Estuarine, Coastal and Shelf Science 164 (2015) 253–264

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

A model for optimization of the productivity and bioremediation efficiency of marine integrated multitrophic aquaculture

Fani Lamprianidou*, Trevor Telfer, Lindsay G. Ross

Institute of Aquaculture, University of Stirling, Stirling FK9 4LA, UK

ARTICLE INFO

Article history:
Received 14 January 2015
Received in revised form
12 June 2015
Accepted 30 July 2015
Available online 4 August 2015

Keywords:
IMTA
Ulva
Paracentrotus lividus
Dynamic energy budget
Nitrogen
Modelling

ABSTRACT

Integrated multitrophic aquaculture (IMTA) has been proposed as a solution to nutrient enrichment generated by intensive fish mariculture. In order to evaluate the potential of IMTA as a nutrient bioremediation method it is essential to know the ratio of fed to extractive organisms required for the removal of a given proportion of the waste nutrients. This ratio depends on the species that compose the IMTA system, on the environmental conditions and on production practices at a target site. Due to the complexity of IMTA the development of a model is essential for designing efficient IMTA systems. In this study, a generic nutrient flux model for IMTA was developed and used to assess the potential of IMTA as a method for nutrient bioremediation. A baseline simulation consisting of three growth models for Atlantic salmon *Salmo salar*, the sea urchin *Paracentrotus lividus* and for the macroalgae *Ulva* sp. is described. The three growth models interact with each other and with their surrounding environment and they are all linked via processes that affect the release and assimilation of particulate organic nitrogen (PON) and dissolved inorganic nitrogen (DIN). The model forcing functions are environmental parameters with temporal variations that enables investigation of the understanding of interactions among IMTA components and of the effect of environmental parameters. The baseline simulation has been developed for marine species in a virtually closed system in which hydrodynamic influences on the system are not considered. The model can be used as a predictive tool for comparing the nitrogen bioremediation efficiency of IMTA systems under different environmental conditions (temperature, irradiance and ambient nutrient concentration) and production practices, for example seaweed harvesting frequency, seaweed culture depth, nitrogen content of feed and others, or of IMTA systems with varying combinations of cultured species and can be extended to open water IMTA once coupled with waste distribution models.

1. Introduction

The constantly increasing demand for seafood, during a period of overexploitation of the fisheries sector can only be met by sustainable growth of aquaculture. This growth is limited by the environmental impacts and economic requirements of intensive monoculture of fed species. Moreover, rapid and uncontrolled expansion of the aquaculture sector challenges the realization of an Ecosystem Approach to Aquaculture (Soto et al., 2008). It has been proposed that expansion of marine aquaculture in parallel with environmental protection can be achieved using Integrated Multi-Trophic Aquaculture systems (IMTA) (Chopin et al., 2001; Neori et al., 2004). IMTA has the potential to be an economically viable solution to the problems of dissolved and particulate nutrient enrichment, since the waste from fed species aquaculture is exploited as a food source by extractive organisms of lower trophic levels giving added value to the investment in feed by producing a low input protein source as well as increasing the farm income. In order to promote more resilient growth of the Scottish aquaculture industry a draft Seaweed Policy Statement that examines the cultivation of seaweed as part of IMTA systems was introduced in 2013 (Marine Scotland, 2013). Large-scale seaweed cultivation has been suggested as a means to mitigate the nutrient enrichment environmental impact of marine fish farms (Abreu et al., 2009; Wang et al., 2013). As a very large area is required for the cultivation of sufficient seaweed biomass for complete nutrient bioremediation, doubt remains as to whether complete bioremediation by seaweed cultivation is practically feasible (Broch and Slagstad, 2012). However, there is a general agreement that cultivation of seaweed as part of an IMTA is a promising way for partial removal

* Corresponding author. Tel.: +44 1786 7878.
E-mail address: fani.lamprianidou@stir.ac.uk (F. Lamprianidou).

http://dx.doi.org/10.1016/j.ecss.2015.07.045
0272-7714/

of dissolved fish farm effluent (Broch et al., 2013; Jiang et al., 2010; Reid et al., 2013; Wang et al., 2013). Similarly, sea urchins can filter sea cage effluent (Kelly et al., 1998; Schuenhoff et al., 2003) and it has been shown that *Paracentrotus lividus* can assimilate fish farm waste and can achieve high growth and survival rates near salmon cages (Cook and Kelly, 2007).

IMTA systems design needs to encompass the characteristics of both the site and the selected organism and optimizing synergies requires advanced understanding of the system at a specific site. A major factor restricting the efforts to optimize open water IMTA, is the lack of knowledge on how IMTA systems operate coupled with the lack of data from large scale extractive cultures and thus the need to extrapolate results from small-scale studies (Troell et al., 2003). Due to limited knowledge of IMTA system properties, the placement of the extractive organisms is often driven by availability of space as opposed to nutrient uptake maximization (Hughes and Kelly, 2001).

Lack of knowledge or inaccurate IMTA design might impact the health and growth of the finfish or the surrounding environment or the extractive organism flesh might be of inferior quality. For example, the use of organic extractive organisms can lead to additional nitrification of the water column, because most of the organic material ingested by the organic extractive organisms returns to the water column as nutrients (Nizzolli et al., 2005) and pseudofaeces produced by filter feeders may collect on the sediment impacting benthic communities. Also, the extractive cultures may interfere with the water movement, changing the particle dispersal patterns and reducing the water flow through the sea cages. Farming different species within the same system can increase the exposure to pathogens; mussels for instance bioaccumulate and shed harmful bacteria (Pietrak et al., 2012). Other limitations of open water IMTA include the need for high stocking densities and the need for deployment of the organic extractive organisms lower in water column near the primary source of particulate waste.

The maximum production of an organic extractive species crop is limited by food availability (e.g. Grant and Filgueira, 2011). Increasing crop biomass beyond this carrying capacity causes food depletion and thus crop production cannot be maximized (Cranford et al., 2013). There needs to be a balance between waste production and uptake where the waste is sufficient to feed the extractive organisms and concurrently as much of the waste as possible is removed from the ecosystem. An efficient IMTA farm allows the profitable use of each of the culture modules with minimum waste (Neori et al., 2004). In order to achieve this the standing stocks of all the cultured organisms have to be maintained, considering nutrient requirements of each and the rates of excretion and uptake of the important solutes by each of them (Granada et al., 2015).

From a biological point of view, the choice of extractive species in an IMTA system is crucial because their physiological and ecological attributes determine the rate of particle or nutrient consumption and assimilation, their growth rate and in capabilities in terms of biofiltration. Species are chosen based on specific culture performance traits, for which quantitative information needs to be available, with respect to nutrient uptake efficiency and secondary considerations (e.g. yield and protein content). The marketability of the extractive species is largely dependent on the location, with the Western world showing less demand for food species that are low in the trophic chain. Nevertheless, dried seaweed products can always be exported and seaweeds can be processed to produce cosmetics, fertilizers, animal feed, biogas and others.

The environmental benefits, matter and energy flux within an IMTA farm as well as between the environment and the IMTA system, need to be qualified and quantified prior to the establishment of a marine IMTA system. The aim of this study was to provide a tool for designing IMTA farms at any site by creating a modelling tool that can be used to fine-tune IMTA designs for maximising yields and nutrient removal.

Without a thorough understanding of the dynamics of the system, the environmental and economical benefits of IMTA cannot be achieved. However, field measurements of nutrient and Particulate Organic Matter (POM) concentrations in open-water systems are challenging due to the highly diluting, dynamic nature of open-water systems, presenting high spatial and temporal variation both diurnally and seasonally. The model described in this study determines the temporal availability of nutrients and POM released by the different IMTA components and thus the amount available for uptake by different groups of extractive organisms. Because of the site specificity of waste distribution, this model focuses on simulation of a virtually closed system, within which the nitrogen is homogenously distributed. The species used in this study are Atlantic salmon (*Salmon salar*), a sea urchin (*P. lividus*) and the sea lettuce (*Ulva lactuca*), though it will be possible to re-parameterise the model for a range of different species.

