

Macroalgae model notes

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This is version 0.1[*DRAFT*] of the document

1 Background

1.1 Scope and design philosophy

The model is required by the funder to predict the potential yield of macroalgae from European waters on a 1x1km grid. The funder wishes for the assessment of 3 different species of macroalage and requires (external to this model) to ensure that the downstream effects of nutrient utilisation are accounted for in terms of productivity of downstream seaweed farms.

This model is designed to run independently from any geospatial dynamics or interactions which will be handled at the next level up in the software stack being built to meet the requirements of the project.

The model is designed to be flexible enough to be run as a single macroalgal farm ‘sub-unit’ e.g. 1x1m horizontal extent in a nested multi-scale model of a farm in order to investigate within-farm nutrient and productivity dynamics as may be required. However it is envisaged that the model will be run once for each 1x1 km grid square, with a simple farm density scaling parameter to represent the reality that seaweed farms cannot occupy the entirety of a 1x1km grid square, but may be more productive spread out over an area rather than intensively farmed in one compact unit. Beyond this, as the funder wishes for ‘potential’ yield the model will not consider practical aspects of limits to seaweed production (distance from coast, maximum possible harvesting frequency, line density, conflicts with other uses of the sea etc.) as these are out of scope. Similarly the effect of grazing, bacterial or viral pressure on macroalgal productivity or the potential impacts of storms or harmful algal blooms are not considered with the scope of this model (although some of these may be identified as risk factors for aquaculture activities within the geospatial framework that this model will operate).

The model is driven by nutrient inputs, light and temperature and is sufficiently simple that it is possible to represent the behaviour of any species of macroalgae by parameter modification without changing the model code. It is derived from a recent simple multi-species model of macroalgal growth by Hadley et al. (2015).

2 Model description

2.1 Model equations

The model presented here is based on the model of Hadley et al. (2015), which follows (Adridge2009?) and further (Solidoro1997?). The model currency is nitrogen, with 2 inorganic forms, ammonium (NH_4) and nitrate (NO_3) in water. Algae are able to take up these into a store (N_s) for conversion into fixed nitrogen (N_f), i.e. biomass nitrogen. These 4 nitrogen pools (all with units of mg N m^{-3}), plus Detritus, D in g dw m^{-3} are the state variables of the model. An additional technical state variable, Yield, tracks the quantity of macroalgal material harvested (detailed in Section 2.2.3)

2.1.1 Farm dimensions and nutrient supply

A farm (Fig. 1) is described by its horizontal and vertical dimensions. Horizontal dimensions are aligned to a notional flow direction, where x_{farm} and y_{farm} are the sizes of the farm in the flow direction and perpendicular to the flow direction, respectively. For the current application these would typically be fixed at the size of the grid box (1000m). A farm density term, ρ_{farm} , defines the proportion of the total farm area where seaweed is growing (to account for spacing between lines or cages, plus space for access or the transit of other marine craft through the farm area). Typically this value should be no greater than 40% (vanderMolen?). In order to maximise nutrient availability, macroalgal lines are assumed to extend to the full width of the farm perpendicular to flow (y_{farm}) with notional spacing between lines in the x direction allowing for a density < 1 .

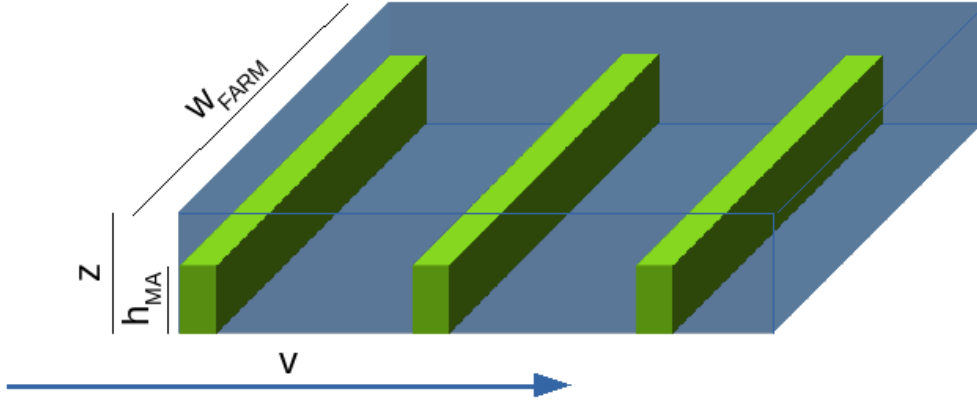


Figure 1: Schematic of macroalgal farm

The cultivation depth, z_{farm} is defined as the distance from the water surface to the base of the seaweed. The volume of macroalgae within the the farm is given by:

$$V_{MA} = y_{\text{farm}} \cdot x_{\text{farm}} \cdot \rho_{\text{farm}} \cdot h_{MA} \quad (1)$$

Where h_{MA} is the height of the macroalgae (a fixed, species specific parameter).

The water within the farm volume, extending to the water surface, is considered to be well mixed in all cases. However, the flow of water through the farm horizontally by advection and via vertical mixing introduces new water (and therefore nutrients), affecting both the available concentration of nutrient to drive macroalgal growth and the resulting effect of such growth on the water concentration. Given input terms of horizontal advective flow, v , and vertical mixing, t_z (both in length units), an effective volume of influence, V_{eff} can be defined as:

$$V_{EFF} = y_{\text{farm}} \cdot (x_{\text{farm}} + v) \cdot (z_{\text{farm}} + t_z) \quad (2)$$

The ratio $\frac{V_{MA}}{V_{EFF}}$ is used to scale the nutrient uptake within the farm to the net effect on concentration within the effective volume of water. Furthermore, as nutrient flow will tend to restore nutrient concentration back to the ambient concentration, the inverse term ($\frac{V_{EFF}}{V_{MA}}$) can be used to determine the nutrient concentration restoration rate to the farm volume, with a maximum value of 1 (per timestep).

Ammonium and nitrate concentration in the model are a function of the restoration of nutrients to ambient concentration by the input of new water, their biomass-specific uptake by seaweed ($f(NX_x, Q) \cdot B$); remineralisation of detrital material, $r_L \cdot D$; nitrification of NH_4 to NO_3 ($r_N \cdot NH_4$); and a mortality term, $d_M \cdot N_f$, that returns stored nitrogen to the ammonium pool.

$$\frac{dNH_4}{dt} = \min(1, \frac{V_{EFF}}{V_{MA}}) \cdot (NH_{4_ext} - NH_4) + (r_L \cdot D + d_M \cdot N_f - f(NH_4, Q) \cdot B - r_N \cdot NH_4) \cdot \frac{V_{MA}}{V_{EFF}} \quad (3)$$

$$\frac{dNO_3}{dt} = \min(1, \frac{V_{EFF}}{V_{MA}}) \cdot (NO_{3_ext} - NO_3) + (r_N \cdot NH_4 - f(NO_3, Q) \cdot B) \cdot \frac{V_{MA}}{V_{EFF}} \quad (4)$$

The pool of internal nitrogen stored by the macroalgae, N_s is controlled by the uptake of NH_4 and NO_3 into the store, the light, temperature and nutrient dependent growth rate (i.e. the uptake from stored inorganic N to fixed biomass N (N_f)) and the mortality term.

$$\frac{dN_s}{dt} = (f(NH_4, Q) + f(NO_3, Q)) \cdot B - \min(\mu \cdot g(E, Q, T) \cdot N_s, PO_{4V_{EFF}} \cdot N : P_{MA}) - d_M \cdot N_f \quad (5)$$

Here, the term $\mu \cdot g(E, Q, T) \cdot N_s$ represents the nitrogen, temperature and light dependent conversion of stored nitrogen to fixed nitrogen (i.e. biomass growth). When the total available phosphate within the effective volume of influence ($PO_{4V_{EFF}}$) is less than the phosphate requirements to support the calculated conversion of N_s to N_f , growth is limited to this phosphate availability.

