be maintained between 50 and 200 mg chlorophyll *a* m⁻² to protect benthic biodiversity and angling values, respectively, and below 30% filamentous algal cover to protect aesthetic values (Biggs 2000, Suren et al. 2003, Sabater and Admiral 2005). The National Policy Statement for Freshwater Management (NPS-FM) mandates characterisation of periphyton status by comparing monthly monitoring of river periphyton biomass against target biomass bands (NZ Government 2017).

High periphyton biomass is associated with high nutrients, high light, warm temperatures, and low velocities, while periphyton biomass is reduced by grazing invertebrates, unstable substrate and fast water velocities (Biggs 1996). In-river nutrient concentrations are often the main driver amenable to management of point and non-point nutrient. The NPS-FM requires regional councils to develop nutrient criteria to meet specified periphyton biomass targets. Thus, reducing observed periphyton abundance and preventing future proliferations are of high priority for regional councils.

Models that simulate periphyton abundance with respect to growth and loss functions would be useful in developing land and water management plans to meet target biomass bands. The main management question to be addressed using a river periphyton model in New Zealand is:

What environmental conditions are required to meet river periphyton biomass (chlorophyll *a*) targets?

This report provides a review and assessment of the potential for using mathematical, process-based (mechanistic) models for predicting river periphyton biomass (measured as chlorophyll *a*). While empirical models correlate periphyton biomass with relevant environmental variables, they are constrained in their ability to predict beyond the range of observed conditions. Mechanistic models, however, can predict changes outside of the range of conditions that have been observed provided that the underlying ecosystem processes are well defined.

All mechanistic periphyton biomass models in current use account for some biomass growth drivers such as nutrients, light, temperature, biomass carrying capacity (related to spatial constraints), and loss processes such as respiration, grazing, physically induced and autogenic detachment. The mechanistic models reviewed in this report include early (1970s) periphyton biomass river models, international river models, and the Tukituki River Model (TRIM) which was developed and has been applied in New Zealand. Model applications, benefits, limitations, and some technical details such as the programming environment, inputs and outputs, key modelled mechanisms and calibration parameters, and temporal and spatial scale were summarised and compiled.

This report provides a summary of existing mechanistic models and preliminary guidance for advancing mechanistic river periphyton modelling in New Zealand. The following steps are recommended to inform nation-wide periphyton management using mechanistic periphyton models:

- 1) **Identify** several high priority **rivers** with distinct characteristics (geomorphology, nutrient concentrations, flows, temperature, light conditions/shading, etc.).

- 2) Using the high priority rivers identified in step 1), develop, calibrate, and confirm **river-specific** mechanistic periphyton **models** based on the parsimonious river model (Chapra et al. 2014). Steps for developing a mechanistic periphyton model are outlined in Appendix B. To improve site-specific river periphyton modelling, I recommend focusing on the following:
 - a. Collecting high resolution data (hydraulics, temperature, light, nutrients, periphyton) using cutting-edge technology such as remote sensing to support model calibration, confirmation, and data assimilation; and
 - b. Better defining physical and biological periphyton processes (esp. nutrient delivery and uptake, biological senescence, and physical detachment) by performing laboratory and *in situ* experiments at the species or periphyton community level.
- 3) Apply the calibrated and confirmed, river-specific models to rivers with similar characteristics. Recalibrate the models as necessary. Create a **look-up table** of tested ranges of parameter values for specific river classes. The parameter tables should be readily available to every periphyton modeller and routinely updated so that models can be judiciously applied with an adaptive management approach.
- 4) Simulate a suite of possible temporally variable hydraulic, nutrient, light, and temperature conditions for a river of interest. Using the results, develop river-specific stressor–receptor **response curves** (periphyton biomass vs. steady state in-river nutrient concentration). Those curves can then be used to define site-specific nutrient criteria to meet periphyton biomass targets in endpoint (extreme) conditions. The main limitation of this approach is that it sets criteria for **steady-state conditions**.

Ultimately, coupled atmospheric, catchment, hydrodynamic, sediment transport, nutrient, and multi-trophic level ecosystem and social/economic models must be used to resolve temporal and spatial variability. While challenging, model coupling must be advanced to capture system responses to natural and anthropogenic perturbation and inform management decisions. In the meantime, management decisions have to be made based on assumed endpoint steady-state conditions.

1 Background and objective

The term periphyton refers to the community of algae and other organisms (e.g., fungi, bacteria) that grows attached to riverbeds. While periphyton is a natural part of rivers ecosystems, excessive periphyton can lead to degradation of habitat, water quality and in-river values (Biggs 2000a).

Proliferations of periphyton or “blooms” can be caused by environmental changes including nutrient enrichment (generally nitrogen and/or phosphorus), elevated temperatures, and alterations to flow regimes that increase periods favouring the accrual of periphyton.

In-river nutrient concentrations (mass per volume, usually in mg L^{-1}) drive local periphyton growth but they in turn are controlled by nutrient inputs or loads (flux as mass per time, usually in kg d^{-1}) from land, from upstream, and sometimes from the river bed (sediments). Thus, management of nutrient concentrations in rivers targets nutrient sources, both point and non-point.

1.1 Freshwater management context

The National Policy Statement for Freshwater Management (NPS-FM, NZ Government 2017) sets out a National Objectives Framework (NOF) that includes an attribute for periphyton. The attribute defines four periphyton states that reflect ecosystem health, ranging from rare (Band A attribute state) to regular (Band D attribute state) periphyton blooms.¹ For derivation of the attribute, refer to Snelder et al. (2013). Grading against the NPS-FM periphyton attribute requires monthly monitoring of river periphyton biomass (measured as chlorophyll, chl a) by regional councils at key sites.² The NPS-FM also specifies that periphyton biomass targets (i.e., the thresholds separating the four periphyton states) are to be met by setting nutrient (dissolved inorganic nitrogen, DIN, and dissolved reactive phosphorus, DRP) criteria. To manage nitrogen and phosphorus inputs to and concentrations in rivers to control or avoid the damaging effects of excessive river periphyton, the following questions are relevant:

- 1) What in-river concentrations of DIN and DRP are required to yield 50, 120 and 200 $\text{mg chl } a \text{ m}^{-2}$ (NPS-FM biomass thresholds)?
- 2) Does DIN or DRP loading (nutrient input from a catchment to a river) reductions affect total periphyton biomass?
- 3) Does spatially variable DIN and DRP limitation in a river determine the effectiveness of nutrient loading reductions?
- 4) Would nearly complete elimination of anthropogenic P and/or N loads (especially during high irrigation seasons with high runoff) result in river-wide reductions in periphyton levels?

To answer these questions and set nutrient targets as mandated in the NPS-FM, the use of predictive periphyton models has been recommended (MPI and MfE 2018). While it is unrealistic to expect any model to be able to accurately predict total periphyton biomass (as chl a) at daily intervals at the reach scale for all New Zealand rivers in the near future, models are nonetheless useful tools for comparing different nutrient loading scenarios in support of decision making in adaptive freshwater management.

¹ The periphyton attribute is included for protection of the ecological values of waterways and is specified in terms of chlorophyll a per square metre of river bed. States (bands) are $\leq 50 \text{ mg/m}^2$ (A), $>50 \leq 120 \text{ mg/m}^2$ (B), $>120 \leq 200 \text{ mg/m}^2$ (C), and $>200 \text{ mg/m}^2$ (D). The metric required for assignment of a river to a band is the 92nd percentile of monthly observations of chlorophyll a , based on at least three years of data. Thus, for a site to fall into band D, chlorophyll a would exceed 200 mg/m^2 in at least 4 of 36 monthly surveys.

² Here, “key sites” refers to sites identified by regional councils as representing conditions in the freshwater management units defined in each region.

Previous nutrient guidelines for managing nuisance river periphyton in New Zealand were reviewed in recently published draft guidelines on how to address the Periphyton Note of the NPS-FM, i.e., setting nutrient targets to manage nuisance periphyton in surface waters (MPI and MfE 2018). Nutrient guidelines first set by MfE in 1992 did not focus directly on managing periphyton biomass but on sewage fungus and water column dissolved organic matter (MPI and MfE 2018). Later, nutrient guidelines were developed based on linear regression (empirical) models derived from data collected for 30 hill-fed, cobble-bed New Zealand rivers (Biggs 2000a). Recently available data from regional councils are being used to develop regional guidelines following an approach similar to that of (2000b). Inclusion of additional variables where appropriate allows for development of region-specific models (Kilroy et al. 2017, 2018b). Models that were recently considered by MPI and MfE (2018) for setting target nutrient guidelines include the mechanistic model TRIM (Rutherford 2011a,b, 2013a,b), statistical Bayesian Network models (Matheson et al. 2012, Storey et al. 2017), broad scale models based on data from the National River Water Quality Network (Larned et al. 2015, Elliott et al. 2016), and non-linear quantile regression (Matheson et al. 2016).

In this report, I consider two types of quantitative models: empirical (data-based) and mechanistic (process-based) periphyton models. The application of empirical models to predict periphyton biomass is the focus of a companion report (Kilroy et al. 2019). The primary objective of this report is to assess the potential for the use of mechanistic models for predicting nuisance river periphyton biomass at a national scale in New Zealand, with a focus on the following:

- 1) **comparison** of benefits and limitations of existing empirical and mechanistic modelling approaches, including early (1970s) periphyton biomass river models, internationally developed and applied models, and specifically the Tukituki River Model (TRIM) for New Zealand;
- 2) **description** of mechanistic drivers used for modelling periphyton growth, i.e., the role of nutrients, light and shading, temperature, substrate, respiration and mortality, grazing, and sloughing (senescence and detachment);
- 3) **recommendations** and preliminary guidance on steps forward for periphyton model development and application across scales in New Zealand.

1.2 Common mechanistic periphyton modelling approaches

The questions raised in Section 1.1 can be re-framed. First, it must be acknowledged that nutrients are not the sole controlling factor and several other environmental controls affect periphyton growth and nutrient conditions themselves. Assuming that the other periphyton controlling factors are not amenable to management and focusing on nutrient management, the following overarching question motivates river periphyton modelling:

What in-river nutrient loads and/or concentrations will allow us to meet target river periphyton biomass (chlorophyll a) levels in a river?

The general mechanistic modelling strategy for relating nutrients to algal growth and biomass is to employ rate equations that represent physical and biochemical processes, which depend on site-specific model parameters and forcing, initial, and boundary conditions (Reckhow and Chapra 1999).

Periphyton growth models attempt to quantify the gains and losses of biomass and the associated sources, transformations and sinks of the controlling nutrients (Figure 1-1). Periphyton growth refers to specific productivity (the amount of biomass produced per existing biomass over time). Biomass is

usually quantified as chlorophyll *a* (Uehlinger et al. 1996, Labiod et al. 2007, Flynn et al. 2013), ash-free dry mass (AFDM, Boulêtreau et al. 2006, Bellmore et al. 2014, Graba et al. 2014), carbon (Rutherford et al. 2000, Buzzelli et al. 2000, Ambrose et al. 2006, Rutherford 2011a), or the number of algal cells (Asaeda and Son 2000, 2001) per unit area. Periphyton accrual refers to the accumulation of biomass over time and is mediated by several factors (Figure 1-2). Physical factors that drive or impede periphyton growth are substrate, flow, light, and temperature. Biogeochemical cycling of macro- and micronutrients can drive or impede growth. Ecological resistance to periphyton growth occurs via grazing by macroinvertebrates.

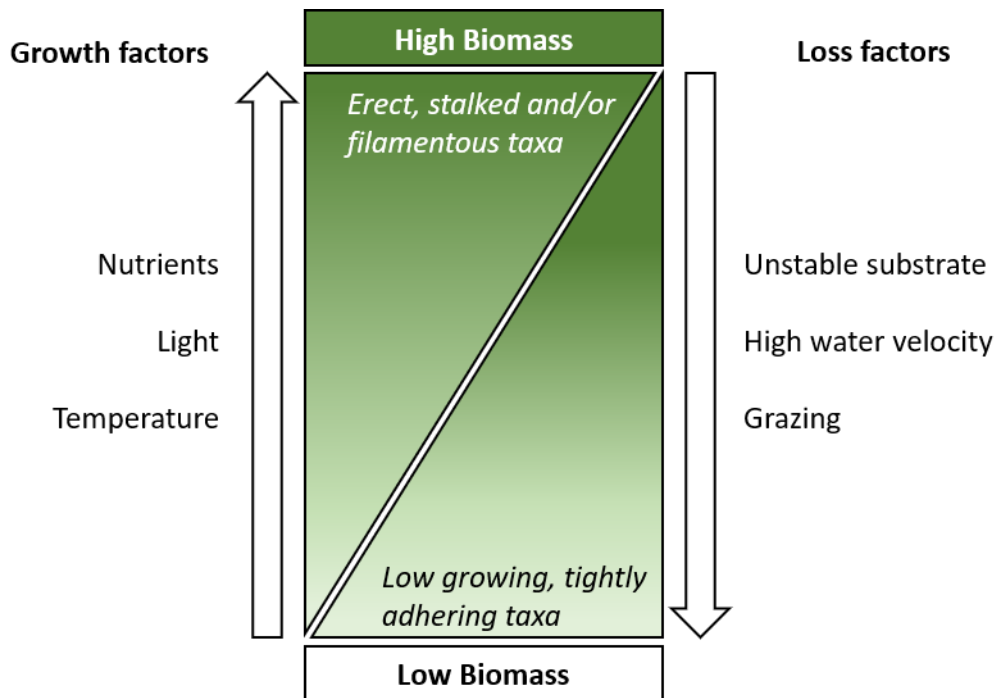


Figure 1-1: Periphyton biomass accrual is controlled by environmental factors that can enhance or impede growth. Physical factors include light, temperature, hydraulic, and substrate characteristics and biogeochemical and biological factors include nutrient concentrations and grazing pressure. Increases in nutrient concentrations, light, and temperature usually drive growth, while increasingly unstable substrate, high water velocity, and grazing pressure usually impede growth. Adapted from Biggs (1996, Figure 2).

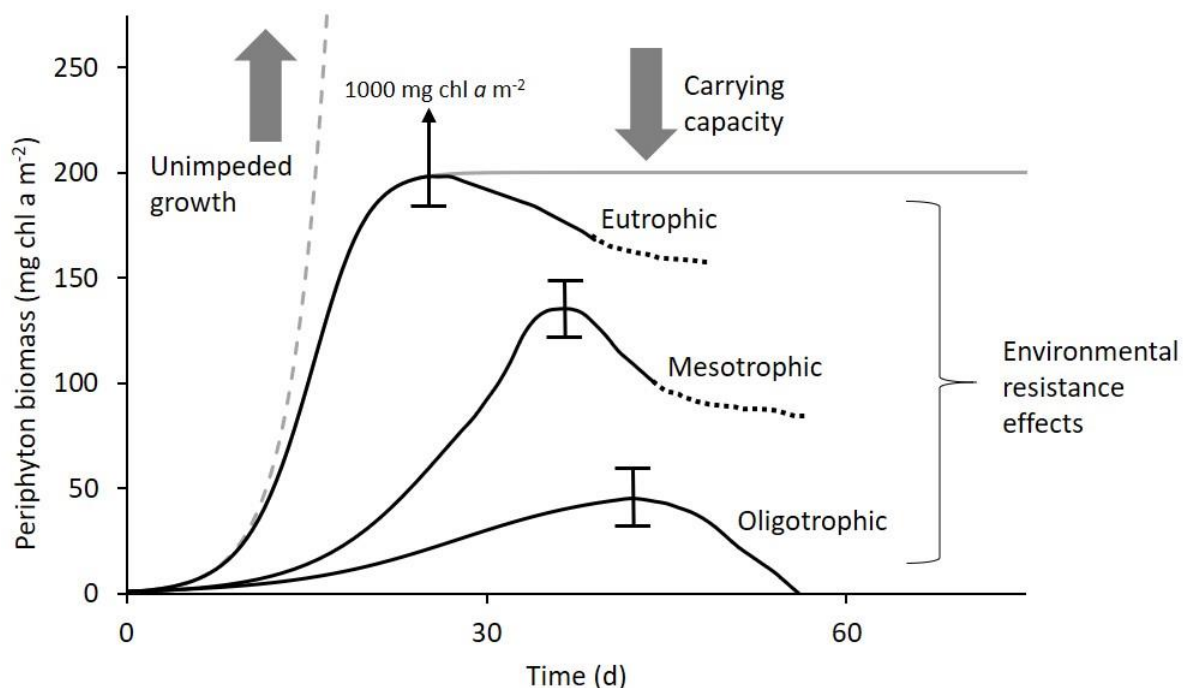


Figure 1-2: Idealised periphyton biomass accrual mediated by environmental conditions in the context of simple exponential (dotted grey line) and logistic (solid grey line) modelling approaches. Unimpeded growth is modelled with an exponential growth function. Growth limited by carrying capacity is modelled with a logistic growth function. In reality, growth is mediated by environmental conditions, which – when stable – result in temporary equilibria reflecting different levels of nutrient concentrations (high – eutrophic, medium – mesotrophic, low – oligotrophic). Biomass levels can be as high as $1000 \text{ mg chl } a \text{ m}^{-2}$. Figure adapted from Larned et al. (2016, Figure 10.4).