2. Model development

The model was implemented using the visual simulation package Powersim™ Constructor Studio 8 (Powersim Software AS, Bergen). An 18-month period time horizon was used, to simulate the at-sea phase of salmon production cycle, which lasts between 14 and 24 months (Marine Harvest, 2012). The model is typically operated with a one-day time step and the model differential equations are solved using a third order Runge–Kutta integration method. The selected time-step reflects accurately the time dependent environmental changes (accurate integration) with low computing effort.

An extensive literature review was carried out for model parameterization for *Ulva* (Table 1) and for *P. lividus* (Add_my_pet, 2014), while the model for *S. salar* was parameterized using data acquired from commercial Scottish salmon farms. For the parameters where a range of values was available in the literature, the most representative value was used. It is evident that the inclusion of many proxy variables from the literature propagates uncertainties through the model, affecting the overall model accuracy. Since the model is deterministic, its output is entirely determined by the input parameters and structure of the model. Due to the high structural complexity of the model and high degree of uncertainty in estimating the values of many input parameters, a detailed sensitivity analysis was performed by varying each input parameter by ± 10% and quantifying the effect on eight output variables (Table 2). The selected output variables reflect the objectives of the research with respect to nitrogen bioremediation and yield productivity. Within the sensitivity analysis all model parameters and initial values of state variables (50 input variables) were varied in order to determine the response of the following eight effect variables: harvested seaweed, salmon and sea urchin biomass, nitrogen accumulated by seaweed, salmon and sea urchins, DIN and PON available at the IMTA site at the end of the simulation. The sensitivity analysis results are presented as a normalized sensitivity coefficient (NS) (Fasham et al., 1990):

$$NS = \frac{DV/V_b}{DP/P_b} \quad (1)$$

where $DV = (V_b - V)$ is the change of a response variable, V_b is the value of a response variable for the base run, V is the value of a

Table 1
Parameterization of constants and time series variables used at the seaweed growth submodel.

Variable	Description	Value range in literature	Value used	Units	Reference
μ_{max}	Maximum growth rate	0.8–18	10	% Day^{-1}	Neori et al., 1991; Luo et al., 2012; Perrot et al., 2014
N_{max}	Maximum intracelular quota for N	36-54	50	mg^{-1} N g dw^{-1}	Fujita, 1985; Cohen and Neori 1991; Perrot et al., 2014
N_{min}	Minimum intracelular quota for N	10 to 13	10	mg^{-1} N g dw^{-1}	Fujita, 1985; Cohen and Neori 1991; Perrot et al., 2014
T	Water Temperature	Site specific	6.8–13.7[a]	°C	n/a
q_{10}	Seaweed temperature coefficient	2	2	n/a	Aveytua-Alcázara et al., 2008
I_0	Water surface light intensity	Site specific	50-190[a]	W m^{-2}	n/a
I_{opt}	Optimum light intensity for macroalagae	50	50	W m^{-2}	Perrot et al., 2014
k	Light extinction coefficient	Site specific	1	m^{-1}	n/a
z	Culture depth	Farm practice	2	m	n/a
V_{max}	Maximum N uptake rate	0.44–2.2	1.32	mgN g^{-1} dw h^{-1}	Lapointe and Tenore 1981; Perrot et al., 2014
K_N	N half saturation	0.06–0.55	0.31	mg L^{-1}	Perrot et al., 2014
Wet/Dry	Wet to dry weight ratio	6.7–10.15	8.43	n/a	Neori et al., 1991; Angell et al., 2012
M	Mortality	0.009–0.02	0.015	d^{-1}	Aveytua-Alcázara et al., 2008; Perrot et al., 2014
T_{ref}	Reference temperature for seaweed growth	n/a	15	°C	Neori et al., 1991; Luo et al., 2012; Perrot et al., 2014
Ω	Decomposition rate and natural biomass loss	n/a	M/2	d^{-1}	n/a
D	Loss rate due to environmental disturbance	n/a	M/2	d^{-1}	n/a
S	DIN concentration in seawater	Site specific	0.594	mg m^{-3}	n/a

[a] Time series variable.

response variable for the sensitivity analysis run, $DP = (P_b - P)$ is the change in a model parameter, P_b is the baseline value of a model parameter and P is the value of a model parameter for the sensitivity analysis run.

When the value of NS for a parameter +10% is negative then there is a negative correlation between parameter and effect. When it is negative for a parameter −10% then there is a positive correlation between parameter and effect.

2.1. Model outline

The model determines the nutrient recovery efficiency and biomass production of IMTA based on a baseline simulation, components of the model can be altered or removed for the simulation of particular scenarios. Following re-parameterization, the model can simulate IMTA systems consisting of different combinations of finfish, sea urchin (or other grazing invertebrate) or seaweed species. The present model incorporates an ecosystem model consisting of three submodels that interact with each other and with their surrounding environment via nutrient cycling (Fig. 1). The submodels consist of growth models for *S. salar*, *Ulva* sp. and *P. lividus* that interact with each other through modelled nitrogen release and subsequent assimilation (Fig. 1).

Salmon growth was modelled using the Thermal-unit Growth Coefficient (TGC) (Iwama and Tautz, 1981), the seaweed growth model is based on Droop's model for nutrient-limited algal growth (Droop, 1968) and sea urchin growth was modelled using the Dynamic Energy Budget (DEB) theory (Kooijman, 1986).

The TGC is a simple model widely used in aquaculture, based on three basic assumptions, which may be violated under certain conditions (Jobling, 2003). The TGC can present errors when the temperature deviates far from the optimum for growth (Jobling, 2003), but this is not a setback given the temperature range used in the present simulations. For the organic extractive organisms a bioenergetic model was used in order to link the environmental variables, mainly food availability and temperature, with feed intake, growth, excretion and faeces production. For the simulation of salmon growth and nutrient uptake and release, the TGC was preferred to a bioenergetic model because under intensive aquaculture conditions feed is not limiting growth. Furthermore, salmon is well studied and daily time series data for the TGC and food conversion ratio (FCR) as well as sources of data for excretions and faeces production were available in the literature. Finally, as salmon are grown at sea for only for a part of their production, data are not required for the full life cycle, which is the strength of the DEB approach.

The model includes daily time steps for a better understanding of the process affecting the IMTA productivity and nutrient removal efficiency. Due to the dynamic design of the model the bioremediation potential of different production scenarios can be estimated by altering various production parameters of the baseline simulation. These include site-specific environmental conditions (temperature, irradiance and ambient nutrient concentration) and production practices (seaweed harvesting frequency, seaweed culture depth, nitrogen content of feed, initial stocking biomass of extractive organisms etc.). The maximum seaweed and sea urchin biomass that can be sustained at any given time can also be estimated based on the daily amount of nitrogen within the IMTA system that is available for uptake.

The complete model is used to determine the overall ability of the IMTA system to reduce the nutrient and POM waste of fed-species taking into account the quantity of nutrients and POM that are released and the quantity that could be potentially absorbed/consumed by the extractive organisms if all the waste remained within the virtually closed system. The only nitrogenous input to the seaweed and sea urchin submodels is the daily waste released to the sea from the salmon submodel. This is used to calculate the amount of particulate (suspended) and dissolved nitrogen released from the salmon farm for a given fish production over 18 months, as well as the potential for decreasing the nutrient released by converting salmon monocultures into IMTA systems. The model considers fish growth and consequent feed input and waste release, and the uptake and release of DIN and PON by the different IMTA components. The growth models are combined with nutrient transfer/cycling and this way the virtually closed system bioremediation efficiency is estimated (Fig. 1).

2.2. Salmon growth submodel

The growth rate of fish fluctuates throughout an individual life cycle and is mainly influenced by feed availability, temperature and photoperiod (Austreng et al., 1987). Salmon growth was simulated using a thermal growth coefficient:

$$TGC = 1000\frac{\sqrt[3]{W_t} - \sqrt[3]{W_0}}{T*t} \quad (2)$$

where W_0 is the smolts initial wet weight, W_t is the fish's wet

Table 2
Most sensitive parameters (with NS ≥ 1) for the effect variables a) Nitrogen accumulated in harvested salmon b) Harvested salmon biomass c) DIN accumulated in harvested seaweed d) Harvested seaweed biomass e) Nitrogen accumulated in harvested sea urchin biomass f) Harvested sea urchin biomass g) DIN available at the IMTA site h) PON available at the IMTA site, by descending absolute normalized sensitivity coefficient (NS) for either + or − 10% of the effect parameter's value.

