Numerical Modelling Course

@Marine Benthic Ecology 2019

Modulation of global change impact by biotic interactions, bioinvasion and parasitism

Anja Eggert

Contents

Introduction

Ecosystems are complex and due to this complexity it remains difficult to grasp how they are modified by climate change, like ocean warming. We have a fairly good understanding of temperature effects on single process rates of e.g. growth, photosynthesis, grazing or mortality. Thermal performance curves became standard lab procedures to evaluate the physiological performance of species. However, temperature effects on communities remain difficult to quantify. Increased temperatures may have a negative impact on one process, but could be beneficial for another process and the net-community effect is not clear at first glance.

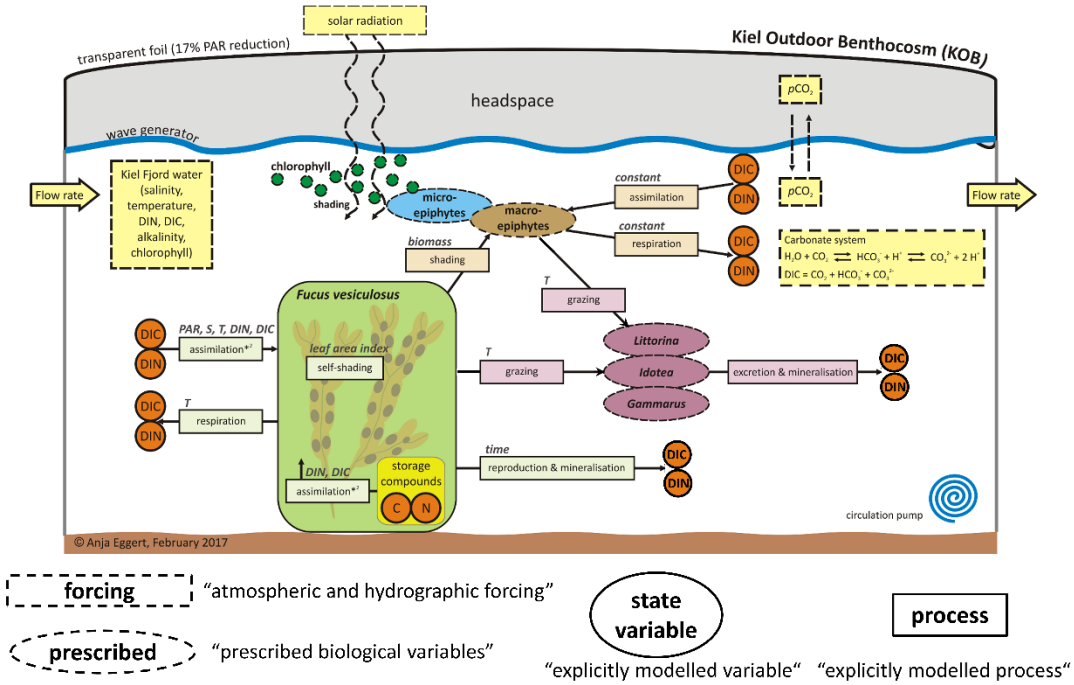
In this practical, you performed ecological experiments with key species of the benthic community in the Western Baltic Sea and you got to know the Kiel Indoor/Outdoor Benthocosms (KIBs and KOBs). Indeed, well-designed experiments in mesocosms are an excellent tool to study community effects of climate change. You can consider a numerical model as a tool to integrate experimental results (of laboratory, mesocosm and field studies) in a very systematic way. It can improve our mechanistic understanding of the impacts of climate change.

In this two-days course on numerical modelling you will learn how to develop a box model. Box models are also called 0D-models as we only consider one grid cell, i.e. neither vertical nor horizontal transport. Nevertheless, we will consider temporal changes. In this exercise we will run simulations over two months.

We will develop an ecological box model from scratch to simulate the temporal development of a benthic community in a mesocosm experiment (KOB). You will need to define the key species of the community, which act like nodes in a network. Mathematical equations must be derived to describe the connecting processes and biotic interactions, which are the arrows in the network. You will use the Code Generation Tool (CGT), developed by Hagen Radtke @IOW (https://ergom.net). The CGT comes along with an editor (CGT-EDIT) for conveniently editing textfiles of the formal description and which does not require skills in programming.