Several mechanistic river periphyton models are summarised and some technical information about these models is presented in Appendix A, Table A-1 and Table A-2. A range of simple to complex models that include some or all controlling factors are described in the following subsections.

Following this section on background information and objectives of this report, Section 2 introduces empirical and mechanistic modelling, Section 3 describes and compares common mechanistic approaches to modelling periphyton processes. Section 4 discusses further considerations for mechanistic periphyton modelling. Section 5 provides conclusions and recommendations based on the reviewed literature.

2 Introduction

It is recognised that worldwide, eutrophication is increasing in response to anthropogenic and climate change pressures (Janssen et al. 2019) and there is a need for predictive tools to help identify drivers and test management scenarios. The susceptibility of rivers to nuisance periphyton depends on river characteristics including hydraulic conditions (flow, shear velocity, depth), substrate type and mobility, natural nutrient supply, light/shading conditions, water temperature, and invertebrate grazing pressure. These drivers are generally well understood (Larned 2010) and some or all are components of mathematical biomass prediction models (e.g., River Water Quality Model, Reichert et al. 2001; Tukituki River Model, Rutherford et al. 2011a,b; Parsimonious River Model, Chapra et al. 2014).

Predicting the effects of nutrient loading and other environmental factors on algal accrual have been assessed via two interconnected approaches: empirical and mechanistic modelling. There are few purely empirical (data-based) or purely mechanistic (process-based) models, and most models include elements of both (Reckhow and Chapra 1999).

2.1 Empirical vs. mechanistic modelling

Periphyton modelling has historically been dominated by empirical approaches. Structured empirical modelling has a long history in limnology to predict algal biomass (phytoplankton) with respect to nutrients in lakes (Vollenweider, 1968, 1975; Rast et al. 1983). Sawyer (1947) first suggested inorganic nutrient thresholds to manage nuisance algal growth in lakes. Regression models relating periphyton biomass to nutrient concentrations and other variables have been used for Missouri rivers (Lohman et al. 1992a), a Montana river (Dodds 1997), and New Zealand rivers (Biggs 2000b). The Biggs (2000b) regression relationships linked maximum annual chlorophyll *a* to mean annual DIN or DRP and mean annual accrual time (calculated from flood frequency). The regression equations were used to propose mean annual DIN and DRP concentrations necessary to prevent maximum chlorophyll *a* from exceeding specified levels (Biggs 2000b). Recently, the Biggs (2000b) approach was used to develop refined empirical relationships for the Canterbury and Manawatu-Wanganui regions (Kilroy et al. 2017, 2018). In addition, machine learning models such as boosted regression trees (BRTs) and random forest (RF) models have become popular in the scientific literature (Wagenhoff et al. 2017). A companion report (Part 1) focuses on data analysis and empirical modelling approaches to predict periphyton biomass (Kilroy et al. 2019).

The main benefits of simple regression-based empirical models are that they often yield straightforward relationships that are easy to understand and apply in management and are often sufficiently accurate for environmental management and planning. Regression techniques are used to fit an equation to observational data. Simple regression models can account for variability by using annual medians or means, assuming that an annual average represents the general nutrient status or trophic state of a river (e.g., Biggs 2000b and Dodds et al. 2002b). Empirical models do not have to be linear but can also be built using more complex equations (e.g., first order polynomials, exponential). In addition, machine learning techniques generally have superior predictive ability, but work best with very large datasets, use complex algorithms and can be difficult to interpret.

The main drawback of empirical models is that they do not necessarily identify cause and effect relationships and rely on historical data, so that extrapolation (predictions for never observed input conditions) becomes highly uncertain. Simple regression models cannot capture nutrient dynamics, which are driven by physical mass transport and nutrient cycling, which can in turn control

periphyton biomass. For example, periphyton biomass can be constant while water column nutrient concentrations decrease with distance from a source, as in Chapra et al. (2014). Similarly, Whitehead et al. (1997) tested a neural network model and a mechanistic model given data for six sites on the River Thames. The models performed similarly well, but the data-based neural network model required reach-specific definition of 5 model parameters for 5 reaches (i.e., 25 calibration parameters), while the mechanistic model required one set of 9 river-wide model parameters. Thus, empirical models cannot be confidently applied to predict the response of systems to conditions beyond the range of data used to develop the model (extrapolation). On the other hand, mechanistic models are built based on physical, chemical, and biological process understanding and can thus be used to predict environmental responses to conditions that have never been observed before (Rastetter et al. 2003).

Empirical models use aggregated data representing average conditions to reveal average system level responses based on correlations. Mechanistic models use disaggregated data representing specific conditions to reveal system level responses based on an understanding of underlying processes. “As with any ecosystem, modes of inference about river processes are subject to a tension between aggregation to reveal system level behaviours vs disaggregation to understand mechanisms” (Reijo et al. 2018). Though there can be tension between empirical and mechanistic modellers, the two approaches overlap: empirical models are not solely based on correlation but implicitly model mechanisms, and mechanistic models cannot avoid using some empirical information. Examples of empirical models and some advantages and disadvantages are summarised in Table 2-1.

Table 2-1: Some empirical model types, advantages and disadvantages, and examples.

Model Type	Advantages	Disadvantages	Examples
<p>Regression models:</p> <ul style="list-style-type: none"> ▪ simple ▪ multiple ▪ general linear models (GLMs) ▪ general additive models (GAMs) 	<ul style="list-style-type: none"> ▪ Easy to produce and interpret ▪ Ignore any prior process understanding and recognise linear patterns in data 	<ul style="list-style-type: none"> ▪ Do not necessarily identify cause and effect, only correlation ▪ Data that are not normally distributed must be transformed to normality ▪ Wide data range required for best results ▪ Model coefficients are not biophysically meaningful; “black box model” with no (or little) process understanding (Whitehead 1997) 	<ul style="list-style-type: none"> ▪ Periphyton in Missouri streams (Lohman et al. 1992a, Aizaki and Sakamoto 1988) ▪ Periphyton in Montana rivers (Dodds 1997) ▪ Periphyton in New Zealand rivers (Biggs 2000b)
<p>Multivariate machine learning models:</p> <ul style="list-style-type: none"> ▪ classification trees and boosted regression trees (BRTs) ▪ Random forests (RFs) ▪ Artificial neural networks (ANN) ▪ Bayesian belief networks (BBN) ▪ Genetic models 	<ul style="list-style-type: none"> ▪ Probability distribution of input data does not have to be known as for traditional regression analysis ▪ Data may vary seasonally and cyclically (Maier and Dandy 1996) ▪ Highly non-linear (Maier et al. 1998) ▪ Perform well even with noisy or incomplete data sets (Tang et al. 1991, Burke and Ignizio 1992) ▪ Can help identify the most important drivers in a particular system (e.g., flow and temperature, Maier et al. 1998) ▪ Can ignore a lot of prior process understanding and recognise patterns in data ▪ Include multiple indicators, i.e., more evidence to make the model more robust (BRT) 	<ul style="list-style-type: none"> ▪ Do not establish cause and effect, only correlation → “black box” issue (only inputs and outputs are known but not internal processes) ▪ Parameters are not biophysically meaningful ▪ Parameters are location-specific when derived for data obtained for one location ▪ Neural networks require less pre-existing understanding, but their predictions are not necessarily superior to those of other approaches (Whitehead et al. 1997) 	<ul style="list-style-type: none"> ▪ BRT: setting in-river phosphorus objectives using nutrient, sediment, and environmental variables (Wagenhoff et al. 2017) ▪ ANN: <i>Anabaena</i> in River Murray in South Australia (Maier et al. 1998) ▪ ANN: 7 types of algae in Saldenback Reservoir in Germany (French and Recknagel 1994) ▪ ANN: various algal species in Lakes Kasumigaura in Japan, Biwa in Japan, and Lake Tuusulanjärvi in Finland, Darling River in Australia (Recknagel et al. 1997) ▪ ANN: algae in River Thames in England (Whitehead et al. 1997) ▪ BBN: water quality (Maren et al. 1990, Tang et al. 1991, Burke and Ignizio 1992, Quinn et al. 2013)

2.2 Simple mechanistic model forms

The simplest growth model upon which all mechanistic periphyton biomass models are built is the exponential growth model, which does not include any growth inhibition resulting in unrealistic, infinite biomass predictions over time. The second simplest growth model is the logistic growth model, which includes growth inhibition resulting in a steady-state biomass over time. These two most simple growth models are highlighted red in Table A-1.

2.2.1 The exponential growth model

Idealised periphyton biomass accrual over time is depicted in Figure 1-1. The simplest mechanistic biomass or population growth model is the exponential growth function, which represents unimpeded growth (dashed grey line in Figure 1-2) driven by an independent, constant growth rate (biomass produced per biomass per unit time):

$$\frac{dX}{dt} = \mu_{max} X \quad (1)$$

where X represents biomass (e.g., mg chl a m^{-2}), t is time (d) and μ_{max} is the gross specific growth rate, i.e., the maximum rate of biomass produced per unit of biomass per day at optimal conditions (here in units of d^{-1}). The exponential growth model leads to unrealistic biomass predictions as time increases and is driven by μ_{max} , a key coefficient in any mechanistic model but that cannot easily be measured, because truly perfect growth conditions seldom occur.

Growth rate estimates are derived from measurements; e.g., net growth is estimated as the difference between **gross primary productivity** (GPP, based on measurements of oxygen released during photosynthesis) and **respiration** (based on oxygen consumed during respiration). Modelers generally acknowledge the importance of the maximum growth rate (e.g., Rutherford 2013b) and measurements from laboratory and chamber studies attempting to represent ideal growth conditions support a commonly used range of 0.2–3.0 d^{-1} for this parameter (Uehlinger et al. 1996, Schuwirth et al. 2008, Fovet et al. 2010, Benedini and Tsakiris 2013, Graba et al. 2010, 2014).

2.2.2 The logistic growth model

An improvement to the exponential growth model which leads to unrealistic biomass predictions as time increases, is the logistic growth model takes the form of an S-shaped biomass curve. This function modifies the simple exponential growth equation with a maximum biomass or carrying capacity value that dictates the maximum achievable biomass. The logistic growth model accommodates space and resource limitation by capping biomass at a prescribed carrying capacity that forces the biomass curve to bend and level off (solid grey line in Figure 1-2):

$$\frac{dX}{dt} = \mu_{max} \left(\frac{X_{max} - X}{X_{max}} \right) X \quad (2)$$

where X_{max} is the maximum attainable biomass and $\frac{dX}{dt}$, the rate of change in biomass, approaches zero as X approaches X_{max} . A population or biomass carrying capacity represents any kind of limitation that increases with biomass. This biomass-related growth limitation could be caused by limited space, disease, predators for populations and the restricting environmental factors shown in Figure 1-1 (e.g., nutrients, further discussed in Section 3.1.3). The logistic growth model assumes

that, at some point in time, an equilibrium occurs between driving and restricting environmental factors. This may not occur in practice because drivers (e.g., light, temperature, nutrients) usually vary with time.

While mathematically efficient, the maximum sustainable biomass is not a universal constant but inconveniently site-specific and difficult to define. In addition, this model does not account for biomass losses and only for one growth cycle that ends when the maximum biomass is reached and sustained. However, the basic logistic growth model can be modified and enhanced. For example, Rodriguez (1987) tested three simple models for estimating periphyton growth parameters: (1) the logistic model, (2) a logistic-like model including colonization, and (3) a model including colonization and secondary epiphytism. He tested the models on seven data sets and concluded that model 2 was the most appropriate, retaining enough complexity to be more realistic than the simple logistic model (model 1) but simpler than model 3. However, he noted that model 2 should not be applied where sloughing and grazing losses are significant. Others have applied the logistic model and noted that it does not account for the effects of light, temperature, or nutrients on periphyton growth (Bothwell 1988, Momo 1995, Tsujimoto and Tashiro 2004, Ateia et al. 2016). Some model details are summarised in Table A-1 (red background colour indicates this group of models).

When values for μ_{max} and X_{max} are determined by calibration and confirmation using site-specific biomass measurements, logistic growth models represent steady state conditions. Because effects of light, temperature and nutrients are not included, simple logistic growth models cannot be used to answer our guiding water quality management question: What in-river nutrient loads and/or concentrations will allow us to meet target river periphyton biomass (chlorophyll *a*) levels in a river?

3 Mechanistic model processes

When substrate, space requirements, temperature, light, and nutrient availability, hereafter termed environmental forcing conditions, are favourable, the rate of periphyton biomass production increases. The term μ_{max} in Equation (1) is the maximum growth rate that occurs under optimal forcing conditions and when biomass is low. In practice, the effective (net, actual) growth rate is less than μ_{max} because temperature, light or nutrients are usually sub-optimal. In addition, high biomass causes self-shading and/or affects the diffusion of nutrients (see Section 3.1.3).

The basic form of a growth model that includes growth mediation and biomass removal terms is as follows:

$$\text{Rate of change in biomass} = \frac{dX}{dt} = \overbrace{\mu_{max} \cdot \phi_T \cdot \phi_I \cdot \phi_N \cdot \phi_X \cdot X}^{\text{Growth}} - \overbrace{(R + G + S + M)}^{\text{Losses}} \quad (3)$$

where the mediation functions for temperature T , light I , nutrient concentration N , and biomass X ($\phi_T, \phi_I, \phi_N, \phi_X$, respectively) attenuate the maximum specific growth rate μ_{max} and respiration R , grazing G , flow-induced sloughing (detachment) S , and mortality and autogenic sloughing M are removal processes. When the resulting net growth rate or the difference between growth and removal rates is positive, biomass is gained (accumulated); when it is negative, biomass is lost. The modelling challenge lies in describing and quantifying the effects of each term in Equation (3) well enough to predict biomass at an acceptable level of accuracy. The growth-mediating factors and associated processes are described in detail in Sections 3.1 and 3.2.

Typically, biomass accrual follows an oligotrophic, mesotrophic, or eutrophic shape (Figure 1-2). While the shape of the biomass accrual curve is similar in different rivers, the rate of biomass accrual depends on nutrient concentrations. Increasingly high to low nutrient conditions are referred to as eutrophic or nutrient-rich, mesotrophic, and oligotrophic or nutrient-poor, while peak biomass depends on both growth and loss processes (e.g., grazing by macroinvertebrates, sloughing and scour by high flows).

3.1 Biomass growth mediation

Models that are higher in complexity compared to the logistic model incorporate light, temperature, and nutrient mediation and sometimes loss mechanisms (models shaded yellow Table A-1, Table A-2). These models were developed based on specific experimental or observational data. Among the first of such models were those developed by McIntire, Horner, and colleagues (1970s–1990s). Horner et al. (1983) conducted flume experiments over a range of DRP concentrations (2–75 $\mu\text{g L}^{-1}$) and velocities (5–75 cm s^{-1}) and modelled periphyton biomass accrual in the channels. While this model was deemed unsuitable for application to management, the Uehlinger model (1996, see Table A-1, first model in yellow), which stems from prior work by McIntire and Colby (1978), has been applied and modified for sites in Europe, the United States, and Japan. This group of models accounts for several environmental forcing conditions and some incorporate nutrient cycling, grazing, and physical removal mechanisms. However, with respect to eutrophication management, Chapra et al. (2014) emphasize two deficiencies in these models: 1) “they do not explicitly account for the impact of algal uptake on the concentration of the limiting nutrient (i.e., the limiting nutrients are not modelled explicitly)” and 2) “most are not designed to model spatial effects (e.g., the distribution of biomass downstream of nutrient sources).”

This group of models relies on several model parameters and prescribed environmental forcing conditions such as light intensity and temperature, site-specific calibration, and validation. These models are not spatially explicit (i.e., OD models), but linkage to a spatially explicit hydrodynamic model may aid in setting nutrient load limits to meet in river periphyton biomass objectives.