Fixed (biomass) nitrogen, N_f is then:

$$\frac{dN_f}{dt} = \min(\mu \cdot g(E, Q, T) \cdot N_s, PO_4 \cdot N : P_{MA}) - d_M \cdot N_f \quad (6)$$

Finally, the detrital pool is determined from the inflow of detrital material, the loss of N_f due to mortality and the remineralisation of detritus to NH_4 .

$$\frac{dD}{dt} = \min(1, \frac{V_{EFF}}{V_{MA}}) \cdot (D_{ext} - D) + (d_M \cdot N_f - r_L \cdot D) \cdot \frac{V_{MA}}{V_{EFF}} \quad (7)$$

2.1.2 Growth dynamics

Uptake from inorganic nutrients into the fixed nitrogen pool, N_f is controlled by standard Monod / Michaelis Menten kinetics, whereby the uptake is dependent on the maximum specific uptake rate V_{NX_x} per unit biomass, the concentration of NH_4/NO_3 and the half-saturation constant for the species of interest (K_{NX_x}), scaled between minimum and maximum value by the internal nutrient quota, Q :

$$f_{NX_x} = \frac{V_{NX_x} \cdot NX_x}{K_{NX_x} + NX_x} \cdot \frac{Q_{\max} - Q}{Q_{\max} - Q_{\min}} \quad (8)$$

Nitrogen is fixed from the internal nutrient pool to the fixed nitrogen pool through a specific maximum growth rate, μ , scaled by temperature, light and internal nutrient availability.

$$\mu \cdot g(E, Q, T) = \mu \cdot g_E \cdot g_Q \cdot g_T \quad (9)$$

where g_Q scales the maximum growth rate according to the internal nutrient reserves:

$$g_Q = \frac{Q - Q_{\min}}{Q - K_c} \quad (10)$$

The temperature scaling term used by Hadley et al. (2015) only inhibits growth at temperatures below the optimum temperature, T_o . However, it is well known that macroalgal species growth rate declines also at temperatures above their optimum. Therefore we adapt the scheme of (Martin2002?) which has a ‘bell curve’ temperature dependence.

$$g_T = e^{-2.3 \left(\frac{T - T_o}{T - T_x} \right)^2} \quad (11)$$

Where $T_x = T_{max}$ for $T > T_o$ and $T_x = T_{min}$ for $T < T_o$.

The light-dependent scaling as described by Hadley et al. (2015) could not be successfully implemented here, possibly due to a reporting error in their paper (see appendix).

The daily maximum angle of incident light is calculated as a function of latitude (L) and ordinal day of the year (d_{ord}):

$$\theta = 90 - L - 23.45 \cos\left(\frac{360}{365} \cdot (d_{ord} + 10)\right) \quad (12)$$

The light intensity at the top of the macroalgae is then calculated as:

$$I_{top} = I_{surf} \cdot e^{(-K_d \cdot \frac{z_{farm} - h_{MA}}{\sin(\theta)})} \quad (13)$$

and the mean irradiance throughout the height of the macroalgae, accounting for self-shading is then calculated as:

$$I_{avg} = \frac{I_{top}}{\frac{K_d \cdot h_{MA}}{\sin(\theta)} + \frac{N_f \cdot a_{cs}}{(\sin(\theta))}} \cdot (1 - e^{-(\frac{K_d \cdot h_{MA}}{\sin(\theta)} + \frac{N_f \cdot a_{cs}}{(\sin(\theta))})}) \quad (14)$$

The growth scaling function g_E is then

$$g_E = \frac{I_{avg}}{I_{sat} + I_{avg}} \quad (15)$$

where I_{sat} is the species specific saturation irradiance value of the macroalgae.

2.2 model structure and ins/outs

The model is implemented as a series of differential equations, solved in R using the `deSolve` package (`deSolve?`) in file `macroalgae_model.R` (see Section 2.1). The same file also contains functions for creating time-varying forcing functions from input data (Section 2.2.2); and functions for managing harvesting of the macroalgae under various management options 2.2.3.

For testing or other individual runs, the model can be initialised and run using the `run_MA.R` script in the same directory as the model code. When operationalised within the wider modelling environment it will be initialised and run from a pything script which will pass boundary forcings, parameter values and run control settings directly to the model and retrieve outputs.