Parameter symbol	Parameter name	Parameter baseline value	Effect for parameter +10%	NS for parameter +10%	Effect for parameter −10%	NS for parameter −10%
a) Nitrogen accumulated in harvested salmon: effect baseline value is 24.66 tonnes						
TGC	Thermal-unit growth coefficient[a]	2.33	30.55	2.42	19.61	2.07
FCR	Feed conversion ratio[a]	1.04	24.92	0.1	20.39	1.73
b) Harvested salmon biomass: effect baseline value is 1000 tonnes						
TGC	Thermal-unit growth coefficient[a]	2.33	1242	2.45	808	1.95
c) DIN accumulated in harvested seaweed: effect baseline value is 17.09 tonnes						
N_{state}	Nutrient state of seaweed at harvest[b]	10	3.18	−7.93	10.59	3.97
μ_{max}	Max seaweed growth rate	0.13	19.78	1.57	13.71	1.98
T	Water Temperature[a]	10.89	18.01	0.54	12.96	2.41
V_{max}	Maximum N uptake rate	1.32	19.18	1.22	13.50	2.10
W/D	Wet/dry ratio	8.43	19.19	1.23	13.49	2.10
z	Culture depth	2	19.39	1.35	14.32	1.62
N_{excr}	Nitrogen lost via excretion	0.45	16.80	−0.17	15.09	1.17
d) Harvested seaweed biomass: effect baseline value is 341.84 tonnes						
μ_{max}	Max seaweed growth rate	0.13	395.69	1.58	274.19	1.98
T	Water Temperature[a]	10.89	360.20	0.54	259.27	2.41
V_{max}	Maximum N uptake rate	1.32	383.68	1.22	269.92	2.11
W/D	Wet/dry ratio	8.43	383.73	1.23	269.88	2.11
z	Culture depth	2	387.89	1.35	286.49	1.62
N_{min}	Min intracellular quota for N	10	303.32	−1.13	358.39	−0.48
N_{max}	Max intracellular quota for N	50	307.66	−1.00	360.90	−0.56
e) Nitrogen accumulated in harvested sea urchin biomass: effect baseline value is 0.96 tonnes						
T	Water Temperature[a]	10.89	1.119	1.65	0.640	3.33
$\{Px\}$	Maximum surface-specific feeding rate	578.55	1.248	3.00	0.723	2.47
K_o	Reference reaction rate at 288 K	1	1.229	2.80	0.734	2.35
T_A	*P. lividus* Arhenius temperature	8000	0.793	−1.74	1.172	−2.21
μ_{cj}	Ratio of carbon to energy content	83.30	0.876	−0.88	1.068	−1.13
f) Harvested sea urchin biomass: effect baseline value is 20.02 tonnes						
T_L	*P. lividus* lower boundary tolerance	273	0.08	−9.96	n/a	n/a
T	Water Temperature[a]	10.89	23.01	1.15	13.37	3.32
$\{Px\}$	Maximum surface-specific feeding rate	578.55	26.01	2.99	15.00	2.50
K_o	Reference reaction rate at 288 K	1	25.36	2.67	15.39	2.31
T_A	*P. lividus* Arhenius temperature	8000	16.59	−1.71	24.21	−2.09
$[E_G]$	Volume specific cost of *P. lividus* growth	2748	18.28	−0.87	22.02	−1.00
g) DIN available at the IMTA site: effect baseline value is 12.38 tonnes						
N_{state}	Nutrient state of seaweed at harvest[b]	10	23.31	0.22	16.95	0.18
TGC	Thermal-unit growth coefficient[a]	2.33	18.05	4.64	5.55	5.59
FCR	Feed conversion ratio[a]	1.04	11.82	−0.45	6.82	4.49
N_{excr}	Nitrogen lost via excretion	0.45	15.60	2.60	10.65	1.40
μ_{max}	Max seaweed growth rate	0.13	9.69	−2.17	15.77	−2.74
$N_{content}$	Nitrogen content in feed	0.057	15.66	2.63	10.59	1.44
T	Water Temperature[a]	10.89	11.46	−0.74	16.53	−3.35
V_{max}	Maximum N uptake rate	1.32	10.29	−1.69	15.98	−2.91
W/D	Wet/dry ratio	8.43	10.30	−1.68	15.97	−2.90
z	Culture depth	2	10.08	−1.86	15.15	−2.24
N_{min}	Minimum intracellular quota for N	10	14.32	1.57	11.56	0.66
h) PON available at the IMTA site: effect baseline value is 9.65 tonnes						
TGC	Thermal-unit growth coefficient[a]	2.33	12.07	2.54	7.41	2.35
FCR	Feed conversion ratio[a]	1.04	9.68	0.03	7.78	1.94
$N_{content}$	Nitrogen content in feed	0.0576	10.70	1.08	8.61	1.07

[a] Time series variable. The time series parameters where increased/decreased by 10% at each time step.
[b] For the parameter 'Nutrient state of seaweed at harvest' we used N_{min} instead of N_{max} at the column labelled as +10% and $(N_{min} + N_{max})/2$ at the column labelled as −10%.

weight at time t, T is the temperature and t is time in degree-days.

Solving for W_t we obtain:

$$W_t = \left[\sqrt[3]{W_0} + \frac{TGC*T*t}{1000}\right]^3 \quad (3)$$

The total salmon biomass was calculated as individual weight multiplied by the number of individuals. The model also accounted for natural mortality, modelled as a time series variable since mortality decreases with fish size, using empirical data from Scottish salmon farms.

The amount of waste released from the salmon farm in the form of excretion, faeces production and feed loss was assumed to be as calculated by Wang et al. (2012) for Norwegian salmon farms, with the exception that the feed nitrogen content was set to be 5.76% of the feed weight, since to date crude protein content is around 36% (Skretting, 2015). We assume that every day of the simulation 2% of feed nitrogen is released in the environment as feed loss, 45% as dissolved excretions and 15% as faeces, while the remaining 38% is assimilated into salmon biomass and removed from the ecosystem

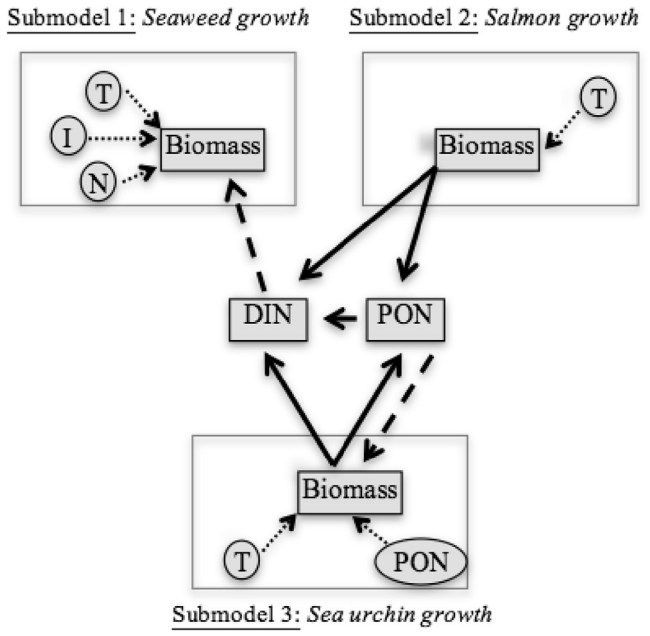

Fig. 1. Conceptual diagram of the model showing the major state variables (squares) and forcing functions (circles) of each submodel as well as the interactions among the submodels. The dashed lines represent nitrogen assimilation and the solid lines nitrogen release. *T, I* and *N* represent temperature, irradiance and nitrogen, respectively.

when the fish are harvested.

2.3. Seaweed growth and nitrogen uptake

Seaweed biomass *(B)* increases with a varying growth rate and decreases due to natural causes and periodic harvesting. The basic processes affecting seaweed biomass form the differential Equation (4):

$$\frac{dB}{dt} = (\mu - \Omega)^*B - (D + H)^*B \tag{4}$$

where μ is the specific growth rate, Ω the specific decomposition rate, D the loss rate due to environmental disturbance and H the harvesting rate. Biomass is calculated as wet biomass, for the conversion of seaweed wet to dry weight an 8.43 to 1 ratio was used (Angell et al., 2012; Neori et al., 1991). At the baseline simulation due to lack of data in the literature for the specific decomposition rate and the loss due to environmental disturbance for *Ulva* sp. the term mortality (M) is used, where $M = \Omega + D$ and $\Omega = D$ (Table 1).