3.1.1 Temperature and light effects (ϕ_I and ϕ_T)

Temperature and solar radiation drive photosynthesis and respiration, processes that convert carbon dioxide, nutrients, water, and energy in the form of sunlight into oxygen, biomass, and energy. Sub-optimal light and temperature conditions can dampen or inhibit photosynthesis (DeNicola 1996, Hill 1996). The Arrhenius equation describes temperature-dependent chemical reaction rates and is frequently employed in mechanistic algal biomass models to describe the effects of temperature, but other formulations have also been used (Table 3-1).

Periphyton growth is strongly dependent on the light intensity of photosynthetically active radiation (PAR), the visible range of the electromagnetic spectrum. Periphyton community or species-specific photosynthesis-irradiance (P-I) curves are often experimentally developed (Table 3-1). Several of these P-I equations, sometimes including photoinhibition³ and often experimentally developed for marine phytoplankton, are described by Hill (1996); some are simple with constant parameters (e.g., Ryther 1956), while others are more complex (e.g., Pahl-Wostl and Imboden 1990). A hyperbolic relationship with an asymptotical maximum rate of photosynthesis is often used (Jassby and Platt

³ Inhibition of photosynthesis at high light intensity, resulting in a peak in the PI curve with declining P with increasing I.

1976). Some models include a photoinhibition term to account for inhibition of the rate of photosynthesis at high light intensity (Platt 1980).

In situations where light conditions at the water surface (incident irradiance) are not approximately equal to those at the surface of the periphyton mat, light attenuation through the water column is simulated using the Beer-Lambert Law.

In a periphyton mat as opposed to a film, only the cells on the surface of the mat are fully illuminated, while lower layers are shaded by those above. Higgins (2005) and Martin et al. (2014) accounted for light attenuation through both the water column and through the periphyton mat using the Beer-Lambert Law, where the controlling model parameters are the light extinction coefficients through the water column and the periphyton mat (k_e and k_{alg}).

Table 3-1: Common formulations for temperature (T) and light (I) mediation (ϕ_I and ϕ_T , respectively) in mechanistic periphyton models.

Equation	Model parameters	References
<p>Eppley for temperature:</p> $\phi_T = \frac{0.851}{P_S^B} (1.066)^T$ <p>T = water temperature</p>	P_S^B = max rate of photosynthesis	Eppley (1972)
<p>Arrhenius for temperature:</p> $\phi_T = \theta^{T-T_0}$ <p>T = water temperature</p>	θ = constant T_0 = reference temperature, usually 20 °C	Goldman and Carpenter (1974), Chapra (1997), Asaeda and Son (2000), Ambrose et al. (2006), Fovet et al. (2010), Bellmore et al. (2014),
<p>Asymmetric Gaussian distribution for temperature:</p> $\phi_T = \exp\left(-\left(\frac{T - T_{opt}}{\Delta T_{lower}}\right)^2\right), T_{min} < T < T_{opt}$ $\phi_T = \exp\left(-\left(\frac{T - T_{opt}}{\Delta T_{upper}}\right)^2\right), T_{opt} < T < T_{max}$ <p>Assuming that $\phi_T = 5\%$ at both T_{min} and T_{max}:</p> $\Delta T_{lower} = \frac{T_{opt} - T_{min}}{\sqrt{\ln(20)}}$ $\Delta T_{upper} = \frac{T_{max} - T_{opt}}{\sqrt{\ln(20)}}$	T_{max} = maximum temperature T_{opt} = optimal temperature T_{max} = maximum temperature	Rutherford et al. (2000)
<p>Cerco and Cole for temperature:</p> $\phi_T = e^{-K_1(T-T_{opt})^2} \text{ for } T \leq T_{opt}$ $\phi_T = e^{-K_2(T-T_{opt})^2} \text{ for } T > T_{opt}$ <p>T = water temperature</p>	T_{opt} = optimal temperature K_1 and K_2 = shape parameters defining growth as a function of temperature above and below T_{opt}	Cerco and Cole (1994)

Equation	Model parameters	References
Michaelis-Menten for light: $\phi_I = \frac{I}{k_I + I}$	k_I = light half-saturation constant	Uehlinger et al. (1996), Buzzelli et al. (2000), Bellmore et al. (2014)
Beer-Lambert Law for light: attenuation through water column: $I = I_0 e^{-k_e H}$ <i>h</i> = water depth from surface to mat <i>I</i> ₀ = incident light (at water surface)	k_e = light attenuation coefficient (sometimes several are used for attenuation through the water column and periphyton mat)	Ryther (1956), Chapra (2006), Asaeda and Son (2001)
Steele's Law for light: $\phi_I = \frac{I}{I_{opt}} e^{1 - \frac{I}{I_{opt}}}$	I_{opt} = optimum light intensity for growth	Asaeda and Son (2000), Fovet et al. (2010), Steele (1962)
Hyperbolic P-I curve: $\phi_I = \frac{P^B}{P_S^B} \tanh\left(\frac{\alpha I}{P_S^B}\right)$ <i>P</i> ^B = rate of photosynthesis	α = constant characterizing the photochemical reactions of photosynthesis, defines the initial slope of the curve P_S^B = max rate of photosynthesis	Jassby and Platt (1976)
Half-sinusoid for light: $\phi_I = \frac{I}{I_k} \text{ for } 0 < I < I_k$ $\phi_I = 1 \text{ for } I > I_k$ Assume radiation follows a half-sinusoid during the day, average for daily mean: $\overline{\phi_I} = \frac{Day}{12\pi} \left[\frac{I_{max}}{I_k} - \sqrt{\left(\frac{I_{max}}{I_k}\right)^2 - 1} + \frac{\pi}{2} - \sin^{-1}\left(\frac{I_k}{I_{max}}\right) \right] \text{ for } I_{max} > I_k$ $\overline{\phi_I} = \frac{Day}{12\pi} \left(\frac{I_{max}}{I_k}\right) \text{ for } I_{max} < I_k$ <i>I</i> _{max} = daily maximum radiation	I_k = saturating radiation	Rutherford et al. (2000)

Equation	Model parameters	References
P-I curve with photoinhibition : $\phi_I = \frac{P^B}{P_S^B} \left(1 - e^{-\frac{\alpha I}{P_S^B}} \right) \cdot e^{-\frac{\beta I}{P_S^B}}$ P^B = rate of photosynthesis	α = constant characterizing the photochemical reactions of photosynthesis, defines the initial slope of the curve β = constant characterizing photoinhibition, defines the final slope of the curve P_S^B = max rate of photosynthesis without photoinhibition	Platt (1980), Hill (1996), Dodds et al. (1999)
DYPHORA photosynthesis model for phytoplankton	9 parameters, model based on hyperbolic P-I curve	Pahl-Wostl and Imboden (1990)
Periphyton community or type-specific light and temperature mediation surfaces: polynomial functions	(2D surfaces fitted to experimental data)	Graham et al. (1982), Biggs et al. (1999)

3.1.2 Internal and external nutrient effects ϕ_N

Assuming optimal light, temperature and physical conditions, periphyton growth is controlled by nutrient availability. The macronutrients that most commonly limit algal growth in marine and freshwater systems are bioavailable nitrogen (N) and phosphorus (P). Increases in N or P leads to freshwaters due to anthropogenic activity often result in eutrophication, i.e., increases in periphyton production (Biggs 1988, 2000a,b) and to large diurnal variations in DO and pH which adversely affect sensitive organisms). The bioavailable forms of N and P are dissolved inorganic N (DIN, i.e., the sum of nitrate, NO₃-N, nitrite, NO₂-N, and ammonium, NH₄-N) and dissolved reactive P (DRP, mainly phosphates, PO₄-P). Fractions of dissolved organic N and P (DON and DOP) and particulate N and P (PN and PP) can also become bioavailable when they are broken down by bacteria and enzymes (e.g., Hu et al. 2016, Lambert et al. 2015). The rates at which some forms of these nutrients are taken up are variable and nutrient uptake has been extensively studied in North America but not in New Zealand (Kilroy et al. 2018).

Nitrogen and phosphorus control of periphyton has been extensively researched and several reviews have been published (e.g., Francoeur et al. 1999, Francoeur 2001, Larned 2010, Keck and Lepori 2012). In North America, nutrient management has historically focused on P, primarily as a result of research on eutrophication in lakes. More recently, co-limitation by N and P has prompted recommendations for both N and P management in rivers (Dodds and Smith 2016). In New Zealand, simultaneous N and P management has been advised since at least the 1980s (e.g., Lake Rotorua, Rutherford et al. 1989, Wilcock et al. 2007). The focus on P over N controls and application of the limiting nutrient (Liebig's law of the minimum⁴, von Liebig 1840) concept for managing cultural eutrophication has recently become a contentious academic discussion topic, but the discussion is more focused on phytoplankton in lakes rather than periphyton in rivers (e.g., Lewis and Wurtsbaugh 2008, Schindler et al. 2012, Schindler et al. 2016, Cotner 2016, Schindler et al. 2017). Based on

⁴ Carl Sprengel first conceived the idea (1828), which was later formalized by Justus von Liebig (1840). The principle states that biological growth is not limited by a total amount of available resources but only by the scarcest of all required resources, the limiting factor (e.g., sunlight or a particular nutrient).

nutrient diffusing substrate (NDS) experiments, it has been shown that primary nutrient limitation can vary from reach to reach along a river (e.g., Kilroy and Wech 2015).

Mechanistic models usually simulate nutrient limitation (ϕ_N) using Michaelis-Menten kinetics in which the growth rate increases with increasing concentration of a limiting nutrient (model input) in the surrounding water up to a maximum at high concentrations. Each potentially limiting nutrient requires a Michaelis-Menten formulation, and the smallest (minimum) of the Michaelis-Menten terms is often used to represent nutrient limitation – consistent with Liebig’s law of the minimum. Michaelis-Menten kinetics require knowledge of the external (water column) nutrient concentration and the half-saturation constant for the limiting nutrient. The latter is defined as the nutrient concentration at which half of the maximum specific growth rate is achieved and is often a model calibration parameter although it can be estimated from field and/or laboratory experiments (Table 3-2). This method of modelling nutrient limitation ignores variation in stored nutrient content (cell quota), which is the mass of nutrient stored inside algal cells per total algal mass, usually expressed as a percent. Stored nutrients are determined by particulate nutrient analysis and the total algal mass is usually taken as the dry mass (DM) and sometimes as the ash-free dry mass (AFDM).

When stored nutrient content is a state variable, the rates of nutrient uptake and loss determine nutrient accumulation in periphyton. The nutrient uptake rate depends on internal and external nutrient concentrations (Rhee 1973, Brown and Harris 1978, Gotham and Rhee 1981). For example, Lohman and Priscu (1992) measured nutrient uptake rates ($\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$, and $\text{PO}_4\text{-P}$ in $\mu\text{g gDM}^{-1} \text{h}^{-1}$) by the green filamentous alga *Cladophora* in Clark Fork of the Columbus River in Montana in 1989-1990 and found that uptake rates could be related to water column nutrient concentrations using the Michaelis-Menten equation, which is more often termed the Monod equation when used to model nutrient uptake. Monod kinetics are commonly used in mechanistic periphyton models (e.g., DeAngelis et al. 1995, Dent and Henry 1999). Models that use Monod kinetics assume a constant cell quota and that uptake is physiologically controlled and not limited by nutrient delivery; however, external/in-river and internal/stored nutrient concentrations as well as flow conditions/turbulence influencing uptake (Section 3.1.3). In addition, differences in alkaline phosphatase activity, an indicator of P-limitation, and P uptake by P-limited algae grown under different light intensities and wavelengths have been observed (Wynne and Rhee 1988).

Nutrient uptake rates used in models are generally defined based on benthic chamber experiments or in-river measurements to derive metabolism rates (carbon production and consumption) from changes in dissolved oxygen (Young et al. 2008). Nutrient uptake rates can be measured during the same benthic chamber experiment. Substrate covered by periphyton is placed into a chamber with river water that is continuously pumped through the chamber. Nutrient uptake is measured by difference in the water nutrient concentration over time. For example, Rutherford (2011a) reported DRP, DOP, DIN, and DON uptake and release rates derived from chamber experiments and applied those measurements in TRIM. Similarly, Dent and Henry (1999) used nitrogen uptake, release, and mineralization rates based on measurements by others (e.g., Busch and Fisher 1981, Grimm and Fisher 1984, Mulholland and DeAngelis 2000). Points of caution concerning the derivation of nutrient uptake rates from chamber experiments include that periphyton are invariably disturbed as substrate is removed from the river and placed in the chamber, conditions inside the chamber (velocity, flow, temperature) differ compared to those in the river, and the scaling of such small-scale measurements up to river reaches likely introduces error (Young et al. 2008). Chamber experiments are nonetheless useful because conditions can be controlled. Single chamber experiments may not be useful for modelling, but suites of experiments across light, temperature, and external and stored

nutrient gradients for different types of periphyton can be conducted to define the uptake rate as a function of those variables.

Another, more complicated mechanistic approach to simulate nutrient limitation is by means of Droop kinetics (Droop 1973, Table 3-2) in which the growth rate depends on external (water column) nutrient concentration and on the concentration of nutrient stored within the periphyton; i.e., nutrient-saturated periphyton (high cell quota) have a higher growth potential or capacity to multiply than starved periphyton (low cell quota). In the Droop model, cell quota can either be an input or another modelled state variable (like biomass). The periphyton cell quota increases as a result of nutrient uptake from the surrounding water and decreases as nutrients are used for periphyton growth.

Cerucci et al. (2010) tested both modelling approaches (Michaelis-Menten and Droop kinetics) within the WASP model on a river in New Jersey and found that predictions were better when Droop kinetics, were applied to simulate periphyton growth. Droop kinetics account for luxury nutrient uptake, which refers to nutrient uptake beyond an alga's nutrient requirements to maintain cell structure and storage of those nutrients (e.g., as polyphosphates) for future cell division. It can be thought of as nutrient storage during times of plenty for nutrient use during times of drought.

Table 3-2: Common formulations for nutrient (N) mediation (ϕ_N) in mechanistic periphyton models.

Equation	Model parameters	References
<p>Michaelis-Menten (and/or Monod):</p> $\phi_N = \min_i \left(\frac{N_i}{k_{N_i} + N_i} \right)$ <p>N_i = nutrient concentration (e.g., i = N or P)</p>	<p>k_{N_i} = nutrient half-saturation constant</p>	<p>McIntire (1973), Buzzelli et al. (2000), Fovet et al. (2010), Rutherford (2011a), Bellmore et al. (2014), DeAngelis et al. (1995), Dent and Henry (1999), Boulétreau et al. (2006)</p>
<p>Droop:</p> $\phi_N = 1 - \frac{q_0}{q}$ <p>q = cell quota</p>	<p>q_0 = minimum cell quota, internal nutrient concentration stored in algal cells (expressed as % of dry mass)</p>	<p>Droop (1973) Auer and Canale (1982), Flynn et al. (2013), Flynn (2014), Asaeda and Son (2000), Son and Fujino (2003), Ambrose et al. (2006), Cerucci et al. (2010)</p>

3.1.3 Nutrient dynamics and carrying capacity ϕ_x

At optimal light and temperature, periphyton productivity is controlled by hydraulics and geomorphology. Flow, water velocities, shear stress, substrate size, stability and roughness (Murdock and Dodds 2007) and time mediate colonization and adequate nutrient delivery from the water column to the benthic biomass. River hydraulics and mat thickness also affect nutrient uptake.

Nutrient delivery to algal cells in periphyton and its dependence on water column nutrient concentrations and hydraulic conditions were investigated by Whitford (1960) and Larned et al. (2004). Whitford (1960) concluded that diffusion was limited at velocities under 15 cm s^{-1} ; and Larned et al. (2004) conceptually modelled positive (enhancing nutrient delivery) and negative (increasing potential for detachment) effects of turbulence on periphyton growth. Contrasting slow molecular diffusion through the periphyton mat and turbulent diffusion in the main river affect

nutrient access for periphyton. At low velocities, mass transfer through a thick boundary layer controls nutrient delivery; at high velocities, transport across algal cell membranes (active transport systems) controls nutrient delivery (Larned et al. 2004, Jumars et al. 2001). In riverside channel experiments, maximum growth rates were achieved at lower nutrient concentrations for thin periphyton mats (Bothwell 1989), which suggests no hydraulic limitation of nutrient delivery. For dense mats, however, higher nutrient thresholds were required to saturate growth (Bothwell 1989), consistent when nutrient transport through the mat is limiting. Nutrients diffuse more readily into and out of the surface layers than those below the surface. Nutrient limitation due to delivery is generally implicitly accounted for by a biomass-dependent carrying capacity term.