2.2.1 Parameter values

2.2.1.1 Species-specific macroalgal parameters Species-specific algal parameters are listed in Table 1.

```
##
## Attaching package: 'bvpSolve'

## The following object is masked from 'package:stats':
##
##   approx

## Loading required package: shape

## -- Attaching packages ----- tidyverse 1.3.1 --

## v ggplot2 3.3.5      v purrr  0.3.4
## v tibble  3.1.6      v dplyr  1.0.8
## v tidyr   1.2.0      v stringr 1.4.0
## v readr   2.1.2      v forcats 0.5.1

## -- Conflicts ----- tidyverse_conflicts() --
## x dplyr::filter() masks stats::filter()
## x dplyr::lag()    masks stats::lag()
```

2.2.2 Environmental forcings

2.2.2.1 PAR

2.2.3 Harvesting functions and yield calculation

2.2.4 Model ins and outs

2.2.5 Run control parameters

2.3 Characterising model behaviour

Model behaviour is characterised by considering 4 regime types which challenge the model to work at the extreme cases of nutrient concentration and availability: 1) low nutrient, low flow; 2) high nutrient, low flow; 3) low nutrient, high flow and 4) high nutrient high flow. The model is run with default parameter set for ulva and all other parameters set to default values (Section 2.2.1). Input values are simulated sinusoidal parameters representing annual cycles for PAR, ammonium and nitrate. Phosphate is kept in excess. Fixed values of the other forcings are used. Common to all runs, PAR varies between 200 and 1000 $\mu\text{mol m}^{-2}\text{s}^{-1}$, K_d is fixed at 0.1 m^{-1} and latitude (used to calculate solar angle) is 50 degrees. The remaining forcings differ between each run and are summarised in Table 2.

Selected model outputs for each of the four reference runs are presented in Fig. 2. These demonstrate a number of important characteristics of the model (which are also characteristic of macroalgal growth in reality). Firstly it is clear from panel B (dry weight of biomass in g per metre of rope) that flow rate has a

Table 1: Species specific parameter values for macroalgae, including default values for ulva and alaria

| parameter | description | units | ulva | saccharina |
|-----------------------------------|---------------------------------------|--|---------|------------|
| μ | maximum specific growth rate | d^{-1} | 0.45 | 0.06 |
| V_{NH_4} | maximum ammonium uptake rate | $\text{mg(N) g}^{-1}(\text{dw}) \text{d}^{-1}$ | 124 | 100 |
| V_{NO_3} | maximum nitrate uptake rate | $\text{mg(N) g}^{-1}(\text{dw}) \text{d}^{-1}$ | 39 | 200 |
| K_{NH_4} | half saturation constant for ammonium | mg(N) m^{-3} | 700 | 11 |
| K_{NO_3} | half saturation constant for nitrate | mg(N) m^{-3} | 70 | 200 |
| Q_{max} | maximum internal nitrogen | $\text{mg(N) g}^{-1}(\text{dw})$ | 42 | 22 |
| Q_{min} | minimum internal nitrogen | $\text{mg(N) g}^{-1}(\text{dw})$ | 13 | 10 |
| $\text{N} : \text{P}_{\text{MA}}$ | N to P ratio of macroalgal biomass | - | 12 | 12 |
| K_c | half growth constant | $\text{mg(N) g}^{-1}(\text{dw})$ | 7 | 8 |
| T_o | optimum growth temperature | $^{\circ}\text{C}$ | 12 | 12.5 |
| T_{min} | minimum temperature for growth | $^{\circ}\text{C}$ | 1 | 0 |
| T_{max} | maximum temperature for growth | $^{\circ}\text{C}$ | 25 | 20 |
| I_{sat} | saturation irradiance | $\mu\text{mol m}^{-2} \text{s}^{-1}$ | 200 | 90 |
| a_{cs} | nitrogen-specific shading | $\text{m}^2 \text{mg(N)}^{-1}$ | 0.00033 | 0.00036 |
| d_M | mortality rate | d^{-1} | 0.0003 | 0.0003 |
| h_{MA} | height of macroalgae | m | 0.2 | 2 |
| w_{MA} | width of macroalgae e.g. on rope | m | 1 | 0.3 |
| r_L | remineralisation rate | d^{-1} | 0.1 | 0.1 |
| r_N | nitrification rate | d^{-1} | 0.1 | 0.1 |