The gross growth rate was defined as a function of water temperature, availability of Photosynthetic Active Radiation (PAR) and nutrient concentration in the water column and in the plant tissues. The joint dependence of growth on environmental variables is defined by separate growth limiting factors, which range between 0 and 1. A value of 1 means the factor does not inhibit growth (i.e. light is at optimum intensity, temperature is optimum and nutrients are available in excess). The limiting factors are then combined with the maximum gross growth rate at a reference temperature as in Equation (5) (Solidoro et al., 1997):

$$\mu = \mu_{max(T_{ref})}{}^*f(T)^*f(I)^*min(f(N), f(P)) \tag{5}$$

where $\mu_{max(Tref)}$ is the maximum growth rate at a particular reference temperature (T_{ref}) under conditions of saturated light intensity and excess nutrients, $f(T)$, $f(I)$, $f(N, P)$ are the growth limiting functions for temperature, light and nutrients (nitrogen and phosphorus).

The major nutrients required for growth are nitrogen and phosphorus, while carbon is often available in excess and micronutrients such as iron and manganese are only limiting in oligotrophic environments. Typically, in marine ecosystems, nitrogen is the element limiting algal growth (Lobban and Harrison, 1994). Thus in the baseline simulation it is assumed that phosphorus is not limiting, so Equation (5) becomes:

$$\mu = \mu_{max(T_{ref})}{}^*f(T)^*f(I)^*f(N) \tag{6}$$

The Photosynthetic response to light is based on Steele's photoinhibition law (Steele, 1962):

$$\frac{P}{P_{max}} = \frac{I}{I_{opt}} exp\frac{1 - I}{I_{opt}} \tag{7}$$

where P is the photosynthetic response at a given light intensity I (W m^{-2}) for an organism that has a maximum photosynthetic rate P_{max} at the optimal (saturating) light intensity I_{opt} and I is the light intensity at a given depth (z). Light intensity at a given depth is an exponential function of depth, seaweed and phytoplankton standing biomass and is given by:

$$I(z) = I_0 e^{-kz} \tag{8}$$

where k is the light extinction coefficient (m^{-1}).

After mathematical integration of the light limitation factor Equation (8) we obtain:

$$\begin{aligned} F(I) &= \int_0^z \frac{P}{P_{max}} dz = \int_0^z \frac{I(x)}{I_{opt}} exp\frac{1 - I(x)}{I_{opt}} dx \\ &= \int_0^z \frac{I_0 e^{-kx}}{I_{opt}} \exp\frac{1 - I_0 e^{-kx}}{I_{opt}} dx \\ &= \frac{1}{k}{}^*\exp\left(\frac{1}{I_{opt}}\right)^*\left[\exp\left(-\frac{I_0}{I_{opt}}{}^*\exp(-z^*k)\right) - \exp\left(-\frac{I_0}{I_{opt}}\right)\right] \end{aligned} \tag{9}$$

The temperature, like the light, limitation factor follows an inhibition law.

$$F(T) = q_{10}^{0.1(T - T_{ref})} \tag{10}$$

where q_{10} is a temperature coefficient and T_{ref} is the reference temperature at which the seaweed growth rate was measured.

The nitrogen limitation factor Equation (11) is given by the range of internal nitrogen concentration, with a feedback effect on the uptake function (Aveytua-Alcázar et al., 2008; Coffaro and Sfriso, 1997; Solidoro et al., 1997). It can range between 1, when $N = N_{max}$ and uptake is saturated and 0 when $N = N_{min}$ and maximum uptake rate is possible, all measured in mgN g^{-1} dry seaweed. Internal nitrogen quota/concentration *(N)* refers to the concentrations in algal cells as opposed to external concentrations that refer to the concentration in the water column.

$$F(N) = 1 - \frac{N_{max} - N}{N_{max} - N_{min}} \tag{11}$$

For calculation of *(N)*, a quota-based model was used developed from Droop's original formula (Droop, 1968):

$$\frac{dN}{dt} = V^*F(N) - \mu^*N \tag{12}$$

where V is the nitrogen uptake rate (mg g^{-1}dw h^{-1}) and μ is the

specific growth rate.

Nutrient uptake rates *(V)* are proportional to nutrient concentration in the water according to Michaelis–Menten kinetics:

$$V = \frac{V_{max}S}{K_N + S} \tag{13}$$

where V_{max} is the maximum nitrogen uptake rate under the site's prevailing conditions (mg g^{-1}dw h^{-1}), S is the total DIN concentration in the seawater (mg l^{-1}) and K_N is the half-saturation coefficient for nitrogen uptake (mg l^{-1}).

By combining Equations (11)–(13) we obtain:

$$\frac{dN}{dt} = \frac{V_{max}S}{K_N + S}\frac{N_{\max} - N}{N_{max} - N_{min}} - (\mu^{*}N) \tag{14}$$

The bioremediation effect of IMTA is closely dependent on the biomass of extractive organisms harvested. However, the maximum biomass is restricted by culture practicalities such as the potential alteration of water currents and by the availability of nutrients. The maximum biomass is site and species dependent. For the baseline simulation presented here, the maximum seaweed biomass permitted on site at any given time was set at 35 tonnes wet weight. The area required for the culture of 35 t of *Ulva*, with stocking density of 1.6 kg m^{-2} and two layers of seaweed one at the sea surface and one 3 m deep would be 10,937 m^2. This stocking density was selected because the maximum density permitted to guarantee the greatest uptake of nutrients in *U. lactuca* is 1.9 kg m^{-2} (Neori et al., 1991). The area required for the seaweed culture is used for the estimation of the virtually closed IMTA site's water volume, which is estimated using the following formula:

'IMTA site volume' = 'Average depth' * 'Number of salmon cages' * 'Sea cage area' + 'raft area' * 'number of rafts' * 'Average depth'.

Seaweed is lost due to mortality, harvesting and natural biomass loss (seedling mortality, grazing, epiphytism, sediment abrasion and smothering and removal by wave action). Managing the harvesting rate is of paramount importance for achieving high productivity rates. For optimal results, when the seaweed biomass reaches a predefined level (35 t in the baseline simulation) the seaweed is harvested at regular time intervals. The biomass harvested depends on the forecasted growth and natural mortality rate of the forthcoming days. A discrete flow in the model controls the loss of seaweed biomass due to harvesting; the rate of the flow (harvest rate) is regulated by the following instruction:

IF (start harvesting = 0, 0 ton, IF (current time step * timestep = stoptime − starttime, seaweed biomass, IF (accrued part of 10 days = 1, seaweed biomass − maximum seaweed biomass, IF (accrued part of 10 days = 0, seaweed biomass − maximum seaweed biomass, 0 ton))))where '*start harvesting*' is a level that allows harvesting to start only when the seaweed biomass has surpassed the value of a constant that defined as maximum biomass that can be on site (maximum seaweed biomass). The level 'start harvesting' changes from 0 to 1 when the level '*seaweed biomass*' is equal to or larger than the constant '*maximum seaweed biomass*'. '*Current time step*' is a level that counts the time steps, starting from zero. *Timestep*, *starttime* and *stoptime* are Powersim built-in functions that return the time step of the simulation, the start-time and stop-time of the simulation, respectively. In the final time step all the seaweed in the level *'seaweed biomass'* is transferred to the level *'harvested seaweed'*. '*Seaweed biomass*' is a level that shows the seaweed biomass. *'Accrued part of 10 days'* is a level used for the calculation of 10-day periods. When the value of this level is one, all the seaweed is harvested apart from *'maximum seaweed biomass'*.

The model is effective for perennial seaweed species. However, as the gametophyte stage of *Ulva*, lasts only for a few months, frequent reseeding will be necessary at time intervals dependent on the environmental conditions, epiphytic growth or disease. The numerical parameters used in the seaweed model are summarized in Table 1.