Introduced in Section 2.2.2, a **carrying capacity** term can be used to implicitly model limitation of periphyton productivity by nutrient delivery through the mat. Such a biomass limitation mechanism mathematically curbs exponential growth by decreasing the growth rate to zero with an expression that depends on a defined maximum sustainable biomass (X_{max}), resulting in an S-shaped biomass vs. time curve with a horizontal asymptote at X_{max} . Conceptually, the carrying capacity is the maximum sustainable biomass in the system given biomass-related constraints. Generally light, temperature, and nutrient mediation are modelled separately (see Sections 3.1.1 and 3.1.2) and physical space constraints, self-shading, and any other less tangible growth mediation factors related to biomass density or mat thickness are accounted for in the carrying capacity expression. Biomass limitation may occur due to competition for space (see the Water Quality Analysis Simulation Program WASP7 and WASP8 user manuals, Martin et al. 2006, 2014) and/or nutrient delivery and light constraints at the bottom of a thick periphyton mat (Uehlinger et al. 1996, Higgins et al. 2005). An alternative means of accommodating carrying capacity constraints is by simulating self-shading, which restricts biomass growth as more biomass accumulates and shades cells below the mat surface (e.g., Asaeda and Son 2000, Higgins et al. 2005). Some methods of modelling carrying capacity/biomass limitation are summarised in Table 3-3. All approaches require model parameters that are difficult to define: a maximum sustainable biomass (carrying capacity) or a half-saturation constant for biomass, terms that are system-specific and can hide shortfalls in other model processes. Remembering that “all models are wrong, but some are useful” (Box 1987), these formulations – while not perfectly physically based – can nonetheless be useful for management applications when parameters are appropriately chosen for the site of interest.

Table 3-3: Common formulations for carrying capacity (ϕ_x) in mechanistic periphyton models.

Equation	Model parameters	References
<p>Logistic growth/saturation:</p> $\phi_x = \frac{X_{max} - X}{X_{max}}$ <p>X = biomass</p>	<p>X_{max} = maximum sustainable biomass</p>	<p>Ambrose et al. (2006, WASP7), Canale and Auer (1982), Tomlinson et al. (2010), Higgins et al. (2005), Malkin et al. (2008), Buzzelli et al. (2000)</p>
<p>Modified logistic growth:</p> $\phi_x = 1 - \left(\frac{X}{X_{max}}\right)^2$ <p>X = biomass</p>	<p>X_{max} = maximum sustainable biomass</p>	<p>Martin et al. (2014)</p>

Equation	Model parameters	References
<p>Michaelis-Menten:</p> $\phi_X = \frac{X}{k_X + X} \text{ or } \phi_X = \frac{1}{1 + k_{Xinv}X}$ <p>X = biomass</p>	<p>k_X = biomass half-saturation constant</p> <p>k_{Xinv} = inverse biomass half-saturation constant</p>	<p>Uehlinger et al. (1996), Rutherford et al. (2000), Rutherford (2011a), Bellmore et al. (2004), Boulêtreau et al. (2006)</p>

In addition to nutrient delivery, nutrient cycling via periphyton uptake and release in a river is termed '**nutrient spiralling**' and presents a modelling challenge. It is this process, directly tied to high spatial variability in rivers, that primarily distinguishes river periphyton modelling from lake periphyton modelling (Chapra et al. 2014). Few periphyton models take nutrient delivery and cycling (particulate to soluble forms and vice versa) into account, but some models differentiate between different nutrient concentrations in the laminar sublayer over the periphyton and the overlying mainstream (Saravia et al. 1998, Whitford 1960, McIntire 1968, Horner et al. 1990). DeAngelis et al. (1995) modelled transient storage zones, regions where nutrient concentrations can be mediated by biological communities either via uptake and conversion to organic material or via release through respiration and mineralisation during decomposition. Nutrient uptake and release by periphyton are highly dynamic and heterogeneous along a river, which makes it challenging to model (Rutherford 2011).

The parsimonious river model (Chapra et al. 2014, Table A-1) simulates nutrient pools, incorporates variable nutrient uptake, and offers enough spatial resolution to predict periphyton biomass at a distance downstream from a nutrient point source. This model is based on work by Thomann and Mueller (1987), who assumed 1D, spatially uniform, steady state plug flow⁵ and constant nutrient uptake rates by periphyton. The state variables are periphyton biomass as chlorophyll *a* (α , mg chl *a* m⁻²), bioavailable phosphorus concentration (p , $\mu\text{g P L}^{-1}$), bioavailable nitrogen (n , $\mu\text{g N L}^{-1}$), and organic matter (c , mg C L⁻¹). The organic matter pool represents dead or sloughed periphyton biomass and is assumed to have the same stoichiometry (N and P content) as live periphyton. It is also assumed that the material does not settle but hydrolyses and eventually releases N and P that contribute to the bioavailable nutrient pools. The main benefit of this model is its simplicity, which is analogous to early mechanistic mass balance models for lake management. There is potential for application of this model in setting nutrient loading targets to meet in-river periphyton biomass targets for steady state conditions, following site-specific model calibration and validation. However, the authors emphasise its limitations (Table A-1 and Table A-2) and the need for more complex models in cases where species competition, multiple point and point source loadings, non-steady state flow, and interactions with higher trophic levels are important.

Similarly, moderately complex river periphyton models incorporating nutrient cycling and uptake, self-shading effects, more complex loss mechanisms (sloughing and grazing), and spatial heterogeneity have been developed for specific locations/situations. For example, lateral heterogeneity and self-shading were included to model the growth of the filamentous green alga *Cladophora* in a Montana, U.S. river (Flynn et al. 2013). The Stream Algorithm (SAL) was developed to assess the relative ability of mayflies and snails (grazers) to control periphyton biomass in hill country rivers at Whatawhata, New Zealand (Rutherford et al. 2000). The Tukituki River Model (TRIM) is more complex in that it includes nutrient cycling between different N and P pools (Rutherford 2011a). These models become increasingly complex as more rate coefficients, species characteristics, and

⁵ Plug flow is a conceptualization used in chemical process modelling, where a fluid is assumed to flow uniformly through a pipe with no shearing between layers and "plugs" or segments/packages of chemically distinct fluid flow through without mixing with the preceding or subsequent plugs.

nonuniform channels and hydraulics are included. Model details are summarised in Table A-1 and Table A-2.

3.2 Biomass loss processes

As previously introduced in Section 2 and Figure 1-1, the loss or removal processes in mechanistic models include respiration R , grazing G , flow-induced sloughing (detachment) S , and mortality and autogenic sloughing M . Mass-based (DM, AFDM, or carbon) models include biomass losses due to respiration, mortality, and temperature-induced autogenic sloughing (e.g., Asaeda and Son 2001, Martin et al. 2006, Rutherford 2011a, Bellmore et al. 2014, Boulêtreau et al. 2006, Martin et al. 2014). In contrast, some chl a models only represent autotrophic production and do not include respiration, mortality or autogenic sloughing terms (e.g, Graba et al. 2010).

3.2.1 Respiration R

Respiration occurs both in light and dark conditions and can be modelled as the sum of basal and light-enhanced respiration (e.g., Canale and Auer 1982, Tomlinson et al. 2010). The magnitude of the rate of respiration is mediated by temperature and, in the case of light-enhanced respiration, light. The maximum rate of respiration is either a model calibration coefficient or derived from experiments. Biomass models usually define the respiration term using first order, temperature-mediated kinetics (Table 3-4).

Table 3-4: Common formulations for losses due to respiration (R) in mechanistic periphyton models simulating biomass dry mass (DM), ash-free dry mass (AFDM), or carbon.

Equation	Model parameters	References
<p>Basal and light-enhanced respiration:</p> $R = R_B + R_L$ $R_B = aT + b$ $R_L = R_{max}M_R$ <p>T = water temperature</p>	<p>a, b = fitting parameters</p> <p>R_{max} = maximum light-enhanced respiration rate (d^{-1})</p> <p>M_R = dimensionless multiplier, based on experimental data</p>	Canale and Auer (1982), Tomlinson et al. (2010)
<p>Temperature-mediated respiration:</p> $R = k_{R,ref} \theta_R^{T-T_{ref}} X$ <p>T = water temperature</p> <p>X = biomass</p>	<p>$k_{R,ref}$ = constant</p> <p>θ_R = constant</p> <p>T_{ref} = reference temperature, usually 20 °C</p>	Martin et al. (2006 WASP7, WASP8), Rutherford et al. (2000), Rutherford (2011a), Bellmore et al. (2014)

3.2.2 Grazing G

Grazing is a periphyton biomass loss mechanism (Feminella and Hawkins 1995, Steinman 1996, Hillebrand et al. 2002) that can limit periphyton accrual even in the presence of high nutrient concentrations (e.g., Biggs et al. 1998, Sturt et al. 2011). Several studies have been conducted to measure and simulate grazing. For example, Welch et al. (2000) conducted grazing experiments in outdoor flumes and indoor aquaria and measured mayfly, caddisfly, and snail grazing rates ranging 3.5–20 mg chl a $m^{-2} d^{-1}$; Elwood and Nelson (1972) measured snail grazing rates ranging 14–23 g AFDM $m^{-2} d^{-1}$ in a southeastern U.S. river; and Pinowska (2002) measured grazing rates of one snail species ranging 2.4–45.5 mg AFDM (g snail) $^{-1} d^{-1}$ with respect to three periphyton species. Invertebrate nutrient requirements differ from those of periphyton and invertebrates can exacerbate P-limitation if background P concentrations are low (Bowman et al. 2005). In addition, different

invertebrate species may compete for food, vary in their susceptibility to flood intensity and duration, and have different food preferences (Murdock et al. 2004). The ranges in grazing rate and variability with respect to grazer and periphyton species indicate why invertebrate grazing is not frequently modelled. However, Villanueva et al. (2004) found that, regardless of differences in abundance and mouthpart morphologies, the overall grazing effects of a mayfly and a snail species on periphyton were comparable in a Patagonian river, suggesting that the grazing effect due to different grazer species could be combined in a model. Nonetheless, when grazing is included as a variable periphyton loss rate, a grazer population model and associated nutrient uptake and release greatly increase overall model complexity and uncertainty.

Some models do include grazing mechanisms, generally as a function of grazer biomass, but do not include nutrient uptake and release (McIntire 1973, Rutherford et al. 2000, Graba et al. 2014). The Stream Algorithm (SAL) by Rutherford et al. (2000) includes a grazer biomass (G , gC m^{-2}) sub-model that simulates top-down control of periphyton biomass; the sub-model is driven by rates (in $\text{gC m}^{-2} \text{d}^{-1}$) of food assimilation (Ass), grazer colonization (G_{col}), respiration (Res), activity costs (Act), predation and mortality (Pre), and export loss (attributed to scour, drift, and emergence, Exp):

$$\frac{dG}{dt} = Ass + G_{col} - Res - Act - Pre - Exp \quad (4)$$

SAL model parameters that drive the grazing rate are the maximum search rate and food handling time, which is the time required to digest prey when grazers are not searching. There are 27 model parameters, of which seven were determined by calibration and the others were assumed or taken from the literature (refer to Table 1 in Rutherford et al. 2000). While this model is complex, the authors note that its calibration is site-specific and one of its weaknesses is that it does not simulate detritus or other trophic levels that affect grazers.

There are several more complex river periphyton models that simulate several species (e.g., McIntire and Colby 1978, Abdul-Azis et al. 2010). Results from a study using a longitudinally resolved nutrient-periphyton-grazer model (Spatial Algal Simulation Model, SPASM) indicated that invertebrates had little influence on periphyton abundance but that spate frequency and magnitude played a more important role in the upper reaches of Mangaotama Stream (tributary of Waipa River; Broekhuizen et al., unpublished).

Complex lake ecosystem models simulate phytoplankton losses due to zooplankton grazing, which is analogous to periphyton losses due to invertebrate grazing. Examples of spatially resolved aquatic ecosystem models include DYRESM-CAEDYM (e.g., Jones et al. 2018), ELCOM-CAEDYM (e.g., Trolle et al. 2014), and EFDC (e.g., Sinha et al. 2012).

3.2.3 Physically induced and autogenic sloughing S

As noted in a NIWA review (Kilroy et al. 2018), physical constraints of river periphyton growth in New Zealand has been an extensively researched topic (e.g., Biggs 1995, 1996, Biggs and Gerbeaux 1993, Biggs and Thomsen 1995, Biggs and Stockseth 1996, Biggs et al. 1999). Biggs (1995) investigated the relationship between chlorophyll a and flood frequency and nutrient concentrations with respect to geology and land use and concluded that flood disturbance and nutrient enrichment are likely the most important controllers of periphyton biomass. Biggs and Gerbeaux (1993) used data from six New Zealand river sites to support the ecological theory of large scale “ultimate” controls (climate, geology, and land use) and small scale “proximate” controls (nutrients, hydraulics, and substrate) of periphyton growth (Naiman et al. 1992). Biggs and Thomsen (1995) quantified the shear stress

tolerances of different periphyton assemblages and found non-filamentous diatom communities to be the most resistant. Biggs et al. (1999) investigated the frequency of high velocity events and sediment removal and concluded that the latter plays an important role in periphyton sloughing, apart from water velocity alone.

Listed in the order of increasing water velocity, there are three physical periphyton removal mechanisms (Biggs et al. 1999, Francoeur and Biggs 2006, Hoyle et al. 2017):

- 1) **sloughing** (detachment) due to shear stress exceeding periphyton tensile strength,
- 2) **abrasion** by suspended sediment,
- 3) **molar action**, i.e., movement (rolling/tumbling) of the solid substrate that is colonized by periphyton.

At lower flows that do not mobilize sediment or larger, colonized substrate, sloughing occurs when velocity-induced shear stress exceeds the periphyton holdfast or adhesion strength. The sediment grain size distribution determines bed stability and potential for abrasion and molar action (Hoyle et al. 2017). At stronger flows that mobilize fine sediment (silt, sand), sloughing occurs when the suspended sediment abrades periphyton from the substrate. At high flows that mobilize colonized substrate, sloughing occurs when the larger colonized substrate (cobbles, boulders) rolls on the river bed and that way sheds its periphyton cover. Water velocity induced sloughing and abrasion by suspended sediment may be modelled as a constant or flow- or velocity-dependent sloughing rate that continually decreases periphyton biomass but leaves enough biomass for rapid regrowth to occur. Molar action, however, results from distinct catastrophic events that rapidly reduce periphyton biomass to a minimum and result in slower regrowth after the event. Field measurements have shown that abrasion is likely the most important removal mechanism (Francoeur and Biggs 2006, Hoyle et al. 2017).

The duration of the period during which water velocities are low and substrate is stable determines the **accrual period**, or time during which periphyton biomass grows to a maximum before it is removed by one of the three described mechanisms triggered by flow. Horner and Welch (1981) measured chl *a* accrual on rocks in rivers at various current velocities and were the first to examine the effects of different nutrient/velocity combinations. They found that algal accumulation increased at velocities up to $\sim 50 \text{ cm s}^{-1}$ when DRP concentrations exceeded $40\text{--}50 \mu\text{g L}^{-1}$. Accrual rates decreased with increasing velocities when DRP concentrations were lower. It was hypothesized that accumulation is a result of competing growth rates determined by nutrient availability and velocity-dependent shear stresses: "Relationships of accrual rate with time for the respective rivers generally showed chl *a* accumulation to be inversely related to velocity, except when orthophosphate-phosphorus concentration continuously surpassed $45 \mu\text{g L}^{-1}$." These results agreed with results from McIntire (1966) and Phaup and Gannon (1967). Horner and Welch (1981) also found that "[v]elocity increase apparently assists productivity by improving turbulent diffusion," supporting previously discussed concepts concerning nutrient delivery.