Table 2: Forcing values for reference runs

| forcing | hnhf | lnhf | hnlf | lnlf | units |
|----------------------------|--------------|-------------|--------------|-------------|-----------------------|
| NH_4_{ext} | 60 ± 30 | 2 ± 1.8 | 60 ± 30 | 2 ± 1.8 | mg(N) m^{-3} |
| NO_3_{ext} | 150 ± 90 | 10 ± 8 | 150 ± 90 | 10 ± 8 | mg(N) m^{-3} |
| v | 1000 | 1000 | 10 | 10 | m/d |
| t_z | 10 | 10 | 5 | 5 | m |

much more significant role to play than concentration in driving total biomass production. This is due to seaweed (particularly ulva's) ability to rapidly take up nutrients into its internal store even at relatively low concentrations. Therefore, with high flow the seaweed can keep its internal store full (Q approaches Q_{\max} , panel C) while growing through the winter. In the high nutrient high flow environment this can be maintained year-round and productivity is limited only by temperature and light availability (and the intrinsic growth parameters of the seaweed species being modelled). In the low nutrient high flow scenario the macroalgae relies partially on its internal nutrient reserve in the summer and Q therefore reduces, leading to somewhat slower growth. However in the low flow environment, resupply of nutrient strongly limits uptake and growth, with low biomass yields and $Q \rightarrow Q_{\min}$. To first order, flow rate therefore will be the main determinant of yield for a given species and the importance of properly constraining nutrient uptake and assimilation parameters is key for predicting realistic yields.