The *Fucus* box model

Within the research project BIOACID (Biological Impacts of Ocean Acidification, https://www.oceanacidification.de/), we developed the first *Fucus* box model to simulate the seasonal growth of *Fucus vesiculosus* in its benthic community (Graiff et al., subm.). This work depends to a large extend on experiments performed in the KOBs to study impacts of ocean acidification and ocean warming. The schematic of the model shows you the implemented state variables (nodes) and processes (arrows). We cannot achieve this complexity in a two-days course. However, you will learn how to develop a model like this.



Fucus vesiculosus biomass is a state variable of the model and is represented as 'carbon_in_Fucus' and 'nitrogen_in_Fucus'. Also dissolved nutrients (DIN, DIC) are modelled explicitly and the nutrient exchange in the flow-through system is considered. The implemented processes are shown in rectangles and their dependence on environmental variables is written above. *1 distinction between *Fucus* assimilation based on dissolved nutrients and growth based on storage compounds.

Model currency

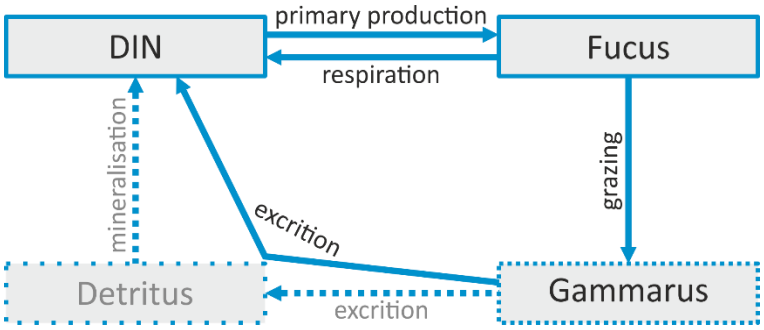
The choice of the model currency is a first and major decision you have to make. As nitrogen is a key nutrient, it is the choice in most large-scale 3D-models. We will also use nitrogen as the model currency. This requires conversion of many measured parameters, like per-capita consumption rates into mol N m^{-3} d^{-1}.

Defining your ecological model

The aim of this model exercise is to develop a numerical model based on the experiments of this practical:

State variable	Process	Factors
macroalga / *Fucus*	growth, primary production	native vs. invasive temperature
mesograzer / *Gammarus*	grazing rate (on *Fucus*), survival, feeding preference	native vs. invasive temperature
predator / *Asterias*	consumption rate (on mussel), growth, survival	salinity, temperature
filter feeder / *Mytilus*	respiration, filtration rate	Short-term temperature fluctuations

It is rather difficult to implement all state variables in a first simple numerical model. Together we will start with including only DIN and *Fucus* as state variables and we will prescribe the *Gammarus* individuals. Thus, we explicitly model dissolved nitrogen (ammonium, nitrate) concentration in the water and *Fucus* growth as nitrogen increase (due to primary production). We let *Fucus* respire, i.e. release ammonium. *Gammarus* is not explicitly modelled, but the given number of individuals grazes on *Fucus* and excretes faecal pellets. As we do neither include detritus nor mineralizing bacteria as state variables, the excreted pellets are directly transferred to DIN. All considered process rates will be temperature-dependent.



Schematic of our first simple biological model. DIN and *Fucus* are state variables, *Gammarus* abundance is prescribed.

Possible extensions:

- Implementation of two *Gammarus* species (native and invasive) with different temperature preferences
- Two *Fucus* species (*F. vesiculosus* and *F. evanescens*) with different temperature-dependence and with different grazing preferences of *Gammarus*
- Run simulations with a global warming set-up.

Possible (other) models:

- Implementation of *Mytilus* and its predator *Asterias*, i.e. mussel filters water with phytoplankton. Consumption rate of the predator is salinity-dependent.