Physical factors drive sloughing in a mechanistic model. Often, sloughing is modelled as a function of biomass, flow, velocity, or bottom shear stress, usually involving at least one tuning parameter (calibration coefficient), and a threshold value above or below which sloughing is triggered. Horner et al. (1983) and Welch et al. (1989) modelled detachment as $D = K_2 V^\Theta$, where *V* is the mean velocity and Θ is an empirical parameter (Table 3-5). Saravia et al. (1998) modelled detachment using a quadratic expression with two model fitting parameters and water velocity to account for shear

stress of the periphyton mat. They fitted model parameters for different sites and seasons. Uehlinger et al. (1996) modelled detachment as a function of flow and biomass, allowing detachment to occur when a specified minimal biomass is exceeded. The detachment rate is directly proportional to flow and biomass, as defined by an empirical detachment coefficient, C_{det} . Additionally, a site-specific catastrophic loss rate, k_{cat} , is used during bed moving spates. Based on the model developed by Uehlinger et al. (1996), Labiod et al. (2007) developed a mechanistic model to simulate biomass produced in laboratory flume experiments in relation to current velocity.

The shear stress of sand on substrate (cobble) is an important factor and has been simulated using several coefficients describing substrate mobility and periphyton- and attachment-specific resistance to detachment and drag forces (Tsujiimoto and Tashiro 2004, Hondzo et al. 2002, Asaeda and Son 2001, Table 3-5). Such models are complicated, can be computationally cumbersome, and introduce more uncertainty with each model fitting parameter or property-specific assumption (e.g., mean cobble and sand diameter, periphyton detachment coefficients, etc.). The influence of velocity and sediments on community structure remains a challenge to model (Flynn et al. 2013).

Less common approaches to model sloughing are to use light and turbidity as indirect triggers. For example, Asaeda and Son (2001) used a light index to estimate algal tensile strength to compare to the water drag force. Fovet et al. (2009) suggested that turbidity can be used as an algal detachment trigger.

Table 3-5: Common formulations for losses due to sloughing (S) in mechanistic periphyton models simulating biomass dry mass (DM), ash-free dry mass (AFDM), or carbon.

Sloughing rate formulations	Model parameters	References
<p>Velocity- or sheer stress-dependent S:</p> $S = k_2 V^\theta$ <p>V = mean water velocity at periphyton mat surface</p>	<p>k_2, θ = empirical fitting parameters</p>	<p>Horner et al. (1983), Welch et al. (1989)</p>
<p> $S = d_t X_t (V_t - V)^2$ <p>V_t = actual water velocity at time t X_t = biomass at time t</p> <p>Critical shear velocity or shear stress beyond which sloughing occurs</p> </p>	<p>d_t = degree of sloughing when current velocity is higher than the mean velocity (V), both are empirical fitting parameters</p>	<p>Saravia (1998)</p> <p>Rutherford (2011a), Fovet et al. (2010, 2012), Toda et al. (2005)</p>
<p>Flow- and biomass-dependent S (continuous removal and by catastrophic events):</p> $S = c_{det} Q (X - X_0) + k_{flood} Q (X - X_0)$ <p>where catastrophic detachment is</p> $k_{flood} = \begin{cases} 0 & \text{for } Q < Q_{crit} \\ k_{cat} & \text{for } Q \geq Q_{crit} \end{cases}$ <p>X = biomass X_0 = initial (or residual) biomass after spates Q = discharge/flow rate</p>	<p>c_{det} = empirical detachment coefficient ($s \text{ m}^{-3} \text{ d}^{-1}$) Q_{crit} = critical discharge for the onset of bed load transport, $40 \text{ m}^3 \text{ s}^{-1}$ k_{cat} = 100 d^{-1}, empirical catastrophic detachment value</p>	<p>Uehlinger (1996), Labiod (2007)</p> <p>Similar approach: Bellmore et al. (2014)</p>

Sloughing rate formulations	Model parameters	References
<p>S depending on shear stress driven bed load transport and sheltering:</p> <p>1)</p> $S = (24 \cdot 3600)\alpha W_x$ <p>where workload of collision between sand and substratum cobble is</p> $W_x = \gamma q_B d_s^{1/3} u_{*e}^{2/3}$ <p>And bedload discharge q_B is approximated by</p> $\tau_{*e} = f(\delta)\tau = \frac{f(\delta)u_*^2}{\left(\frac{\sigma}{\rho} - 1\right)gd_s}$ <p>where $f(\delta) = 1 - \delta$ and $\delta = \Delta_c/d_c$ τ_{*e} = non-dimensional (effective) tractive force δ = non-dimensional exposure height of cobbles σ = density of sand ρ = density of water g = gravitational acceleration u_* = shear velocity, calculated from depth-averaged velocity, sand roughness (depending on water depth, Δ_c, and d_s)</p> <p>2) Sediment mobility vs. critical flow threshold</p> $\tau_{crD_i} = \tau_{crD_{50}} \left(\frac{D_i}{D_{50}}\right)^{1-\gamma}$ <p>$\tau_{crD_{50}}$ = critical shear stress to mobilize the median grain size, $N\ m^{-2}$</p> $\tau_{crD_{50}} = \tau_{cr}^*(\rho_s - \rho)gD_{50}$ <p>τ_{cr}^* = Shields number ρ = water density, $kg\ m^{-3}$ g = gravitational acceleration, $m\ s^{-2}$</p>	<p>α = "resistant coefficient of algae detachment" taken as $1.23 \times 10^{-4}\ N^{-1}\ m$ for <i>Cladophora glomerata</i> (Kitamura et al. 2000)</p> <p>γ = cobble material property coefficient, $4.94 \times 10^5\ N\ m^{-4}\ s^{2/3}$</p> <p>$\Delta_c$ = exposure height of cobble d_c = cobble diameter, 10 cm d_s = sand diameter, 1 mm</p> <p>D_i = grain size of interest, m D_{50} = median grain size, m γ = hiding coefficient (dimensionless, no hiding $0 \rightarrow 1$ equal mobility across size classes) ρ_s = sediment density, $kg\ m^{-3}$</p>	<p>Tsujimoto and Tashiro (2004) and references within:</p> <p>Skuka et al. (2013)</p> <p>Hoyle et al. (2017)</p>

Sloughing rate formulations	Model parameters	References
<p>S depending on shear and fluid forces:</p> $\bar{U} = \frac{U_*}{\kappa} \ln\left(\frac{y}{y_0}\right) + B$ <p>\bar{U} = riverwise time-averaged velocity at depth y (cm/s) U_* = shear velocity (cm/s) κ = von Karman constant, 0.41 y = distance from flume bed (cm) y_0 = roughness height (cm) B = constant</p> $F_D = \mu(F_G + F_C - F_B - F_L)$ <p>F_D = forces acting on periphyton along mean flow $\mu = \tan\alpha$</p> <p>Additional equations for: F_G = gravity force F_C = periphyton attachment force F_B = buoyancy force F_L = lift force</p> <p>Assume drag and lift forces around cylindrical filaments, use boundary shear stress function based on fluid-velocity function and <i>Shields</i> (1936) relationship on critical shear stress to mobilize sediments</p>	<p>α = angle between bed plane and periphyton filament C_D = drag coefficient ρ_p = periphyton density d = periphyton diameter L = periphyton filament length σ_C = attachment coefficient C_L = lift coefficient</p>	<p>Hondzo et al. (2002)</p>
<p>S depending on shear stress, type of attachment and periphyton (several equations):</p> <ol style="list-style-type: none"> 1) detachment condition for bottom-attached filaments 2) detachment condition for laterally attached filaments 3) detachment rate for non-filamentous periphyton 4) recovery time since last scour event 	<p>C_D = drag coefficient S = surface area of filamentous cell V = biovolume of filamentous cell L = cell filament length f = bottom friction coefficient F_{cr1} and F_{cr2} = critical threshold strengths of filaments</p> <p>Critical velocities beyond which scour is initiated</p>	<p>Asaeda and Son (2001)</p> <p>Martin et al. (2014)</p>

3.2.4 Mortality and autogenic sloughing M

Mortality and autogenic or self-induced sloughing (detachment) are not often explicitly modelled, because flow-induced sloughing usually implicitly accounts for autogenic sloughing. Nonetheless, as periphyton grows dense and senesces, its structural integrity is compromised (e.g., Higgins et al. 2005, Boulêtreau et al. 2006). Autogenic sloughing occurs when the periphyton mat becomes thick, senesces, breaks and detaches. Boulêtreau et al. (2006) incorporated a temperature trigger to activate bacteria that enhance the degradation process and sloughing. In their model, the self-generated detachment rate is a function of the active bacterial density B_b (cells m^{-2}), which is another

state variable modelled by a differential equation involving temperature (Arrhenius)-mediated growth and a loss term. This autogenic sloughing mechanism introduces additional model complexity but was shown to successfully predict two periphyton AFDM peaks, under the condition that the flow-mediated sloughing term was retained. It was also used by Graba et al. (2014).

Table 3-6 Mechanistic model expressions for mortality and autogenic detachment.

Equation	Model parameters	References
<p>Mortality rate:</p> $M = k_{M,ref} \theta_M^{T-T_{ref}} X$ <p>T = water temperature X = biomass</p>	<p>$k_{M,ref}$ = constant θ_M = constant T_{ref} = reference temperature, usually 20 °C</p>	<p>Asaeda and Son (2000, 2001), Rutherford (2000)</p>
<p>Temperature and self-generated or bacteria triggered detachment:</p> $M = c_{auto} Bb(X - X_0)$ $\frac{dBb}{dt} = [\mu_{Bb} e^{\beta_{Bb}(T-T_{0Bb})} - c'_{det} X] Bb$ <p>X = periphyton biomass (AFDM) Bb = active bacterial density T = water temperature</p>	<p>c_{auto} = self-generated X detachment coefficient X_0 = minimum residual biomass μ_{Bb} = bacterial growth rate β_{Bb} = temperature mediation coefficient for bacterial growth T_{0Bb} = reference temperature for bacterial growth c'_{det} = flow-dependent X detachment rate</p>	<p>Boulêtreau et al. (2006), Graba et al. (2014), Flynn et al. (2013)</p>

4 Considerations for mechanistic river periphyton modelling

Preceding sections focused on the background, motivation, and general, and specific periphyton modelling approaches. In section 1, the need for models to support freshwater management with respect to periphyton was established. In section 2, benefits and challenges of empirical (statistical) and mechanistic (process-based) modelling approaches and foundational mechanistic model forms were introduced and **compared**. In section 3, specific model formulations for periphyton biomass growth and loss processes were **described**. This section **describes** further mechanistic modelling aspects in addition to specific process formulations.

4.1 Periphyton biomass and in-river nutrient modelling challenges

Biomass (chlorophyll *a*, dry mass or ash free dry mass) and water column nutrient concentrations are monitoring variables specified in the NPS-FM and are important for calibration and confirmation of models. Though regulations and monitoring programs are all based on periphyton biomass, an important question should be considered with respect to modelling periphyton with the purpose of establishing nutrient management targets to prevent nuisance growth:

What should the model predict as a response variable (e.g., periphyton biomass, internal or external nutrient concentrations, primary production)?

Water column nutrient concentrations can greatly vary in time and space due to variation in nutrient supply and in-river cycling. Nutrient supply is linked to landscape and can vary on the order of hours to months, while in-river nutrient variability occurs on the order of hours or days. In winter, soils are less capable of retaining nutrients, leading to high nutrient runoff controlling in-river nutrient concentrations. In summer, in-river processes often control in-river nutrient concentrations. Biomass and water column nutrient concentrations are highly dynamic, which makes the assessment of river health challenging.

Stored nutrient content and net primary production may be better indicators than in-river nutrient concentrations and biomass for periphyton nuisance conditions, because they integrate the effects of exposure to certain nutrient/grazing conditions over time. It has been suggested that net primary production (gross primary production – community respiration) based on dissolved oxygen (DO) may be a better means to predict river ecosystem health and trophic state than biomass (net autotrophic or heterotrophic, e.g., Bernhardt et al. 2018, Young and Collier 2008, Young et al. 2009). The ratio of gross photosynthesis and respiration (GP:R) can be used to functionally describe communities based on net metabolism (Odum 1957, Young et al. 2009).

There is feedback between nutrient concentrations in the water column and periphyton biomass. Currently, empirical models developed in New Zealand use annual mean nutrient concentrations to predict annual maximum or peak chl *a* but not vice versa (i.e., relate chl *a* back to nutrient concentrations). Seasonal fluctuations in DIN and DRP can be influenced by in-river uptake by periphyton. These models simulate chl *a* as a function of in-river nutrient concentrations, but in-river nutrient concentrations are taken as independent of chl *a*, a weakness recognised by modellers and managers but difficult to resolve. During summer low flows, DIN and DRP concentrations in lower reaches of a river are often low, while periphyton biomass is high. As periphyton assimilate nutrients (and uptake rates are high), concentrations in the water column are depleted. Regression models developed using data from synoptic, paired water quality/periphyton biomass sampling would often suggest that high nutrient concentrations could lead to low biomass. Munn et al. (2002) presented a

conceptual diagram to describe deviations from expected periphyton biomass vs. nutrient concentration trends. Biggs (2000b) avoided this problem by relating *annual average* DIN and DRP concentrations with *maximum* periphyton biomass. The former is an index of trophic status, while the latter is a measure of the worst-case condition response, the one of interest to managers.

Infrequent spot measurements of water column nutrient concentrations are not necessarily an indicator of periphyton biomass or growth potential because they do not always reveal nutrient supply over time. Spot measurements are more likely to result in negative or no empirical relationships between periphyton biomass and nutrient concentrations, but maximum biomass and annual mean nutrient concentrations result in positive empirical relationships (Figure 4-1). Mechanistic models can resolve sub-annual biomass estimates, accounting for sub-annual variations (e.g., pulses of nutrients coming through the river after a storm).

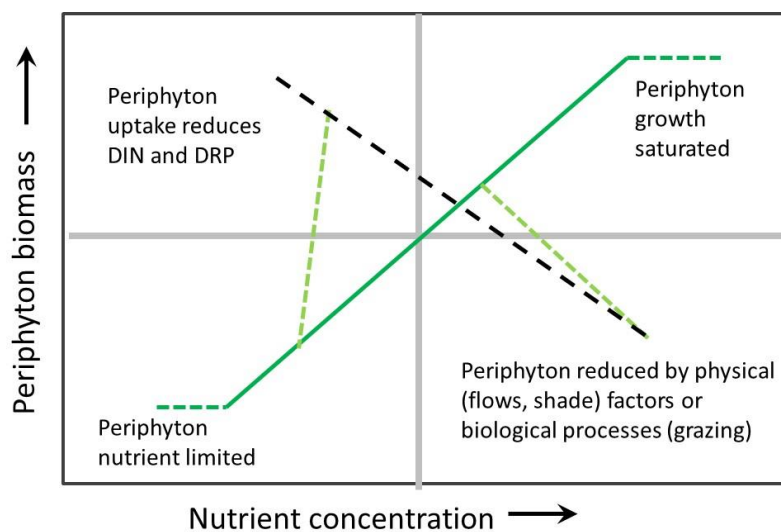


Figure 4-1: Conceptual model of likely relationship between nutrient concentrations and periphyton biomass. The bright green line is the idealised periphyton growth trajectory. Pale green dashed lines indicate deviations from the trajectory under different conditions (four sets of conditions indicated by the grey lines). The black dashed line shows the nutrient–biomass relationship typically revealed from analyses of periphyton over time within sites, or from synoptic surveys of periphyton over a region. Adapted from Munn et al. (2011).

Rather than focusing on measures of in-river nutrient concentrations, nutrients stored in periphyton cells may be considered. Measures of stored nutrient levels (usually measured as grams of nutrient per total grams dry mass, expressed in %) in periphyton can indicate growth potential (related to growth rate). High stored nutrient content (e.g., 0.50 %P in *Cladophora*) indicates historic exposure to high water column nutrient concentrations, while low stored nutrient content (e.g., 0.05 %P in *Cladophora*) indicates growth limitation (e.g., Kuczynski et al. 2016). A measure of stored nutrient content would likely be a better indicator for growth potential than water column nutrient concentrations because the variable fluctuates less and integrates the exposure to high water column concentrations over time. Stored N and P content is determined by particulate N and P analysis on a known mass of periphyton. Given the laborious nature of analysing stored nutrients as opposed to in-river dissolved nutrient concentrations and considering that the NPS-FM mandates that regional councils set annual median or mean limits for DIN and DRP concentrations, a mechanistic model could relate stored N and P content back to mean water column N and P concentrations (e.g., for P, Figure 8a in Tomlinson et al. 2010). This approach should be further explored.