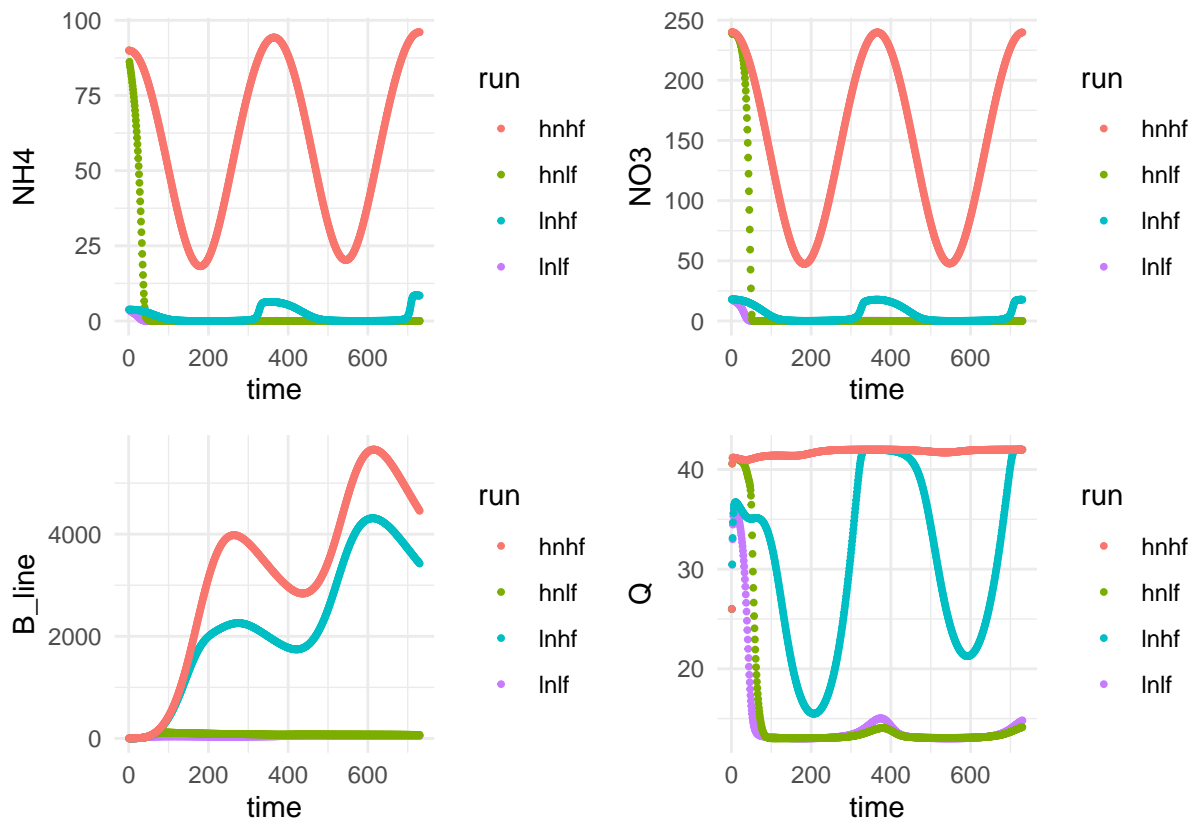


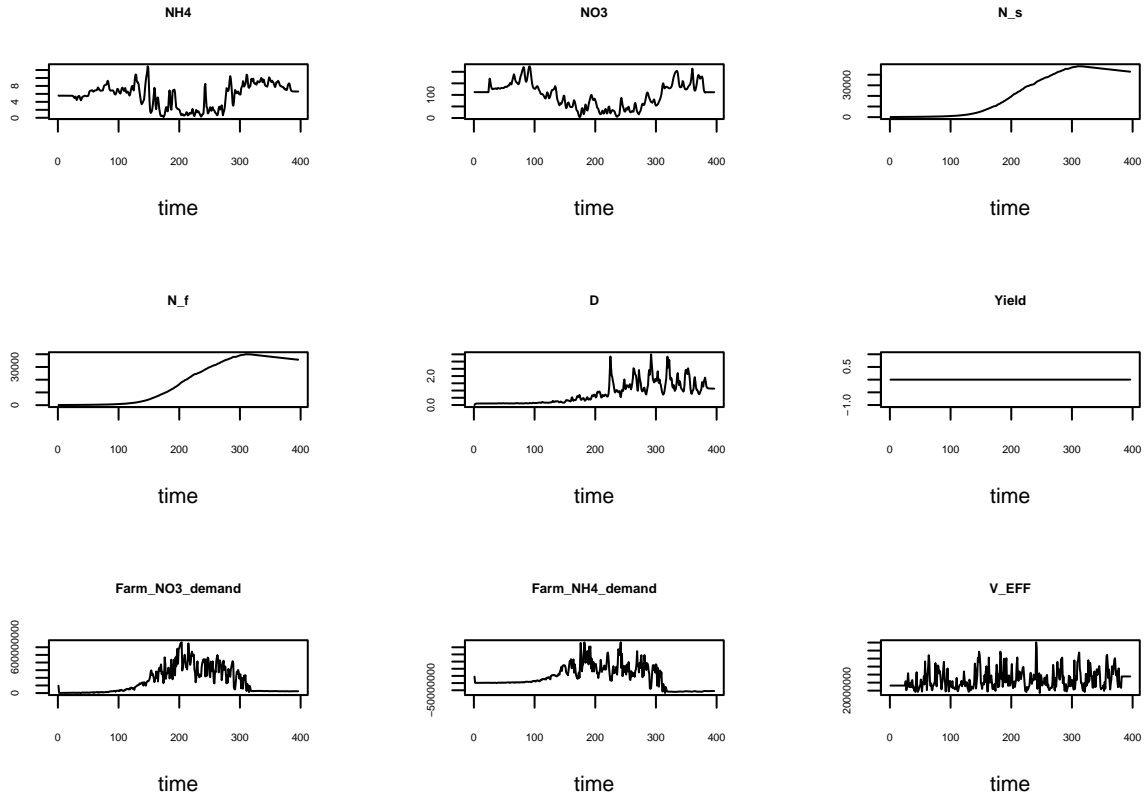
Figure 2: Reference runs of the model showing a) NH_4 concentration in farm outflow, b) nitrate concentration in farm outflow, c) biomass (dry weight) per linear metre and d) nutrient quota, Q of the macroalgal biomass