2.4. Sea urchin growth and nitrogen uptake and release

The sea urchin growth submodel is based on the DEB theory (Kooijman, 1986). DEB theory is based on two state variables: structural volume (V) and energy reserves (E) and on two forcing variables: temperature (T) and food density *(X)*. The basic concept of the theory is that from the food ingested a certain amount is released as faeces and the rest is assimilated. All assimilated food enters a reserve compartment. From there a fixed fraction is spent on maintenance and the rest is spent on maturity or reproduction (Kooijman, 1986). A detailed description of the DEB can be found at Kooijman (2008). Most of the species-specific parameters used for this DEB model were obtained from (Kooijman, 2014).

The initial structural length/diameter of sea urchin juveniles was set to 10 mm, a size suitable for successful transfer of hatchery-reared sea urchins to sea (Kelly et al., 1998). At this length *P. lividus* individuals are characterized as sub adults (Grosjean et al., 1998), so in the baseline simulation the DEB model simulates the growth from late juveniles to mature adults.

The DEB model starts with the ingestion of PON ($mgN\ d^{-1}$) by the sea urchins. This is based on ingestion rate (j_x) (mgC d^{-1}) divided by the C/N ratio of the aquaculture waste. Ingestion rate is proportional to the surface area of the structural volume and follows type-II function response depending on the density of PON. The food that is ingested but not assimilated as biomass is released to the environment as faeces or as excretion by diffusion. The DEB model enables estimation of the potential amounts of excretions released by the sea urchins by estimating the daily production of faeces released into the surroundings this is then divided by the C/N ratio in order to calculate the amount of PON and DIN that is in sea urchin excretions, which is assumed to be immediately added to the PON and DIN pools and is thus available for consumption by the sea urchins and seaweed, respectively. The *P. lividus* N quota *(Q)* was set to 127 mgN mgC^{-1} (Tomas et al., 2005) and sediment N quota *(Qs)* is site specific it was set to 7, which is a representative value for an average Scottish salmon farm site.

The total sea urchin biomass is calculated as individual weight multiplied by the number of individuals. The decrease of the sea urchin stock size, due to mortality, is calculated in Equation (15) where due to the planktonic nature of sea urchin larvae, it is assumed they will be dispersed from the IMTA site and thus reproduction will represent a net energy loss and restocking of sea urchins will be necessary. However, the release of the larvae will contribute to restocking native sea urchin populations.

$$\frac{dN}{dt} = -\delta_r{}^{*}N - \delta_h{}^{*}N \tag{15}$$

where δ_r and δ_h are the sea urchin natural and harvest mortality, respectively. The harvest mortality was zero and at the simulation last time step all sea urchins were harvested, same as in the salmon and seaweed submodels. The natural mortality was set to 0.00102 individuals d^{-1} for sea urchins with test diameter less than 2 cm and 0.00056 individuals d^{-1} for sea urchins with test diameter more than 2 cm (Turon et al., 1995).

During the grow-out stage of *P. lividus* juveniles, the stocking density is approximately 400 individuals m^{-2} (as used in tank cultures; Carboni, 2013). Space is not an issue for the organic extractive component of the IMTA, since for the production of

560,525 individuals only 1401 m^2 would be required and this area would be directly underneath the fish cages and the seaweed rafts.

2.5. Assumptions and simplifications

The key assumption of the overall model is that all nitrogen released by the IMTA components is dispersed homogenously within a quantified water volume defined as the IMTA site water volume (see Section 2.3). It is also assumed that all the nitrogen available in the IMTA site volume is in a form suitable for uptake. Correspondingly, the model does not take into account the interactions between nitrate and ammonium within the environment and organisms, such as the role of sediment and water in the nutrient dynamics or denitrification. The increase of light limitation due to increased self-shading as the seaweed grows was not considered, neither was the shading caused by phytoplankton. Data from Broch and Slagstad (2012) could be used to derive a seaweed self-shading formula from which an add-on model could be used to simulate the changes in k, in this study k is a constant. In the seaweed growth submodel the biomass loss due to mechanical damage caused by harvesting was not included. It is also assumed that nitrogen is the only nutrient limiting seaweed growth. Additionally, the seaweed biomass used as initial biomass is assumed to have an average $((N_{min} + N_{max})/2)$ N quota (this can be regulated by using nitrogen deprived seedlings). When seaweed is harvested it is assumed that the N quota of the harvested seaweed is equal to the maximum N quota due to the high availability of DIN in the virtually closed system. The assumption that the seaweed harvested has this high nitrogen quota might lead to overestimation of the bioremediation efficiency and the effect of lower N quota at harvest was examined in the sensitivity analysis (Table 2). From a farm practice perspective it is assumed, that the relative position of the extractive organisms in relation to the fish cages is such that it ensures high O_2 availability for the fish. For the salmon growth model, excretion, faeces production and feed loss were assumed to be a steady proportion of feed input during the 18 month production period while in reality they change as fish grow.

2.6. Production specifications of the baseline simulation

The results presented are from the IMTA baseline simulation, which was parameterized using data acquired from the literature and from commercial salmon farm sites. The environmental data such as monthly variations in seawater temperature and irradiance were acquired from empirical databases for the West coast of Scotland and the production-specific input data from Scottish commercial salmon farm sites (Figs. 2 and 3). Typically, S1 smolts are transferred to sea in spring (April–May), so April is set as simulation time 0. The baseline scenario farm consists of nine 90 m circular salmon cages with the extractive organisms placed in immediate proximity to those cages. The model simulates a farm that produces 1 000 t of Atlantic salmon in 18 months on-growing, a farm size representative of the Scottish industry.

3. Results

3.1. Growth performance of IMTA components at the baseline simulation

The baseline simulation run estimated that the mean individual fish biomass after 540 days (18 months) was 3.78 kg (Fig. 4A) and the salmon stock decreased by 16,525 individuals from 280,883 to 264,358 individuals (Fig. 4B). During the 18-month production period, 342 t of seaweed and 20.02 t of sea urchins were produced and harvested as well as the targeted 1 000 t of salmon. The seaweed achieved high growth rates, especially during the summer months (Fig. 5). The effect of the growth limitation factors on seaweed growth rate is presented in Fig. 6. The lower seaweed growth rate during the first 300 days (10 months) of the simulation (Fig. 5) can be mainly attributed to low levels of nitrogen available for uptake (Figs. 6 and 9). It is clear that in the hypothetical baseline model scenario, during the first 340 days of the simulation seaweed growth is mainly limited by the availability of nitrogen. Temperature limits growth more during the colder months (October–April) while, the effect of light intensity is rather stable throughout the year (Fig. 6). It should be emphasized here that site specific shading caused by phytoplankton or seaweed self-shading does not contribute to light limitation in the baseline simulation (see Section 2.5).

The aim of the model is to achieve high nutrient bioremediation efficiency in limited space. Sustaining the seaweed biomass at a high density at all times, using the harvesting instruction (described at Section 2.3), played an important role in achieving high bioremediation efficiency (Fig. 7). The first seaweed harvesting occurred 250 days after the simulation start, following which there was sufficient nitrogen available due to the large size of the fish and the environmental conditions were also favourable for the remaining seven months of the simulation (April–October) (Figs. 3 and 6) thus ensuring constant high growth rate and harvesting at 10-day intervals (Fig. 7).

At simulation time zero the site was stocked with 827,900 (0.09 t) sea urchins. During the 18-month production period 20.01 t (wet weight) of sea urchins were produced with average test diameter 4.47 cm (Fig. 8). As a result 0.96 t of nitrogen were

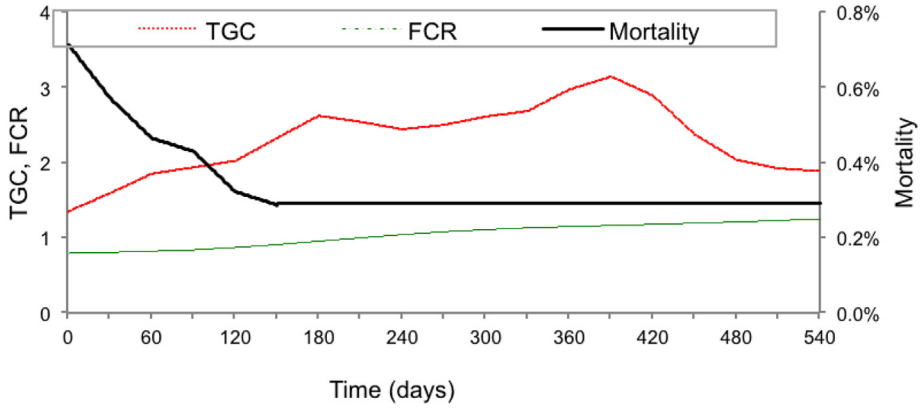

Fig. 2. Baseline scenario values of the time series variables, TGC, FCR and salmon mortality.