4.2 Model resolution

Ultimately, the acceptability of a mechanistic model fit depends on the case-specific question to be answered. In addition to model parameter definition, model resolution is important. Existing periphyton models have a **spatial** resolution at the river reach scale due to observational data availability and representativeness. Periphyton growth in rivers tends to be patchy (from one m² to another m² in one reach) and small-scale heterogeneities are difficult if not impossible to resolve in a model. Periphyton biomass is usually quantified based on the average of ~10 small samples (Biggs and Kilroy 2000), which may not be representative of the sampled river reach (see Kilroy et al. 2013 on representativeness and number of samples). The mechanistic model developed by Uehlinger et al. (1996) simulates periphyton biomass along a deterministic trajectory in a river reach of 2 km and heterogeneities cannot be accounted for (Uehlinger et al. 1996). A spatial scale recommendation of 1 km² for hydrological simulations is recommended by Janssen et al. (2019) as part of their ideal algal prediction model, which focuses on lakes but also includes rivers in the hydrological network.

Most periphyton models simulate biomass at a daily time interval. This is an appropriate **temporal** scale on which changes in biomass can be observed *in situ* and monitoring data can be obtained. Rutherford et al. (2018) recommend a daily-weekly time step because biomass changes at the sub-daily scale are not only difficult to model but are difficult to confidently measure in the field (Kilroy et al. 2013). Furthermore, diurnal, hourly or sub-hourly changes in flow, water column nutrient concentrations, DO, and pH can affect nutrient cycling (e.g., DO affects denitrification and pH affects P adsorption to sediments) and in turn biomass. This means that sub-daily processes cannot always be dismissed and should be modelled at the hourly scale to produce daily biomass estimates. A daily time step is advisable.

The level of **kinetic** (ecosystem process rate) resolution required can be more difficult to determine. Details concerning the level of nutrient cycling, periphyton composition, grazers and potentially higher trophic levels must be selected with the goal of achieving an appropriate balance between model simplicity and complexity, reflected in uncertainty and computational time. When both N and P are modelled, choices must be made in terms of representing their bioavailable fractions and cycling between different forms. For example, dissolved reactive P is considered ~100% bioavailable, while the dissolved organic and particulate fractions vary in their bioavailability. Similarly, different forms of N are more or less bioavailable for algal uptake. When periphyton grows beyond a thin layer of cells into a thick mat, internal recycling processes within the mat may alter periphyton growth rates beyond the influence of nutrient supplies from the water column (Mulholland and Webster 2010). In short, the more nutrient pools (state variables) are included in a model, the more transfer rate coefficients must be defined, and the uncertainty of model predictions increases with the number of model parameters.

To choose appropriate state variables and model processes, their relative importance must be tested. For example, Bellmore et al. (2014) investigated top-down control of periphyton by higher trophic levels. In some situations, salmon can enhance periphyton growth via nutrient supply and in other situations, spawning activity disturbing the river bed can impede periphyton growth (Bellmore et al. 2014). But how important is the role of salmon with respect to periphyton growth? Based on model simulations, the authors found that “salmon did not greatly increase or decrease overall annual periphyton production.” In this case, incorporation of high trophic level organisms (salmon) was not required to improve predictive capability.

4.3 Model evaluation

Model simplicity and complexity must be balanced to reach an appropriate level of accuracy and precision for answering the question at hand. Accurate river periphyton biomass predictions are difficult to make as chl *a* cannot be measured with high precision (Kilroy et al. 2013), but to set nutrient targets, model estimates of biomass should be comparable to observations in magnitude and timing of peak biomass during an accrual cycle. In the spirit of Occam's razor and a quote attributed to Einstein, "everything should be made as simple as possible, but no simpler," the challenge lies in achieving the required model reliability while minimizing costs (Chapra 2008) in data collection, uncertainty, and computing time. A reliable mechanistic model stands on 1) sound physical and biogeochemical principles/formulations and usually on 2) confirmation model runs that produce accurate predictions compared to observational data. Assessing model agreement with observational data is the standard means of calibrating and confirming a model. During this process, managers should focus on a model's ability to predict the relative direction and magnitude of change of the response variable (e.g., biomass) with respect to perturbation rather than its ability to produce precise output values at any point in time or space in a given river.

4.3.1 Goodness of fit

Models are generally calibrated (i.e., tuning coefficients/model parameters are determined) with one dataset and confirmed or validated using the same set of parameters with another, independent data set. Models are calibrated using *in situ* and/or experimental data that are as representative as possible of the conditions to be modelled (i.e., site, species, forcing conditions). Unfortunately, this requires system-specific definitions of parameters such as the sloughing (detachment) rate, critical flow, and gross specific growth rate (Uehlinger et al. 1996). Empirical model parameters are generally defined using optimization methods (e.g., maximum likelihood or least squares). Few empirical and mechanistic models have prediction errors under 30% and can reach well beyond 100% (Reckhow and Chapra 1999). Basic methods for assessing error propagation are Monte Carlo simulation and first order error analysis (Reckhow and Chapra 1999, Hornberger and Spear 1980, Spear and Hornberger 1980).

Various statistical methods are commonly used to evaluate mechanistic model performance or the goodness of fit of model output to observational (measured) data: e.g., the coefficient of determination (r^2), the root mean square error (RMSE), Nash-Sutcliffe efficiency (NSE), the normalized unbiased root mean square difference (NRMSD), and Pearson's chi-squared test (e.g., Uehlinger et al. 1996, Graba et al. 2014). Non-steady state systems can be evaluated by deterministic stability analysis, which uses one or several eigenvalues of the Jacobian, i.e., characteristic values that are sets of model parameter solutions (Saravia et al. 1998, Chapra 2006, Chapra 2012). The Akaike Information Criterion (AIC) is a statistical means of comparing models to aid in selecting a model based on the trade-off between model accuracy or goodness of fit and model simplicity; for example, Boulêtreau et al. (2007) used the AIC to identify an appropriate minimalist model for predicting river epilithon biomass. These methods compare model output with observations but are not necessarily a measure of a model's ability to predict *change*. For these statistical methods of assessing model performance to be useful, a model must be tested using distinctly *different* conditions (environmental forcing conditions, nutrient loadings), which requires observational data (e.g., dry and wet weather conditions).

4.3.2 Sensitivity and uncertainty

Beyond parameter estimation, there is uncertainty in observational data/measurements, setting initial and boundary conditions, process definition, model structure, scenario choice, and numerical approximation; some of the uncertainty is propagated to model predictions and some is not (Dietze 2017). The accuracy and precision of model output heavily depends on that of measured input forcing conditions (e.g., light intensity, water temperature, and water column nutrient concentrations) and calibration data (periphyton biomass and/or other state variables). In addition, the amount and quality of available data (forcing conditions and response variables) for model confirmation tends to be limited. However, new technology can aid in improving the accuracy, precision, and frequency of physical, biological, and chemical data collection.

A sensitivity analysis serves to identify the model parameter(s) with the greatest influence on model output. The modelling paradigm “Garbage in → garbage out” and vice versa “High quality input → high quality output” holds. The result of a sensitivity analysis allows a model user to focus on defining the model parameters that have the greatest effect on model output, because the higher the confidence in the model parameter, the higher the confidence in model output.

Large mechanistic environmental models are often overparameterized due to 1) high structural complexity that seeks to account for process understanding and 2) data limitation for calibration and confirmation; i.e., calibration does not result in a unique set of parameters. Brun et al. (2001) describe two approaches to tackle the parameter identifiability problem of large models and select a parameter set based on model sensitivity to single parameters (via parameter importance indices) and to parameter subsets (via a collinearity index). Rutherford et al. (2018) emphasize that overparameterization does not necessarily make a model unsuitable for informing management and that “even with a paucity of data and high uncertainty, it is possible to support decision makers.”

4.4 Data needs for modelling

The greater the input of **experimental** results and **field** measurements, the better models can be parameterised, calibrated, and confirmed. Intuitively, more data must lead to better models; however, the design of experimental and field work is critical. A periphyton model can only be as good as the data which inform it, i.e., forcing conditions and data-derived parameters.

River periphyton biomass models are intended to serve managers (e.g., regional councils and MfE) in setting periphyton targets and guidelines to protect ecosystem and human health in the face of changes in land cover and land use. New Zealand water quality regulations (NPS-FM) are based on monthly periphyton biomass and nutrient concentration measurements in runs, which are more prevalent in rivers than riffles and pools, although high turbulent dispersion and associated nutrient delivery in riffles can support high periphyton biomass.

Model **parameterisation** requires information that can only be obtained from highly controlled experiments that minimize the number of system variables. As emphasized in a review by Larned (2010), many published results come from studies of periphyton responses to multiple variables, from which temporal and spatial patterns are inferred but mechanisms are rarely identified. Results from highly controlled experiments, however, can be used to describe mechanistic responses. For example, Graham et al. (1982) performed a suite of *Cladophora* growth laboratory experiments resulting in a matrix response to gradients of light and temperature; these results have been used to derive unitless light/temperature response functions that mediate maximum growth and respiration (Tomlinson et al. 2010). The absolute growth and respiration rates (grams dry mass produced per

grams dry mass per day) measured in these experiments do not accurately represent natural ecological responses, but the relative response was identified, normalized, and applied to site- or system-specific maximum growth and respiration rates. Similarly, extensive experimental work has been conducted using chamber (respirometer) and flume experiments (e.g., Biggs and Close 1985, Biggs 1995, Quinn et al. 1997, Matheson et al. 2012b), providing invaluable structural information and data for modelling nutrient-periphyton dynamics.

While experimental results are important for model parameterisation, field measurements are critical for model **calibration** and **confirmation**. Model calibration is the process of choosing model parameters that result in model predictions that agree with measurements of the response variable (periphyton biomass) as well as possible, i.e., tuning the model. Model confirmation is the process of running the model with the same set of calibrated parameters with a different set of forcing conditions, e.g., for a different time, and comparing the model output with measurements. The NPS-FM (2017) mandates monthly periphyton chl *a* monitoring. This temporal resolution (monthly) is coarse and cannot capture periphyton accrual periods, which can range from a few days to several weeks. Monthly data can still be used for model calibration but the input data (environmental forcing conditions) and calibration data (periphyton biomass) are often not reliable enough to achieve a satisfactory model calibration.

Uehlinger et al. (1996) suggested a minimum of 18 months of weekly biomass sampling per river to inform parameter estimation. While cost- and time-intensive, such a biomass sampling regime along with other measurements, depending on the processes simulated in the model, could be used as input forcing conditions for calibration and confirmation of a river-specific mechanistic model. For several models, those additional measurements should ideally include bookend forcing conditions for macronutrient concentrations and physical characteristics: concentrations of N and P forms, flow, velocity, light, temperature, and substrate (grain size distribution) on several sites along a river. New technologies such as near field remote sensing and automated in river nitrogen sensors are being developed and tested to achieve high resolution flow, periphyton, and nutrient concentration data.

More efficient periphyton monitoring methods are in development and could be used to collect model input, calibration, and confirmation data. For example, remote sensing methods using aerial imagery to monitor periphyton hold promise for estimating algal coverage, biomass, and type (e.g., filamentous green, thin film, *Didymosphenia geminata*). For model calibration and confirmation, aerial imagery obtained using drones can greatly enhance spatial resolution, while stationary camera deployments can improve temporal resolution. Multispectral imagery can assist in distinguishing between algal types. Remote sensing techniques hold promise for collecting continuous flow, substrate, and nutrient data.

4.5 Lessons from lake models

Lake water quality modelling with the purpose of managing eutrophication began with an empirical regression model relating phosphorus loading to phytoplankton chlorophyll *a* (Vollenweider 1968, 1975). Since then, empirical and more so mechanistic models have been developed and applied to manage lake eutrophication all over the world, including New Zealand (e.g., Trolle et al. 2014). Most of those water quality models focus on predicting nutrient cycling but some also include suspended algal blooms, i.e., phytoplankton, rather than attached biomass, i.e., periphyton or benthic algae (e.g., Delft3D-WAQ/ECO/BLOOM in the DeltaShell framework, ELCOM-CAEDYM, DRAINMOD, ECM, EwE, GLM, LakeWeb, MIKE 11, MyLake, NiRReLa, PCLake, PROTECH, QUAL2E, SIMCAT, TOPMODEL, WQRRS). Several process-based lake models have been used to predict periphyton biomass, notably

efforts to predict benthic nuisance algal growth in the Laurentian Great Lakes (Great Lakes *Cladophora* Model – Auer et al. 1982, Tomlinson et al. 2010; *Cladophora* Growth Model – Higgins et al. 2005, Malkin et al. 2008). In lakes, residence times determine whether biogeochemical or physical processes drive ecosystem dynamics (Janssen et al. 2019); similarly, in rivers, water velocity and periphyton mat thickness determine the efficiency of nutrient delivery. Several other mechanisms (e.g., self-shading, respiration, and sloughing due to shear stress) that are used to simulate periphyton growth in lentic systems are transferable to lotic ones.

In a review paper, Mooij et al. (2010) identify two main challenges in future lake ecosystem modelling: 1) to avoid “reinventing the wheel” from the bottom up, given that many capable models already exist, and 2) to avoid “tunnel vision” by focusing on one model rather than employing several different models in an ensemble fashion to arrive at conclusions. This perspective is also appropriate with respect to water quality modelling in rivers. Both empirical and mechanistic modelling approaches come with advantages and disadvantages; thus, an ensemble approach that employs multiple models can ultimately improve confidence via converging predictions. One example of ensemble modelling for lake water quality is the work that was completed by an international task team addressing Annex 4 (Nutrients) of the Great Lakes Water Quality Agreement (IJC 2012), where both empirical and mechanistic models were applied to set new phosphorus loading targets for Lake Erie (Annex 4 Objectives and Targets Task Team 2015) in North America. Connecting models is becoming the standard for good practice in lake modelling in New Zealand as well (e.g., ELCOM–CAEDYM links lake hydrodynamics and water quality, Trolle et al. 2014). Models are linked when models are run in series, where one model produces output that serves as one-time input for another model; this is also referred to as running several models “off-line”. Models are coupled when several models are run in parallel, producing output that serves as new input across models at each time step; this is also referred to as running several models “on-line”.

Further, an open source modelling platform for lake and river modellers would enable more rapid testing, parameterisation, and development of lake and river water quality models across spatial and temporal scales. The atmospheric and ocean modelling communities have already been actively collaborating via online platforms to testing and improve large environmental models (e.g., the GEOS-Chem global atmospheric and FVCOM ocean models). Similarly, a large community of researchers across the world recently published results from a study in which the General Lake Model (GLM) was applied to 32 lakes across the world and rigorously tested (Bruce et al. 2018, through the Global Lake Ecological Observatory Network, www.gleon.org). To the best of my knowledge, no such large collaboration exists for river water quality modelling, much less with a specific focus on predicting river periphyton.

5 Conclusions and recommendations

The main purpose of a river periphyton model for New Zealand is to serve as a tool to simulate different environmental scenarios and predict the corresponding periphyton response (biomass). Model predictions will serve to set nutrient criteria to meet biomass targets. Mechanistic models can help identify drivers to be targeted for management in specific situations and, though they may also require case-specific calibration, they are more transferable than empirical models. Mechanistic models can take more investment to develop and test, but the potential benefits for environmental management and natural resource use are significant.

The best mechanistic models are parameterized, calibrated, and confirmed using high quality, high quantity observational data; the best empirical models are also based on high quality, high quantity data and at least some process understanding. It is important to recognise the main limitations of mechanistic models but also embrace the future of predictive modelling based on improved data availability and quality (Reckhow and Chapra 1999). Mechanistic models are often data-limited with respect to parameter selection. Often, expert judgment or literature values (e.g., Bowie et al. 1985) are applied even when those values are site-specific and inappropriate for a given case. This is not only a common issue in mechanistic periphyton modelling (e.g., also in stormwater quality modelling; Al-Amin and Bdul-Aziz 2013). At least two publications have summarised commonly used model coefficient ranges (Horner et al. 1983, Benedini and Tsakiris 2013), but those summaries are either outdated or incomplete.