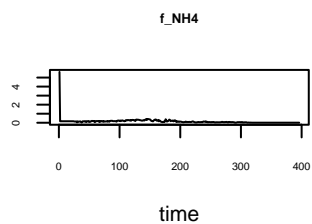
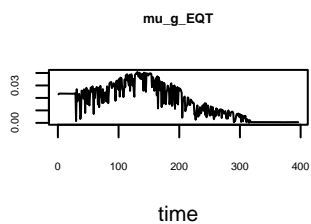
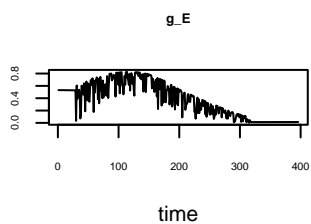
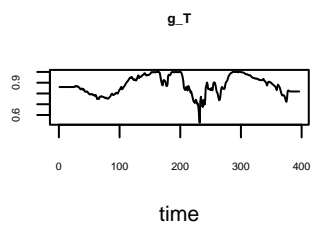
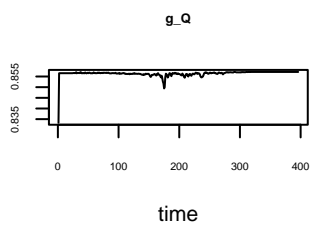
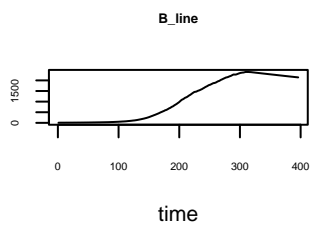
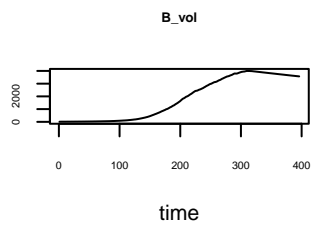
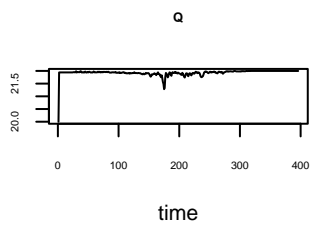
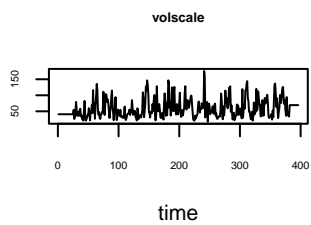
2.4 Model validation

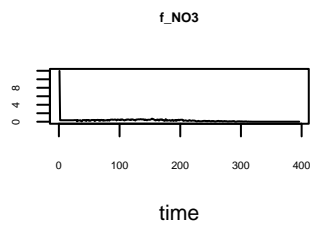
Model validation will be carried out in 2 steps. Firstly, the model will be used to reproduce seaweed yield data from sites around Euro where local environmental data (nutrients, flow, temperature) are available. These sites will capture as great a range of environmental conditions as possible. The work to find relevant datasets is ongoing. These datasets will be used to perform a validation/tuning exercise to ensure that the model is producing reasonable results when the environmental conditions are well constrained. However there are limited data available and we expect only to be able to find a handful of sites with some or all of the necessary data. Therefore in a second step, yield-only data, which is somewhat more easily available, will be used along with environmental forcings derived from CMEMS via the Argans platform will drive the model, thereby validating both the model and the environmental data from CMEMS. While we might not expect

strong quantitative agreement we would hope for order-of-magnitude level model ability and, importantly, good relative agreement between different sites. This work will be ongoing in the second half of the project (post April).

For now, a test run using CMEMS data for Bantry bay is used to demonstrate realistic model behaviour. CMEMS data for 2020-2021 is used to drive the model with a parameter set representative of *saccharina* sp. The model is driven by modelled water current speed, nutrients, temperature and satellite-retrieved PAR (where data gaps exist, substitution is performed for par data according to Section 2.2.2.1). Depth of water mixing (t_z) is set to 10m and the light attenuation coefficient is set to 0.1 (d^{-1}). Figure @ref(fig:bantry_run) presents the full output of the model.







3 References

Hadley, Scott, Karen Wild-Allen, Craig Johnson, and Catriona Macleod. 2015. “Modeling Macroalgae Growth and Nutrient Dynamics for Integrated Multi-Trophic Aquaculture.” *Journal of Applied Phycology* 27 (April): 901–16. <https://doi.org/10.1007/s10811-014-0370-y>.