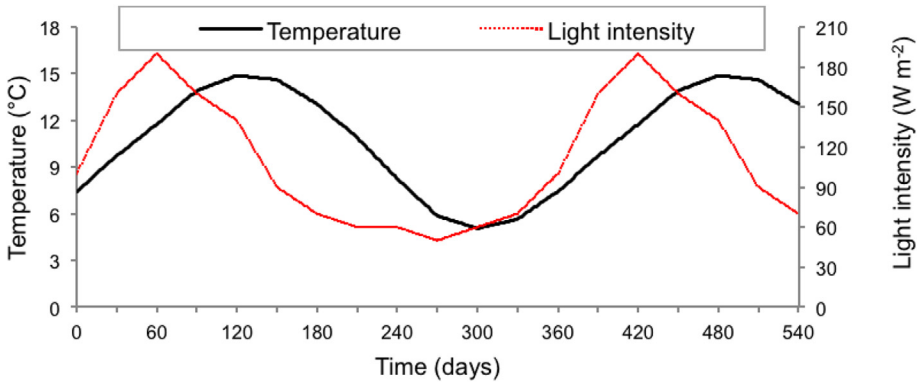

Fig. 3. Baseline scenario values of the time series variables, water temperature and light intensity.

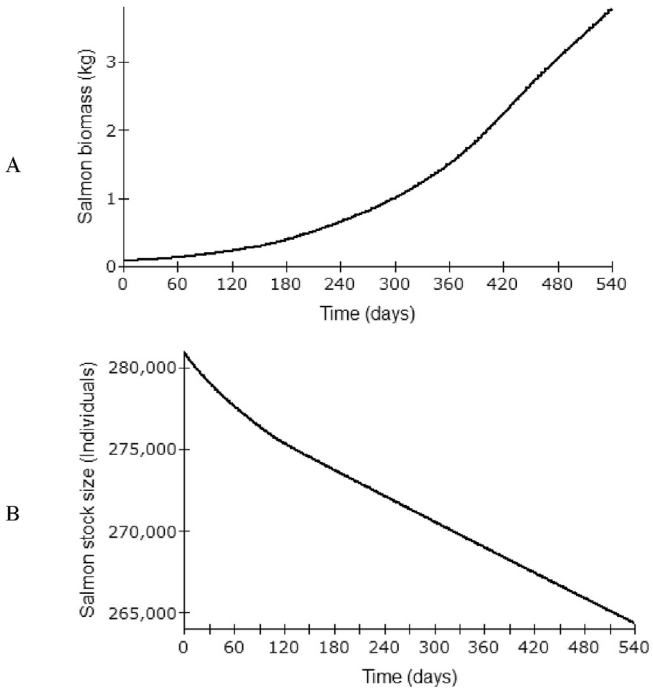

Fig. 4. Simulated output of the salmon: a) individual average biomass, b) stock size, during the 540 days of culture at sea.

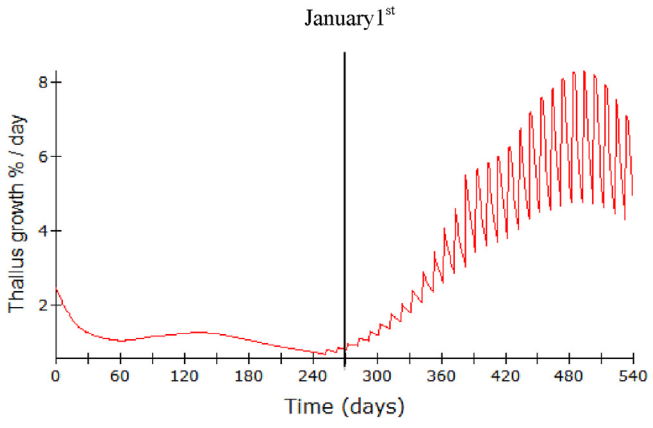

Fig. 5. Seaweed specific growth rate for *Ulva* sp. under the baseline scenario production conditions.

assimilated in the sea urchin biomass and removed from the ecosystem via the process of harvesting.

3.2. Baseline scenario bioremediation potential

For the production of 1 000 t of salmon with an average feed conversion ratio (FCR) of 1.02 and feed nitrogen content 5.76%, the model shows that 65 t of nitrogen are introduced into the system over the 540 day simulated production period. From this 65 t, only 38% is accumulated by the fish and the remaining 62% (40.2 t) is released into the environment. Under the environmental conditions and production method of the baseline scenario the total nitrogen released to the environment from the IMTA site would be 45.2% less (22.03 t instead of 40.2 t) than what would have been released from a salmon monoculture farm of the same capacity. In detail, the amount of nitrogen released from salmon monoculture would be 62% of the exogenous nitrogen input but only 34% in the IMTA system since a large proportion of the nitrogenous waste will be assimilated by the extractive organisms and removed from the ecosystem via harvesting (Fig. 9). Fig. 9 shows the gradual increase in nitrogen within the IMTA system over the simulated production period.

3.3. Sensitivity analysis

All biological, environmental and production parameters were analysed in terms of uncertainty and their relative importance in the model. Due to the large number of input and response variables used in the sensitivity analysis, only the results for the most sensitive parameters (absolute values) are summarized in Table 2. Those parameters are the potential critical assumptions and thus require accurate estimation and/or calibration.

In the salmon submodel, the growth and nutrient uptake is most sensitive to change in the TGC and secondarily to variation in the FCR (Table 2; sections a and b).

In the seaweed submodel, all output variables were most sensitive to parameters affecting growth and nutrient uptake either indirectly through nitrogen uptake and nitrogen content of the seaweed tissues, wet/dry ratio and the culture depth or directly through maximum growth rate, temperature and nitrogen input from salmon excretion. These results show the overall importance of temperature and nitrogen uptake for seaweed growth (Table 2; sections c and d). All parameters, apart from the minimum and maximum intracellular nitrogen quota, were positively correlated with the output variables. Also, increasing parameter values mirrored the effect on the model output of decreasing parameter values, which indicates that most parameters affected growth linearly.

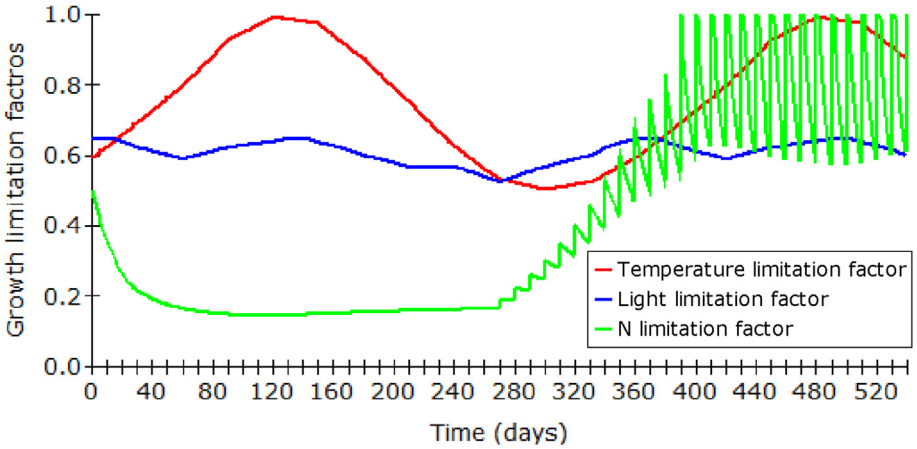

Fig. 6. Seaweed growth limitation factors, under the baseline scenario production conditions. The limitation factors can vary between 0 and 1; where a value of 1 means that the factor does not inhibit growth.