To inform nation-wide river periphyton management using mechanistic models, I recommend the following:

- 1) **Identify** several high priority **rivers** with distinct characteristics (geomorphology, nutrient concentrations, flows, temperature, light conditions/shading, etc.).
- 2) Using the high priority rivers identified in step 1), develop, calibrate, and confirm **river-specific** mechanistic periphyton **models** based on the parsimonious river model (Chapra et al. 2014). Steps for developing a mechanistic periphyton model are outlined in Appendix B. To improve site-specific river periphyton modelling, I recommend focusing on the following:
 - a. Collecting high resolution data (hydraulics, temperature, light, nutrients, periphyton) using cutting-edge technology such as remote sensing to support model calibration, confirmation, and data assimilation; and
 - b. Better defining physical and biological periphyton processes (esp. nutrient delivery and uptake, biological senescence, and physical detachment) by performing laboratory and *in situ* experiments at the species or periphyton community level.
- 3) Apply the calibrated and confirmed, river-specific models to rivers with similar characteristics. Recalibrate the models as necessary. Create a **look-up table** of tested ranges of parameter values for specific river classes. The parameter tables should be readily available to every periphyton modeller and routinely updated so that models can be judiciously applied with an adaptive management approach.
- 4) Simulate a suite of possible temporally variable hydraulic, nutrient, light, and temperature conditions for a river of interest. Using the results, develop river-specific stressor–receptor **response curves** (periphyton biomass vs. steady state in-river nutrient concentration). Those curves can then be used to define site-specific nutrient criteria to meet periphyton biomass

targets in endpoint (extreme) conditions. The main limitation of this approach is that it sets criteria for **steady-state conditions**.

Finally, it must be recognised that periphyton modelling is but one piece of a large puzzle. The performance and reliability of any periphyton model highly depends on the quality of data describing environmental forcing conditions, which are often the output of other physical and biological models. To accommodate temporal and spatial variation those conditions, a periphyton model should be coupled (run simultaneously/in parallel) or linked (run sequentially/in series) with another or several other models that simulate physical conditions (atmospheric conditions, catchment processes, hydrodynamics) and ecosystem processes that affect periphyton (e.g., nutrient cycling and phytoplankton/grazers/higher trophic levels). Both ensemble modelling (running different models independently) and connecting models is becoming increasingly common across the world, including New Zealand. The linkage of atmospheric, catchment, hydrodynamic, sediment transport, nutrient, and multi-trophic level ecosystem and social/economic models remains challenging but must be advanced to capture system responses to natural and anthropogenic perturbation and inform management decisions.

An example of coupled natural and human system modelling, Cobourn et al. (2018) linked several cross-disciplinary models to capture human and natural systems: 1) agricultural land-management decisions, 2) terrestrial nutrient cycling, 3) hydrologic-solute transport through catchments and rivers, 4) aquatic nutrient cycling to simulate water clarity, anoxia, and cyanobacterial blooms in lakes, 5) residential property values, and 6) civic engagement. The application of such a model mosaic may require inclusion of a periphyton model in 3), if periphyton mediate nutrient concentrations in rivers, which affect 4) and 5). Assuming that catchment modelling will not provide daily time series of nutrient loads to rivers in the near future, in the meantime, management decisions have to be made based on assumed steady-state conditions.

This report is intended to serve as a living document for collating information on mechanistic river periphyton modelling and to lay a foundation for future work on predicting periphyton responses to anthropogenically and naturally induced environmental changes.

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Appendix A Mechanistic river periphyton models

Table A-1: Overview of mechanistic river periphyton models from simplest to most complex. Models are grouped into simple models (red), models driven by prescribed environmental conditions (yellow), models featuring some spatial resolution and nutrient cycling (green), complex models (blue), and case-specific models (no colour). Table A-1 is a companion table in Appendix A that summarises further technical details about each model.

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
Logistic growth model and variations		Tested on various periphyton types and monitoring data for Lake Vechten (Netherlands), Lake 240 (ON, Canada), Hortus Botanicus ditches (Netherlands), Lake Jyvasjarvi (Finland), Oak Creek (AZ, USA), experimental trough (Yellowstone N.P., USA), Gwendoline Lake (BC, Canada), Yahagi River (Japan)		<ul style="list-style-type: none"> - simple, not computationally demanding - can be modified/enhanced 	<ul style="list-style-type: none"> - does not explain biomass fluctuations - site-specific max growth rate and max carrying capacity terms - assumes negligible grazing and sloughing - does not include light, temp. or nutrient limitation - min initial biomass 	Bothwell (1988), Rodriguez (1987), Ateia et al. (2016), Tsujimoto and Tashiro (2004), Momo (1995) Free access (equations)
McIntire/Uehlinger river model	- 4th order Runge-Kutta method	Spokane River (WA, USA), Oregon rivers (USA), Necker River (Switzerland), Garonne River (France), Agüera River (Spain), Natori River (Japan), Yahangi River (Japan)		<ul style="list-style-type: none"> - accommodates need for different coefficients for different algal assemblages - uses velocity for nutrient delivery through laminar sublayer and for shear stress - algal detachment as function of friction velocity rather than flow - some versions include grazing, mat buoyancy, algal succession 	<ul style="list-style-type: none"> - 11 empirical parameters - model sensitivity to uptake parameters - not spatially resolved - neglects velocity effect on uptake - must know light extinction coefficient through different types of mats - does not explicitly account for nutrient uptake on concentration of limiting nutrient - Uehlinger model requires specification of recolonization rate or residual algal biomass after a flood - does not simulate grazer-algae-flow interactions 	McIntire (1973), McIntire and Colby (1978), Uehlinger et al. (1996), Saravia et al. (1998), Fothi (2003), Toda et al. (2005), Boulétreau et al. (2006, 2008), Labiod et al. (2007), Graba et al. (2014), Kazama and Watanabe (2018)

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
Horner model	"empirical dynamic periphyton model", 1 epilithic algal group (diatoms) and 1 grazer group (snail <i>Juga</i>)	Oregon rivers	none because "not sufficiently developed for predictive use in management"	- includes current velocity as a variable in continuous time equations	- 1 calibration parameter varies linearly with P (not mechanistically defined) - predictions were high at velocities < 15 cm/s - does not explicitly account for nutrient uptake on concentration of limiting nutrient	Horner et al. (1978, 1983), (McIntire and Colby 1978), Welch et al. (1989)
Hornberger and Spear model	Models <i>Cladophora</i> biomass as P	Murray River, Peel Inlet, Australia		- simple P budget model including P in <i>Cladophora</i> , phytoplankton, sediments, groundwater, and water column - application of Monte Carlo methods to assess parameters	- 19 calibration parameters	Hornberger and Spear (1980), Spear and Hornberger (1980)
Parsimonious River Model, Lateral <i>Cladophora</i> River Model	- assumes 1D, plug flow, spatially uniform, temporally steady state	- Montana (USA) example application to determine nutrient criteria and TMDL wasteload allocation - Yellowstone River, eastern Montana (USA)		- simplicity, fixed stoichiometry - accounts for N and P uptake and bioavailable rather than total N and P - distributes biomass downstream of nutrient sources - agrees with Bothwell (1989) model prediction if Bothwell's log-linear model is replaced with Michaelis-Menten P limitation	- grazing is part of death/sloughing term - unrealistic fixed stoichiometry - assumes steady state conditions - not calibrated/validated because no appropriate data sets were available - does not account for nutrient delivery limitation related to hydraulics	Chapra et al. (2014) and Flynn et al. (2013), based on Thomann and Mueller (1987) but includes nutrient uptake
SAL1 (Stream ALgorithm 1)	1 functional group of diatoms, 1 group of grazers (mayflies)	Hill country rivers at Whatawhata (New Zealand)		- light, temperature, nutrient, grazing, water velocity effects modelled	- does not explicitly account for nutrient uptake on concentration of limiting nutrient	Rutherford et al. (2000)

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
Tukituki River Model (TRIM)	2 submodels: hydraulic and nutrient-biomass	Tukituki River (North Island, New Zealand)		<ul style="list-style-type: none"> - predicts biomass and nutrient peaks timing and order of magnitude - includes several nutrient cycling processes - can turn P exchange with sediments on/off and test effect on water column concentrations - handles 827 river segments (all 4th order or higher) 	<ul style="list-style-type: none"> - uncertainty in calibration parameters - no stored P or Droop kinetics - assumes straight, uniform river segments - phytoplankton not included - cannot resolve sub-daily changes - assumes $DON = PN = (TN - NNN)/2$ and $DOP = PP = (TP - DRP)/2$ - site-specific calibration - assumes fixed internal nutrient stoichiometry and C:N and C:P ratios - nutrients are treated as conservative - hard-wired biomass reseeding after flood - highly dependent on annual input nutrient concentrations transformed into daily (driven by OVERSEER) - assumes worst case scenario (no denitrification) - poor DRP prediction - not enough data for validation 	<p>Rutherford (2011a,b, 2012, 2013a,b)</p> <p>Proprietary access (NIWA)</p>
ISOFLOC (Isotope-based Fluvial Organic Carbon) Model → based on SAL 1	<ul style="list-style-type: none"> - mass balance C isotope fractionation model - C cycling in water column and sediments, sediment transport, hydrology - Suggests that shielding and burial during spates 	Kentucky River Basin (South Elkhorn, KY, USA)		<ul style="list-style-type: none"> - model captures event, seasonal, and annual trends - sloughing driven by shear stress - simulates algal biomass export after detachment 	<ul style="list-style-type: none"> - assumes algae are neutrally buoyant - most sensitive calibration parameters are benthic rates: algal growth, critical shear stress of algae, algal decomposition - does not include rate limiting nutrient conditions - rates must be calibrated for forested, urban and agricultural systems 	<p>Ford and Fox (2015), Ford and Fox (2014)</p> <p>rate values taken from Rutherford (2000), Flynn et al. (2013)</p>

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
	enhances algal stabilization					
TRANSFER (Technology for Removable Annual Nitrogen in Streams For Ecosystem Restoration)	- focus on N cycling - based on ISOFLOC	Kentucky River Basin (South Elkhorn, KY, USA)		- focus on N cycling (denitrification and N spiralling)	- only applicable in non rate-limiting nutrient conditions (i.e., in nutrient-rich urban and agricultural systems)	Ford and Fox (2017b)
AQUATOX	- eutrophication and contaminant fate and transport model - began with CLEAN model (Park et al. 1974) - 4th and 5th order Runge-Kutta integration	Pearl River (LA, USA), Blue Earth River, Rum River, Crow Wing River (MN, USA), Cahaba River (AL, USA), other places in the U.S.	- available in Environmental Protection Agency's (EPA's) Better Assessment Science Integrating point and Non=point Sources (BASINS) platform - used to develop Total Maximum Daily Loads (TMDLs) under U.S. Clean Water Act - assessment of effect of P, TSS, and N levels on benthic chl <i>a</i> - determining nutrient criteria (Carleton et al. 2009) - periphyton and zoobenthos in experimental rivers in France	- user-friendly - does not require much input data - compatible with watershed models HSPF and SWAT to incorporate land use N and P loadings - periphyton submodel calibrated across 20 experiments (EPA, 2000) - includes sediment diagenesis model for remineralization (Di Toro 2001) - peer reviewed by external panel convened by U.S. EPA - extensive parameter library included - can model up to 20 organic chemicals simultaneously	- C cycling based on theory for slow moving water - need more monitoring data (algal biomass) to confirm model calibration parameters - cannot model metals	https://www.epa.gov/ceam/aquatox U.S. EPA (2000) - sediment model DiToro (2001) - WASP 6 Wool et al. (2006) Joyner and Rohli (2013), Carleton et al. (2009), Park et al. (1995, 2008), Rashleigh (2003) Free access

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
QUAL2K (River and Stream Water Quality Model), AT2K, QUAL2Kw	- widely-used, chl a in rivers - 1D steady state flow	Lis River, Portugal		- includes a genetic algorithm for model calibration	- hydraulic removal mechanisms not included - assumes fixed internal nutrient stoichiometry - input data requirements	Pelletier et al. (2006), Pelletier and Chapra (2005), Chapra et al. (2008), reviewed by Cox (2003), Flynn et al. (2015), Vieira et al. (2013), Tsakiris and Alexakis (2012) Free access
CE-QUAL-ICM and CE-QUAL-W2			U.S. Army Corps of Engineers		- complex, lots of data requirements	Cerco and Cole (1994), Rounds and Wood (2001) Free access
Water Quality Analysis Simulation Program (WASP)	- Cerucci et al. (2010) tested Droop vs. Monod kinetics	Raritan River Basin (NJ, USA)	EPA		- does not consider hydraulic removal mechanisms	Park and Clough (2012), Ambrose et al. (2006), Cerucci et al. (2010), Martin et al. (WASP8), Wool et al. (WASP6, 2006), Kish et al. (WASP5) Free access
RWQM, RWQM1 based on activated sludge models ASM1, ASM2, ASM3 (Henze et al. 2000) and QUAL2E (Brown and Barnwell 1987)	River Water Quality Model, based on AQUASIM biofilm model (Wanner and Reichert 1996)	DIN in Crocodile River, South Africa		- can turn off lots of mechanisms to simplify model - more refined than QUAL2E, based on COD similar to Activated Sludge Models (ASM-1, ASM-2, ASM-3) - Model parameters include C, H, O, N, P fractions - Monod kinetics	- constant stoichiometry (C, H, O, N, P) - no changes in organism composition - assumes NO ₃ is always available - complex, many state variables - requires a lot of input data - Crocodile River model most sensitive to microbial biomass and hydraulic parameters, complicated periphyton treatment like a porous matrix, hard to upscale to a reach	Reichert et al. (2001), Deksissa et al. (2004), Debele et al. (2009), Van Griensven (2002)
Deltares modelling suite with 1) hydrodynamic model Delft3D Flexible Mesh	Standalone software for purchase - structured grid model	San Francisco Bay (CA, USA), Rhine River (Germany)		- high spatial (1D, 2D, 3D) and temporal resolution, can be applied for to rivers, lakes, and estuaries - includes sediment dynamics	- not yet well developed for periphyton but has capability	Delft3D FM: Deltares (2015, 2017), Yossef et al. (2008), Li (2009), Los (2009, ch. 7) DELWAQ: van Gerven et al. (2015)

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
(Delft3D FM, succeeds Delft3D 4, SOBEK 2) 2) water quality model framework: DELWAQ (Delft Water Quality)	- includes water quality modelling options for periphyton (DELWAQ, BLOOM)			- physical model has already been applied and tested across the world, especially in estuaries - user-friendly platform (GUI), allows for linking other models - DELWAQ process library and routines available		Proprietary
Buzzelli Everglades N.P. model	Focuses on TP effect on periphyton	Shark Slough, Everglades NP, FL, USA	Applied along with flume experiments to establish P criteria for freshwater in the Everglades (Childers et al. 1999)	- accounts for P recycling (feedback from "periphyton P") - captured correct magnitude of max biomass	- timing of peak biomass was not well simulated - sensitivity to TP half-saturation constant - "Everglades periphyton simulations will not be overly realistic if they follow simple Michaelis-Menten uptake kinetics, over-aggregate state variables of the periphyton complex, and fail to account for changes in the community composition and pH under P enrichment."	Buzzelli et al. (2000)
Transient storage zone (TSZ) model	2 zones: free-flowing water and transient storage zone in the water column Focus on nitrogen cycling	Walker Branch, Oak Ridge Reservation, Tennessee, USA		- successfully simulates nutrient assimilation into biomass via adjusted Monod expression and a self-limiting carrying capacity term - nutrient movement is bidirectional between zones (except labile organic N cannot leave sediments)	- assumes constant transient storage zone and periphyton are only found here - assumes steady state conditions and each zone is well mixed - no available TSZ nutrient measurements for validation - poorly defined sediment-water nutrient exchange - not spatially explicit	DeAngelis et al. (1995)

Model	Notes	Research Application Examples	Management Application Examples	Model Benefits	Model Limitations	References and Access (free/proprietary)
Surface-subsurface exchange model (extended TSZ model)	- based on TSZ model - effects of nutrient transformations in sediments on water column and periphyton - 3 zones: free-flowing water, surface storage zone, subsurface zone	Sycamore Creek, Arizona, USA (N-limited desert river)		- tested at steady state and flood conditions - demonstrates importance of subsurface nutrient recycling (in this case) - identifies importance of measuring labile organic N	- many different nutrient pools (fairly complex nutrient kinetics) - TSZ-free water exchange rates may vary a lot - all parameters were kept constant during post-flood recovery but would vary in reality - hydrologic connection btw. Hyporheic zone and algal mat (nutrients move from sediments into TSZ without uptake by periphyton, likely unrealistic)	Dent and Henry (1999)
Periphyton model added to ProSe, based on RIVE model (Billen et al. 1994)	Hydro-biological river model: RIVE model for C, nutrients and O is coupled with hydrodynamics and a periphyton module	Grand Morin (5 th order river in France)		Focus on biogeochemical cycling, includes 3 water column chl <i>a</i> groups (diatoms, chlorophyceae, detached benthic algae)	- no stored nutrient effects considered - calibration coefficients - model complexity with two bacterial groups and periphyton and P, N, and O cycling	Flipo et al. (2004), Even et al. (1998)
Vertical stream periphyton biomass accumulation model	- filamentous and non-filamentous algae - focus on mat thickness and structure as f(flow)	Calibrated using results from experiments with <i>Achnanthes minutissima</i> , <i>Synedra</i> spp., <i>Spirogyra</i>		- vertically distributed/resolved - filamentous and non-filamentous algae simulated - successfully simulated algal succession and detachment - self-shading, mat depth, Droop kinetics included - drag force, buoyancy of mat considered	- too detailed to model a whole river reach, small scale only - many assumptions and coefficients (e.g., light attenuation through different types of mats) - constant nutrient supply - neglects grazing and respiration - neglects temperature mediation - neglects velocity effect on nutrient uptake, growth, and respiration rates	Asaeda and Son (2000)

Table A-2: Select mechanistic river periphyton model details in addition to those presented in Table 2-1, grouped into simple models (red), models driven by prescribed environmental conditions (yellow), models featuring some spatial resolution and nutrient cycling (green), complex models (blue), and case-specific models (no colour).