Technical description of the KOBs

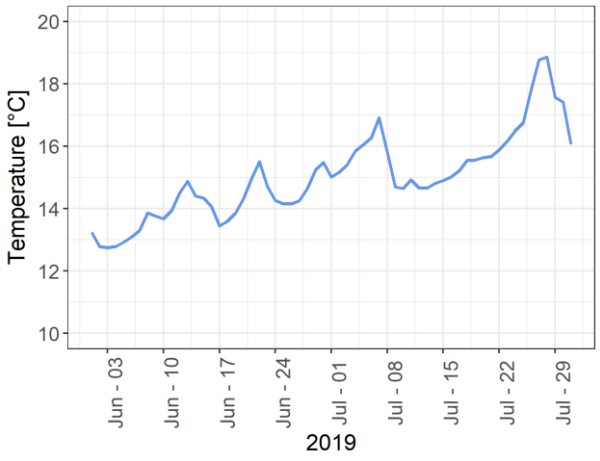
The KOB operates as a flow-through system and its inner dimension is 2 m x 2 m. The KOB runs in an open-circuit mode, i.e. flow-through of natural seawater pumped from Kiel Fjord at 1 m water depth. This needs to be considered in the model.
In this exercise we set the water volume in the tanks to 1.5 m^3 and the flow rate of the pump to 1.8 $m^3\ d^{-1}$, i.e. the water exchange rate was 1.2 d^{-1}.

Forcing factors

All so called forcing factors are prescribed and not explicitly modelled. The time step of the forcing time series (also of the biogeochemical forcing, i.e. 'time-dependent constants') can be different. In the model, start time is defined and the respective value of the variable is used until a new date is reached. I.e. values are not linearly interpolated between time steps, but values are step-wise changed.

Physical forcing:

- Ambient temperature of the Kiel Fjord surface water pumped through the KOBs. Temperatures range between 13 and 19°C in June/July.

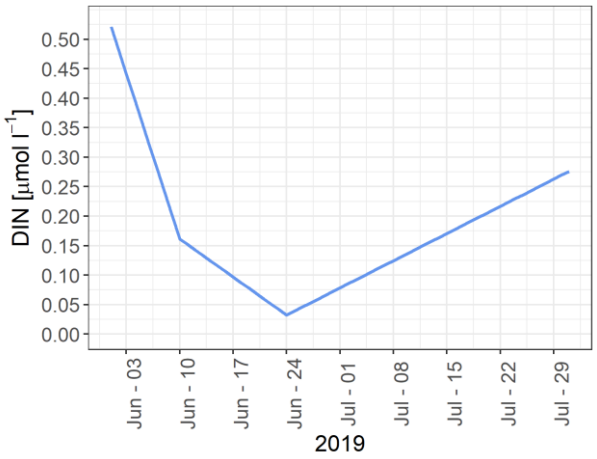


Measured temperature used to force the model.

- We only consider a very simple parametrization of *Fucus* growth, i.e. primary production. It growths during daylight (light=1), but does not in darkness (light=0).
- Effects of salinity are not considered in our model, otherwise we would need salinity data as well.

Biochemical forcing:

- DIN concentration of the Kiel Fjord water pumped through the KOBs. The maximal value is 0.52 µmol l^{-1}, which is far below the considered half-saturation constant of 7.3 µmol l^{-1}. I.e. in June/July, *Fucus* growth is always nitrogen-limited.



Measured DIN concentration in the Kiel Fjord surface water used to force the model.

Biological forcing:

- The mesograzer *Gammarus* grazes on *Fucus*, but number of individuals is prescribed. We consider 333 individuals in one KOB. If the water volume is 1.5 m^3, *Gammarus* concentration is 222 ind. m^{-3}.

Conversion factors (wet biomass, dry biomass, N-content)

As the model currency is "mol nitrogen", we need conversion factors to dry and fresh biomass for all state variables.

- molar mass of N = 14 g mol^{-1}
- mean N-content of *Fucus* = 1.8 g N 100 g^{-1} dm
- thus, mean N-content of *Fucus* = 0.129 mol N 100 g^{-1} dm

- **thus, 1 mol N *Fucus* ≈ 775 g dm *Fucus***

- typical *Fucus* water content = 80.5%
- thus, 100 g fm of *Fucus* = 19.5 g dm of *Fucus*
- thus, 1 g dm *Fucus* = 5.1 g fm *Fucus*

- **thus, 1 mol N *Fucus* ≈ 4000 g fm *Fucus***

Initial values

The model needs initial conditions of its state variables, in our case for *Fucus* biomass and DIN. The initial value of DIN is simply set to the DIN concentration in the flow-through water on day 1 of the experiment (0.0005 mol m^{-3}).