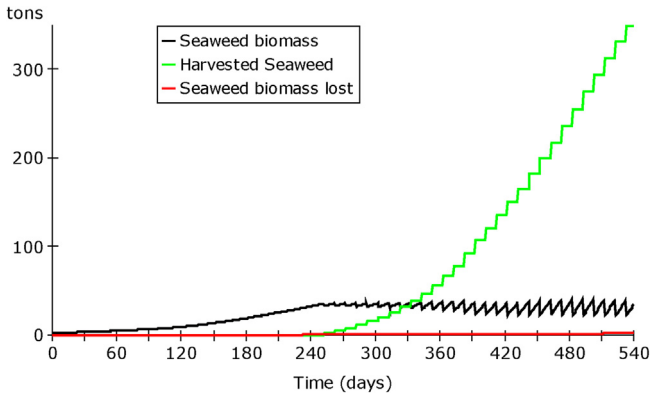

Fig. 7. Seaweed submodel simulation output for *Ulva* sp. produced under the baseline scenario conditions. It illustrates the biomass change over time, the cumulative amount of seaweed biomass lost due to natural causes and the cumulative amount of seaweed biomass harvested.

In the sea urchin submodel the output variables were most sensitive to parameters related to temperature. Other sensitive parameters included the maximum surface-specific feeding rate, the volume specific cost of growth and the ratio of carbon to energy content (Table 2; sections e and f). Overall, this analysis revealed that the DEB model was most sensitive to increases in T_L. Changes in the remaining DEB input variables had little effect on growth (sensitivity < 1).

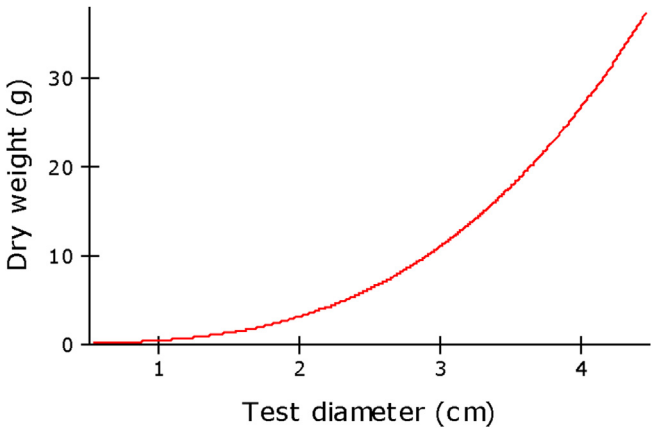

Fig. 8. Sea urchin submodel simulation output for the length – dry weight relationship of *P. lividus*.

The most sensitive parameters within the salmon and seaweed sub-models are also the most sensitive to outcomes of the overall model. The most sensitive parameters of the DEB sub-model do not play such an important role within the overall model performance due to the sea urchin biomass being very small in comparison to that of salmon and seaweed (Table 2; section g and h).

4. Discussion

The aim of this study was the development of a dynamic tool for relative comparison of IMTA scenarios at a given production site, rather than the generation of absolute bioremediation and production estimates. The model results presented are derived from a baseline simulation, which can be re-parameterised to simulate different scenarios.

Results from similar IMTA studies have shown bioremediation potential of a similar scale to the output generated by the present model. Broch and Slagstad (2012) estimated that 0.8 km^2 of *Saccharina latissima* biomass would be needed to sequester all the waste released from a salmon farm producing 1 000 t a year and Abreu et al. (2009) estimated that a 1 km^2 *Gracilaria chilensis* farm would be needed to fully sequester the dissolved nutrients released from a salmon farm producing 1 000 t a year. Sanderson et al. (2012) estimated that 0.01 km^2 of *S. latissima* could remove 5.3–10% of the dissolved nitrogen released from a salmon farm producing 500 t of salmon in two years. However, the results presented, as the results from any other IMTA model or trial, cannot be directly compared with output from similar studies due to the fact that the productivity of an IMTA farm depends on local environmental characteristics, the species combination used, the duration of the grow out seasons and other factors. Moreover, linear interpolation of results from studies with shorter durations can lead to misestimating results. Thus a large variance in production and bioremediation results is natural. The results of this study are in the same order of magnitude as the results acquired from the studies mentioned above; however they suggest higher bioremediation potential, possibly largely due to the harvesting method applied. Specifically, it was estimated that 35% of the total nitrogen released from a salmon farm, with the specifications of the simulated scenario, will be accumulated by the 0.01 km^2 of *Ulva* sp. suggesting a very high bioremediation efficiency. Aiming to achieve 100% bioremediation (i.e. no available nitrogen above the ambient

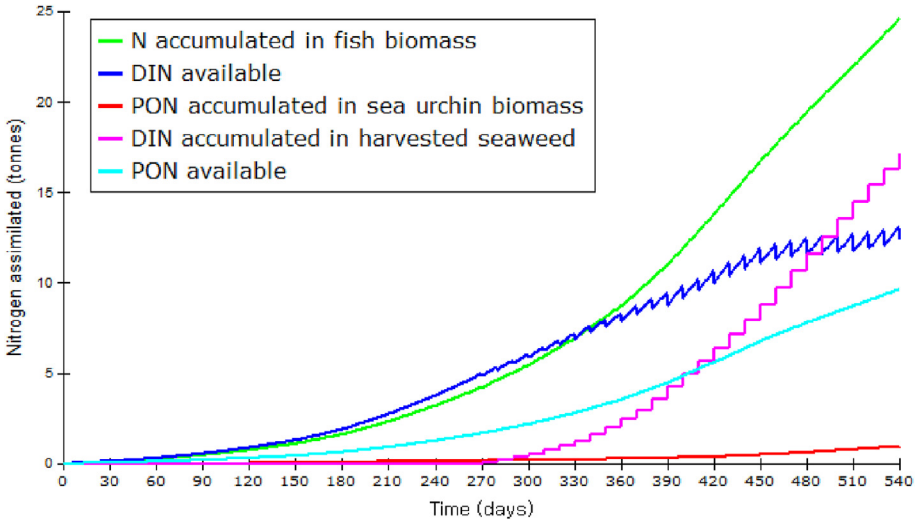

Fig. 9. Modelled output of cumulative amount of nitrogen assimilated by the different IMTA components and the amount of DIN or PON remaining at the IMTA site area at each time step.

concentration occurs at any given time), especially without the addition of external feed sources for the extractive organisms and while sustaining the quality of the extractive organisms, is unrealistic and might only be possible in a fully closed system such as a Recirculating Aquaculture System (RAS). Nonetheless, even at lower bioremediation efficiencies, the model already demonstrates the environmental benefits of IMTA.

The simulated growth for juvenile and adult sea urchins showed good correspondence with literature data (e.g. Cook and Kelly, 2007), although the reference temperature for which all the DEB constants were calculated was 20 °C (Table 1) which is significantly higher than the average temperature (11 °C) at the modelled IMTA site. The sea urchin growth model output is comparable to the results of Cook and Kelly (2007) who concluded that *P. lividus*, with an initial 1 cm test diameter, deployed adjacent to fish cages need approximately 3 years to reach market size (>5.5 cm test diameter). The sea urchins will be approx. one year old when they are deployed and 2.5 years old at the end of the grow out phase at which point their test diameter will be 4.47 cm. At the end of the 18-month grow-out phase of the salmon, the sea urchins will have reached the lower limit of their target market size. The growth rate achieved in this study was similar to that achieved directly adjacent to the sea cages (Cook and Kelly, 2007) and higher than that achieved by Fernandez and Clatagirone (1994) (1.41 mm month^{-1}) where the sea urchins were fed with artificial feed containing fish meal and fish oil at higher water temperature than this study (5–33 °C). After the sea urchins have reached market size a two to three month period of market conditioning at controlled environment is required (Carboni, 2013; Grosjean et al., 1998).

In the first eight to ten months of the IMTA baseline scenario, seaweed and sea urchin growth is limited by nitrogen (Figs. 6 and 8), since the fish are still small and thus require a relatively low feed input. From the eleventh month onwards mainly light and to a lower extent temperature are limiting the seaweed growth. From that point onwards the seaweed growth rate is high as can be seen in Fig. 5. For successful high bioremediation efficiency, at an IMTA farm seaweed growth should not be limited by light or temperature but only by nutrient availability. For this reason IMTA systems could be more efficient in sites further south than the one used for the baseline simulation. It can be seen clearly in Fig. 9 that there is a constant increase of the residual DIN and PON remaining at the IMTA site. This high waste output particularly during the last months of the salmon production is a challenge for achieving very high bioremediation efficiency. The ratio of salmon to extractive organisms used at the baseline scenario is very low, final salmon to seaweed weight ratio was 2.92 and final salmon-sea urchin ratio was 50). From the perspective of space requirement there is the potential for increase of the amount of sea urchins produced, however the quantity of waste available for consumption by the sea urchins decreases with distance from the sea cages and thus increasing the production would mean that some sea urchins would be potentially too far from the food source. Furthermore, limited market demand for marine invertebrates might also pose limitations.