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Logistic growth model and variations	various	Biomass as chl <i>a</i> , C, DM, AFDM	- initial biomass	- growth, carrying capacity, detachment	- max growth rate - biomass carrying capacity	
McIntire/Uehlinger river model	FORTRAN 1973 McIntire model written in MIMIC (digital computer simulation language, Control Data Corporation 1970)	biomass as gAFDM m ⁻² , mg chl <i>a</i> m ⁻²	- mean daily temperature - daily light intensity - minimal biomass - nutrient concentrations	- light and temperature mediated growth - biomass carrying capacity - grazing sometimes included - chronic, catastrophic, and autotrophic (temp. and bacteria driven) detachment - algal succession - Droop kinetics - velocity dependent nutrient delivery	- variable parameterisation for diff. algal assemblages - 11 empirical parameters: max growth rate, biomass half saturation constant, light half sat. const., coefficient of temp. dependence, empirical chronic, catastrophic, and autogenic detachment coefficients - 3 bacteria submodel coefficients	3 h time step
Horner model		biomass as mg chl <i>a</i> m ⁻²	- velocity at algal cell surface	- first order growth - scour - P limitation via Michaelis-Menten kinetics - light limitation according to Steele (1962) - turbulent and laminar flow effects	- max biomass - mass transfer coefficient with turbulent diffusion - mass transfer coefficient in laminar flow - light factor - 3 model fitting parameters	

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Hornberger and Spear model		- <i>Cladophora</i> biomass as g P	- light, temperature, evaporation - flows, river phytoplankton and P concentration (dissolved and particulate), tidal exchange - groundwater flow and P concentration	- linear light- and temperature-mediated growth - Michaelis-Menten P limitation - biomass limitation (carrying capacity with max biomass constant) - combined loss rate to capture losses due to death, respiration, grazing, and sloughing - periphyton model linked to phytoplankton and sediment-water exchange P model	- max growth rate - half-saturation constant for P limitation - max biomass carrying capacity - loss rate - “nutrient source parameter”	daily
Parsimonious River Model, <i>Cladophora</i> River Model		- periphyton biomass as DM mg m ⁻² - available P (mg L ⁻¹) - available N (mg L ⁻¹) - organic matter as C (mg L ⁻¹)	- light, temperature, nutrient loading - river depth and velocity	- zero order periphyton growth, Arrhenius temperature dependence, Michaelis-Menten light and nutrient limitation - periphyton respiration and excretion - periphyton death or sloughing - hydrolysis and decomposition	- max growth rate - fixed stoichiometry for all organic fractions (C:N:P:A of 40:7.2:1:1) - light extinction coefficient - half-saturation constants - reaeration rate - respiration, death rates - max biomass carrying capacity	
Tukituki River Model (TRIM), Stream Algorithm (SAL)	- Visual Basic for Applications in MS Excel - 2-step Huan method (Chapra and Canale 2006)	Periphyton biomass (gC m ⁻²), AMM, DIN, DON, PON, CN from biomass and fixed C/N ratio, DRP, DOP, PP, CP from biomass and fixed C/P ratio, SS, TN, TP	- nutrients, modelled light and temperature - biomass - daily river flows - AMM inflows only from point source discharges	- hydraulics - photosynthesis - respiration - mortality and scour - Monod kinetics for nutrient uptake and limitation - TP adsorption/desorption to bed sediments (TRIM2) - settling of scoured biomass - recycling by respiration and hydrolysis	- 35, greater than the number of independent variables (8) so overdetermined - 22 parameters based on measurements - 13 parameters determined by calibration TRIM2: 25 re-calibrated coefficients, 11 of which strongly influence model predictions but no experimental data or lit values are available	daily averages for each river segment based on sub-daily time step (depends on river velocity and segment length)

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
ISOFLOC (Isotope-based Fluvial Organic Carbon) Model		Carbon: dissolved inorganic (DIC), dissolved organic (DOC), algal particulate organic (APOC), fine particulate organic (FPOC, in silt and clay sized particles)	C concentrations in sediments, DOC, DIC, bathymetry	- hydrology-hydraulics - sediment transport - organic carbon cycling	- inflow DOC, DIC, POC, PIC - carrying capacity parameters - critical shear stress for algal detachment - endogenous mineralization calibration coefficient for algal C and N recycling - TP and N limitations - algal growth and decomposition parameters	Reach scale
TRANSFER (Technology for Removable Annual Nitrogen in Streams For Ecosystem Restoration) 2015	Fortran, Intel Fortran Composer For in Visual Studio	DIN, algal and sediment N species	C from ISOFLOC	- N cycling (NH ₄ and NO ₃ assimilation, denitrification, nitrification, N uptake, N release) - temperature-dependent bacteria degradation	- critical shear stress for algal detachment - endogenous mineralization calibration coefficient for algal C and N recycling	
AQUATOX	- free download of the program - open-source code available online, must be compiled with Delphi 2007 Professional (purchase)	- total nitrogen (TN), total phosphorus (TP), dissolved oxygen (DO) in Joyner and Rohli (2013) - % cyano biomass of sestonic algae, benthic chl <i>a</i> in Carleton et al. (2009)	- site characteristics - nutrient loadings - light, water temp., wind, pH, water volume (or can be state variables)	- chemodynamics of neutral and ionized organic chemicals - bioaccumulation as a function of sorption and biokinetics - biotransformation of daughter products - sublethal and lethal toxicity	- transformation rates	Daily
QUAL2K, AT2K Others: CE-QUAL-ICM and CE-QUAL-W2	- Fortran90 - User interface via Microsoft Excel - Interface operations coded using Visual Basic for Applications	Dry mass, chlorophyll, Carbon (gC m ⁻²), DO, BOD, TN, fecal coliforms, CBOD _u , NH ₄ -N, temperature, pH, SOD, NO ₂ -N, NO ₃ -N, organic and inorganic P	Nutrients, light and temperature, wind speed, hydraulic characteristics of the river (reach length, mean slope, dispersion coefficient, velocity, reaeration constant), loading data	- respiration - mortality - Droop kinetics for nutrient limitation	- C, N, P, DM, chl <i>a</i> , ISS settling velocity - aeration model - CBOD hydrolysis and oxidation rates - N and P transformation rates - kinetic rate parameters (growth, respiration, death rates; half saturation constants) - bottom plant rates and constants, fecal coliform decay and settling rates, COD decay and settling rates	

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Water Quality Analysis Simulation Program (WASP)	Standalone software	biomass as gDM m ⁻²	<ul style="list-style-type: none"> - nutrient concentrations - light - temperature - initial biomass 	<ul style="list-style-type: none"> - based on bottom algae algorithms from QUAL2K - Droop kinetics for nutrient limitation, assuming fixed internal stoichiometry - respiration, mortality 		
River Water Quality Model (RWQM, RWQM1)	MS Excel	<ul style="list-style-type: none"> - up to 24 (11 in simple version) - Ca²⁺ - heterotrophic organisms growing aerobically and anoxically - organisms oxidising ammonia to nitrite - organisms oxidising nitrite to nitrate - algae and macrophytes - consumers 	<ul style="list-style-type: none"> - physical parameters - light, temperature, nutrient loading 	<ul style="list-style-type: none"> - aerobic growth of heterotrophs - anoxic growth of heterotrophs - aerobic endogenous respiration - anoxic endogenous respiration of heterotrophic organisms - growth of 1st stage nitrifiers - growth of 2nd stage nitrifiers - growth of algae - death of algae or consumers - growth of consumers by grazing on algae - hydrolysis - adsorption of phosphate - desorption of phosphate 	<ul style="list-style-type: none"> many (see Reichert et al. 2001) - 13 stoichiometric coefficients - 36 kinetic parameters - 6 equilibrium parameters - 36 mass fractions - more when benthic sediment is included 	variable (can be minutes)

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Deltares modelling suite with 1) hydrodynamic model Delft3D Flexible Mesh (Delft3D FM, succeeds Delft3D 4, SOBEK 2) 2) water quality model framework: DELWAQ (Delft Water Quality)	Standalone software, GUI, can add subroutines in Python or other languages	User defined	varies with selected simulated processes	User defined - hydrodynamics - sediment transport - sediment-water exchange - morphology - water quality and ecological processes within DELWAQ - integrated phytoplankton model for different groups (BLOOM)	varies with selected simulated processes	User defined
Buzzelli Shark Slough, Everglades N.P.		- channel water volume - periphyton P and organic C (compared with measured AFDM) - total P	- temperature - light intensity (modelled mean) - depth - TP loading	- Arrhenius temperature mediation - Michaelis-Menten kinetics for TP and light - logistic density function	- max growth rate - basal respiration rate - fractional respiration - basal mortality rate - max biomass carrying capacity - half sat. constants for TP and light - periphyton mat thickness - periphyton coverage - fraction of recycled periphyton P - assumed atmospheric P source	Daily (with 45 min time step)

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Transient storage zone (TSZ) model		<ul style="list-style-type: none"> - N in living periphyton biomass - N in detritus - N in free-flowing water - N in TSZ 	<ul style="list-style-type: none"> - river flow/discharge - mean subsurface velocity - exchange area - surface water depth - hyporheic sediment depth - pore space - N concentration upstream 	<ul style="list-style-type: none"> - first order mass transfer between 3 zones - uptake based on Monod kinetics 	<ul style="list-style-type: none"> - 2 transfer coefficients: free-flowing water ↔ TSZ, biomass ↔ detritus - rate coefficients: nutrient loss as export/drift away - self-limitation factor in uptake equation 	
Surface-subsurface exchange model (extended TSZ model)		<ul style="list-style-type: none"> - N in living periphyton biomass - inorganic N in detritus - inorganic N in free-flowing water - inorganic N in detritus - organic N in free-flowing water - organic N in TSZ - organic N in TSZ 	<ul style="list-style-type: none"> - hydraulics - inorganic N concentration upstream - organic N concentration upstream 	<ul style="list-style-type: none"> - "stiff system" with high rates of change oth other components - stiff algorithm 	<ul style="list-style-type: none"> - 7 nutrient cycling coefficients 	
Periphyton model added to ProSe, based on RIVE model (Billen et al. 1994)		<ul style="list-style-type: none"> - carbon - biomass as gAFDM m⁻², mg chl a m⁻² 	<ul style="list-style-type: none"> - upstream nutrient loads - light 	<ul style="list-style-type: none"> - light-mediated growth (Beer-Lambert Law, Platt 1980 P/I formulation) - nitrifying bacteria growth in periphyton mat, limited by biomass, oxygen, nutrients (Michaelis-Menten kinetics) - heterotrophic bacteria growth in periphyton mat, limited by organic substrate and oxygen (Michaelis-Menten kinetics) - scour as function of critical slope (depends on critical flow threshold and duration of flood event) 	<ul style="list-style-type: none"> - max growth rates for periphyton and bacteria - photosynthesis/irradiance curve parameters - half-saturation constants for oxygen, bacterial biomass, NH₄, organic substrate - critical coefficients for scouring mechanism 	

Model	Programming environment	State/Output Variables	Key input forcing conditions	Key modelled mechanisms	Key calibration parameters	Temporal/spatial scale
Vertical stream periphyton biomass accumulation model	FORTRAN90, fourth order Runge-Kutta method	filament length, cell density (cells mm ⁻²)	- light - water velocity	- periphyton growth: light and nutrient-limited - internal and external N and P concentrations - self-shading within the mat - mortality - detachment (regular and catastrophic, buoyancy vs drag force, light and community compactness influence tensile strength as by Liebig's Law of the Minimum)	For filamentous and non-filamentous species (each): - light attenuation through the periphyton mat - light half-saturation coefficient - mortality rate - temperature constant - cell biovolume from cell shape and size - reproduction rate (cell divisions per day) - threshold filament strength - surface area of filamentous cells - half-saturation coefficient for max detachment rate	30 day simulations

Appendix B Mechanistic periphyton model development steps

The following steps are recommended to develop a mechanistic river periphyton model such as the parsimonious river model (Chapra et al. 2014) to be used to set nutrient criteria:

- 1) Define **target question(s)** to be answered, characteristics of the specific **river reach(es) of interest**, and associated **assumptions**.
 - The target question may be: What in-river nutrient loads and/or in-river concentrations will allow us to meet target periphyton biomass (chlorophyll *a*) levels in a river reach?
 - To which river reach or system will the model be applied?
 - What are the external (catchment source) and internal (sediment source) loads to the system? Load is defined as mass per time and the product of nutrient concentration (mass per volume) and flow (volume per time). The main assumption would be that nutrients are the management variable.
- 2) Define the required **model resolution**, which often depends on available input and calibration/confirmation data and computational demands.
 - Is the model spatially resolved? If so, over how many dimensions? How is the river reach network resolved? What is the required geographic scale or spatial extent over which the model can be applied?
 - Similarly, what is the required time scale over which the model should be run, including spin-up time (e.g., a year, month, week, day)?
 - What is the required ecosystem process resolution (e.g., total periphyton /periphyton group/periphyton species processes, total grazer/groups of grazer processes, inclusion/exclusion of higher trophic levels, level of detail in nutrient cycling)?
 - What is the required spatial resolution (e.g., 10 km, 1 km, 1 m, 1 mm)?
 - What is the required temporal resolution (e.g., annual, monthly, weekly, daily, hourly)?
- 3) Define the required **model structure**. What are the required state variables (e.g., periphyton biomass, stored nutrient concentrations, in-river nutrient concentrations) and mass balance equations? What are the modelled processes as part of each differential equation describing the rate of change of a state variable? This requires testing various levels of model complexity (number of simulated state variables and processes). In addition, data assimilation methods show promise for improving mechanistic model prediction; they are means to include empirical data or prior model output at each time step (e.g., Shao et al. 2016).
- 4) Choose a **numerical method** to solve the mass balance(s) (e.g., Euler method or higher order Runge-Kutta) and a suitable **computational platform/software** package (e.g., FORTRAN, MATLAB, VBA Excel, R, DeltaShell).

- 5) Define the **data requirements** to run the model. What are the required model inputs, i.e., the environmental forcing conditions (solar irradiance, temperature, etc.) and user-defined initial conditions and model parameters (e.g., starting biomass and maximum specific growth rate)?
- 6) Design and conduct high resolution, long-term **field monitoring** to define site-specific model parameters (especially rate constants) and establish calibration and confirmation data sets. The data should be in the form of the model output (state variables).
- 7) **Calibrate** the model. Run the model and compare model output with observational data. In comparison to measurements, does the model successfully predict the direction and magnitude of periphyton biomass over time? Maximise the goodness of fit using statistical approaches (e.g., minimise the RMSE) to define model parameters (e.g., an acceptable range of values for the maximum specific growth rate).
- 8) **Confirm** the model. Use another dataset similar to but different than that used to calibrate the model (e.g., obtained at a different location in the modelled system and/or at a different time). Run the model for these new conditions without changing model parameters. Compare model output with this second set of observational data. In comparison to this set of measurements, does the model still successfully predict the direction and magnitude of periphyton biomass over time? Repeat the confirmation processes across sites of interest.
- 9) Determine model **sensitivity** and **uncertainty**. Consider the uncertainty in observational data due to field collecting and laboratory analysis methods.