To derive the initial value for *Fucus*, we need to calculate:

- 20 *Fucus* in one KOB
- The individual plants have a fresh biomass of 60 g
- Applying the conversion factor, this is 0.015 mol nitrogen per *Fucus*
- With a water volume of 1.5 m^3, the mean "concentration" of one *Fucus* is 0.010 mol N m^{-3}
- In total, the initial value for *Fucus* is 20*0.010 mol N m-3

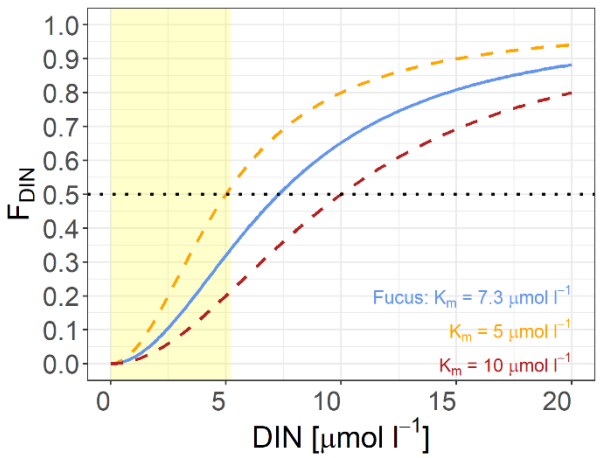
DIN assimilation of Fucus

Nutrient uptake, i.e. DIN uptake, is described with a modified Michaelis-Menten formula with squared arguments (Fennel & Neumann, 1996) which results in a sigmoid functional response:

$$F_{DIN} = \frac{DIN^2}{{K_m}^2 + DIN^2},$$

with K_m being the half-saturation constants of DIN uptake. And F_{DIN} ranges between 0 and 1.

Based on Wallentinus (1984), we choose K_m = 7.3 µmol l^{-1} = 7.3·10^{-3} mol m^{-3}. While typical winter DIN concentrations are 5 to 10 µmol/l, DIN concentrations are always low in late spring/early summer. Thus, in the experimental period, *Fucus* would be strongly DIN-limited. We therefore choose an unrealistic value K_m = 0.2 µmol l^{-1}.



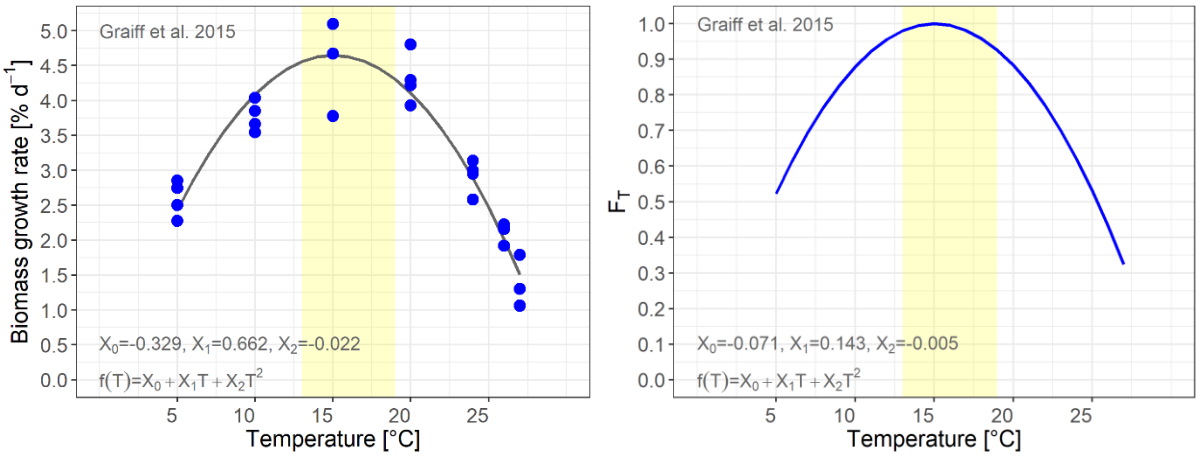
The effect of parameter choices of K_m on the factor F_{DIN}. The yellow box marks the DIN concentrations during the experiment, i.e. *Fucus* growth is DIN-limited and F_{DIN} < 0.35.

Temperature dependence of Fucus growth

Graiff et al. (2015) collected *Fucus vesiculosus* in the Kiel Fjord and measured temperature-dependence of growth (as biomass increase) in laboratory experiments. We fit a quadratic regression model to the growth-temperature-response data.

$$F_T = X_0 + X_1 T + X_2 T^2$$

To obtain F_T ranging between 0 and 1, we normalise the function to a maximum of 1.



Temperature dependence of growth rate of *Fucus* (left) and derived limiting function [0, 1] (right). The yellow box marks the temperature range during the experiment, i.e. *Fucus* growth is not temperature limited (F_T>0.9).

Fucus growth

We consider a very simple light-dependent growth of *Fucus*. It only depends on day/night cycle and the external temperature and DIN concentration.

$$\mu_{fuc} = \mu_0 \cdot \text{light} \cdot F_T \cdot F_{DIN}$$

with μ_0 = 0.047 [d^{-1}], the maximal relative growth rate of *Fucus* (Graiff et al. 2015). Light can be 0 (darkness) or 1 (daylight). F_T and F_{DIN} are the limiting functions [0, 1] as described above.

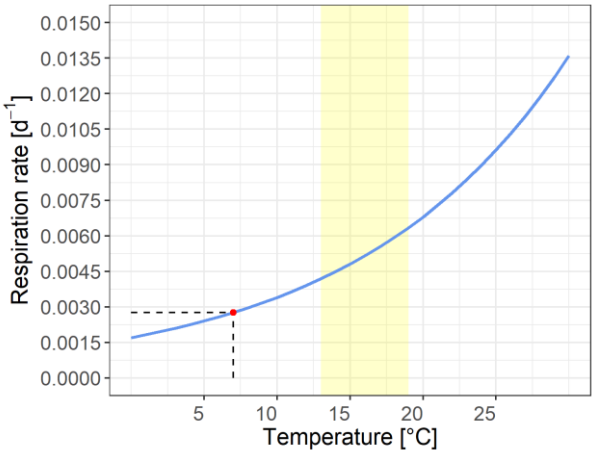
Fucus respiration

Markager & Sand-Jensen (1992) measured at 7°C dark respiration rates of *Fucus serratus* from Denmark of 0.0027 mol C mol^{-1} C cell d^{-1}. We adopt this value for *F. vesiculosus* and for nitrogen. We apply the the van't Hoff's rule to describe the temperature-dependent respiration rate of *Fucus*. We set Q_{10} = 2, i.e. rate increases by factor 2 when temperature increases by 10°C. Accordingly, respiration rate is defined as:

$$resp_{fuc} = r_0 \cdot \exp^{(q_{10} \cdot temp)}$$

with q_{10} = ln(2)/10 = 0.0693 and r_0 is the respiration rate at 0°C.

If respiration rate at 7°C is 0.0027 d^{-1}, we can derive r_0 = 0.0017 d^{-1} at 0°C.



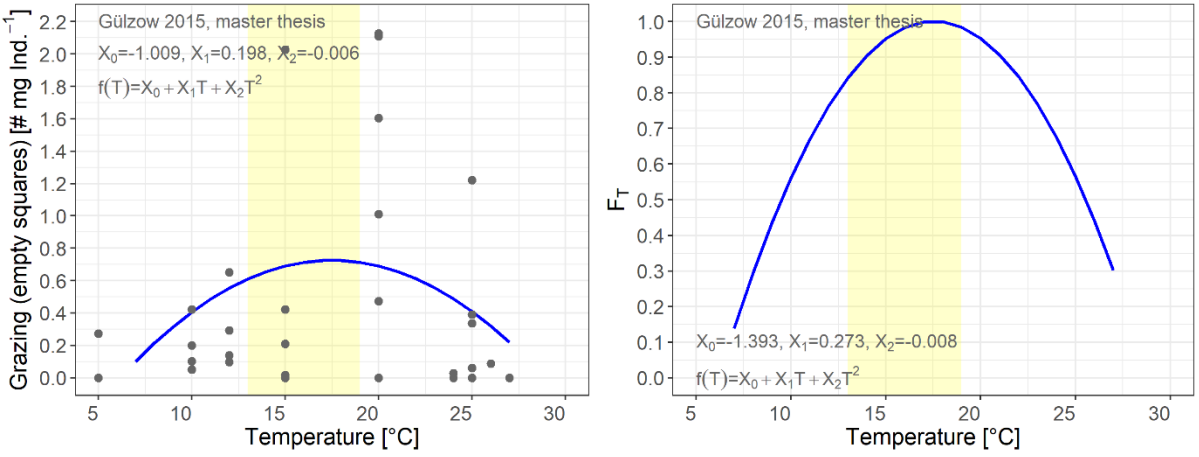
Temperature dependence of respiration rate of *Fucus*. The red dot marks the rate 0f 0.0027 d^{-1} measured at 7°C. The yellow box marks the temperature range during the experiment.

Temperature effect on grazing

We fit a quadratic regression model to the grazing-temperature-response data obtained in laboratory experiments by Elisa Gülzow (master thesis, 2015).

$$F_T = X_0 + X_1 T + X_2 T^2$$

To obtain F_T ranging between 0 and 1, we normalise the function to a maximum of 1.



Temperature dependence of consumption rate of *Gammarus* on *Fucus* (left) and derived limiting function [0, 1] (right). The yellow box marks the temperature range during the experiment, i.e. *Gammarus* consumption is not temperature limited (F_T>0.8).

Grazing rate of *Gammarus*

Göcker & Kall (2003) studied grazing rates of *Gammarus* [mg FM Ind^{-1} d^{-1}]. They determined a mean consumption rate of 0.7 mg FM Ind^{-1} d^{-1}. Using the conversion factors of *Fucus*, this is equivalent to 0.137 mg DM Ind^{-1} d^{-1} and 0.175 10^{-6} mol N Ind^{-1} d^{-1}.

$$graz_{gam} = \#Ind \cdot graz_0 \cdot F_T$$

with #Ind = number of *Gammarus* individuals per m^3, $graz_0$ = maximal grazing rate of 0.175 10^{-6} mol Ind^{-1} d^{-1} and F_T the limiting functions [0, 1].

Number of *Gammarus* individuals is prescribed with 750 Ind KOB^{-1}, i.e. 500 Ind m^{-3}. With $graz_0$ = 0.175 10^{-6} mol Ind^{-1} d^{-1}, this results in grazing rates of approx. 0.08 µmol l^{-1} d^{-1}. This is in our experiment and compared to DIN assimilation rate of *Fucus*, much too low. We therefore choose an unrealistic value of *Gammarus* maximal grazing rate of 15 mg FM Ind^{-1} d^{-1}, 3.75 10^{-6} mol N Ind^{-1} d^{-1}.

As we consider *Gammarus* as a prescribed grazer, i.e. we do not model *Gammarus* growth explicitly, the ingested *Fucus* does not cause increase in *Gammarus* biomass. Furthermore, no detritus state variable is considered, i.e. no mineralisation of detritus takes place. The ingested *Fucus* is directly transferred to dissolved nitrogen.

References

Alexandridis, N., Oschlies, A., & Wahl, M. (2012). Modeling the effects of abiotic and biotic factors on the depth distribution of *Fucus vesiculosus* in the Baltic Sea. Marine Ecology Progress Series, 463, 59–72.

Fennel, W., & Neumann, T. 1996: The mesoscale variability of nutrients and plankton as seen in a coupled model German Journal of Hydrography. 48, 49–71.

Goecker, M. E., & Kall, S. E. (2003). Grazing preferences of marine isopods and amphipods on three prominent algal species of the Baltic Sea. Journal of Sea Research, 50(4), 309–314.

Graiff, A., Karsten, U., Radtke, H., Wahl, M. & Eggert, A. Model simulation of seasonal growth of *Fucus vesiculosus* in its benthic community, submitted.

Graiff, A., Liesner, D., Karsten, U. & Bartsch, I. (2015). Temperature tolerance of western Baltic Sea Fucus vesiculosus – growth, photosynthesis and survival. Journal of Experimental Marine Biology and Ecology 471, 8–16.

Markager, S., & Sand-Jensen, K. (1992). Light Requirements and Depth Zonation of Marine Macroalgae. Mar Ecol Prog Ser, 88(1), 83–92.

Wahl, M., Buchholz, B., Winde, V., Golomb, D., Guy-Haim, T., Müller, J., Böttcher, M. E. (2015). A mesocosm concept for the simulation of near-natural shallow underwater climates: The Kiel Outdoor Benthocosms (KOB). Limnology and Oceanography: Methods, (November), n/a–n/a.

Wallentinus, I. (1984). Comparisons of nutrient uptake rates for Baltic macroalgae with different thallus morphologies. Marine Biology, 80(2), 215–225.