The results of the sensitivity analysis indicate that the model is robust, since variation of key model parameters by ±10% does not cause unexpected changes in the effect parameters. The various model parameters have a different relative influence on the model output, both in terms of harvestable biomass and in terms of nitrogen bioremediation. Thus, depending on the specific study objectives of users, one should consider the precision with which certain parameter values are determined, and whether further tuning is required. This model sensitivity analysis is a useful means for assessing which are the key parameters that increase model uncertainty. Those parameters with high sensitivity have a big impact on the output of the model (e.g. thermal sensitivity parameters T_L in the sea urchin DEB submodel, T in all the submodels and μ_{max} in the seaweed submodel), and therefore future efforts should focus on methods for improving their estimation. In contrast, because parameters with low sensitivity have little influence on the output of the model, their estimation could be simplified. Consequently, despite the large variability observed in some of the parameters, their relative importance may be minor if their sensitivity is low.

Other polyculture and IMTA models developed, to date, include (Nunes et al., 2003; Ferreira et al., 2012; Shi et al., 2011; Ren et al., 2012). The uniqueness of the model developed in this study is that it is a dynamic model developed in a software environment with simple user interface and thus can be used by anyone prior to the setup of an IMTA system. The model presented here is highly adaptable as all the submodels can function independently. By altering model variables the submodels can simulate growth and nutrient assimilation under different environmental conditions or for different species. Altering the values of constants can also help

assess their effect on the IMTA system and in some cases these values can be optimised. For example, all the values related to production practices at the IMTA site, such as seaweed harvesting frequency, maximum seaweed biomass allowed, initial biomass of seaweed or sea urchins, seaweed culture depth and seaweed density, can be optimised for the achievement of higher bioremediation efficiency and/or higher extractive organism production.

The model can be also used to accomplish more general objectives such as: optimization of IMTA culture practices (e.g. timing and sizes for seeding and harvesting, in terms of total production), assessment of the role of IMTA in nutrient waste control and used as input for the evaluation of economic efficiency of various system designs. The present model can be used as a decision support tool for open-water IMTA only after being coupled with waste distribution modelling and environmental sampling for model parameterization. Future versions of the model can link the virtually closed IMTA system to hydrodynamic models for spatial analysis of the waste dispersion and nutrient dilution. Such a model could help develop a balance among the components of the IMTA system and assist in developing an IMTA design for maximum waste uptake in 'open environment systems', as water exchange rate is the key factor influencing the assimilative performance, thus enabling prediction of the effectiveness and productivity of open water IMTA systems.

Acknowledgements

This PhD study to FL was funded by the Marine Alliance of Science and Technology, by the Institute of Aquaculture, University of Stirling and by IKY State Scholarships Foundation of Greece.

References

Abreu, H., Varela, D.A., Henríquez, L., Villaroel, A., Yarish, C., Sousa-Pinto, I., Buschmann, A.H., 2009. Traditional vs. integrated multi-trophic aquaculture of *Gracilaria chilensis* C. J. Bird, J. McLachlan & E. C. Oliveira: productivity and physiological performance. Aquaculture 293 (3–4), 211–220.

Angell, A.R., Pirozzi, I., de Nys, R., Paul, N.A., 2012. Feeding preferences and the nutritional value of tropical algae for the abalone Haliotis asinine. PloS One 7 (6) art. No. e38857.

Austreng, E., Storebakken, T., Åsgård, T., 1987. Growth rate estimates for cultured Atlantic salmon and rainbow trout. Aquaculture 60, 157–160.

Aveytua-Alcázara, L., Camacho-Ibara, V.F., Souzab, A.J., Allenc, J.I., Torres, R., 2008. Modelling *Zostera marina* and *Ulva sp.* in a coastal lagoon. Ecol. Modell. 218, 354–366.

Broch, O., Slagstad, D., 2012. Modelling seasonal growth and composition of the kelp *Saccharina latissima*. J. Appl. Phycol. 24, 759–776.

Broch, O.J., Ellingsen, I.H., Forbord, S., Wang, X., Volent, Z., Alver, M.O., Handå, A., Andresen, K., Slagstad, D., Reitan, K.I., Olsen, Y., Skjermo, J., 2013. Modelling the cultivation and bioremediation potential of the kelp *Saccharina latissima* in close proximity to an exposed salmon farm in Norway. Aquacult. Environ. Interact. 4, 186–206.

Carboni, S., 2013. Research and Development of Hatchery Techniques to Opimize Juvenile Production of the Edible Sea Urchin, Paracentrotus lividus (Ph.D. thesis). University of Stirling, UK.

Chopin, T., Buschmann, A.H., Halling, C., Troell, M., Kautsky, N., Neori, A., Kraemer, G.P., Zertuche-González, J.A., Yarish, C., Neefus, C., 2001. Integrating seaweeds into marine aquaculture systems: a key toward sustainability. J. Phycol. 37, 975–986.

Coffaro, G., Sfriso, A., 1997. Simulation model of *Ulva rigida* growth in shallow water of the Lagoon of Venice. Ecol. Modell. 102, 55–66.

Cohen, I., Neori, A., 1991. *Uloa lactuca* biofilters for marine fishpond effluents. Bot. Mar. 34, 475–482.

Cook, E.J., Kelly, M.S., 2007. Enhanced production of the sea urchin *Paracentrotus lividus* in integrated open-water cultivation with Atlantic salmon *Salmo salar*. Aquaculture 273 (4), 573–585.

Cranford, P.J., Reid, G.K., Robinson, S.M.C., 2013. Open water integrated multi-trophic aquaculture: constraints on the effectiveness of mussels as an organic extractive component. Aquacult. Environ. Interact. 4, 163–173.

Droop, M., 1968. Vitamin B12 and marine ecology. IV. The kinetics of uptake, growth and inhibition in Monochrysis Lutheri. J. Mar. Biol. 48, 689–733.

Fasham, M.J.R., Ducklow, H.W., McKelvie, S.M., 1990. A nitrogen based model of plankton dynamics in the oceanic mixed layer. J. Plankton Res. 48, 591–639.

Fernandez, C.M., Caltagirone, A., 1994. Growth rate of adult *Paracentrotus lividus* in a lagoon environment: the effect of different diet types. In: David, B., Guille, A., Feral, J.P., Roux, M. (Eds.), Echinoderms through Time. Balkema, Rotterdam, pp. 655–660.

Ferreira, J.G., Saurel, C., Ferreira, J.M., 2012. Cultivation of gilthead bream in monoculture and integrated multi-trophic aquaculture. Analysis of production and environmental effects by means of the FARM model. Aquaculture 358–359, 23–34.

Fujita, R.M., 1985. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. J. Exp. Mar. Biol. Ecol. 92, 283–301.

Granada, L., Sousa, N., Lopes, S., Lemos, M.F.L., 2015. Is integrated multitrophic aquaculture the solution to the sectors' major challenges? – a review. Rev. Aquacult. 6, 1–18. http://dx.doi.org/10.1111/raq.12093.

Grant, J., Filgueira, R., 2011. The application of dynamic modeling to prediction of production carrying capacity in shellfish farming. In: Shumway, S.E. (Ed.), Shellfish Aquaculture and the Environment. John Wiley & Sons, Chichester, pp. 135–154.

Grosjean, P., Spirlet, Ch, Gosselin, P., Vaïtilingon, D., Jangoux, M., 1998. Land-based closed cycle echiniculture of Paracentrotus lividus (Lamarck) (Echinoidea: Echinodermata): a long-term experiment at a pilot scale. J. Shellfish Res. 17 (5), 1523–1531.

Hughes, A.D., Kelly, M.S., 2001. Integrated Multi-trophic Aquaculture. Scottish Association of Marine Science, p. 6. http://www.sarf.org.uk/cms-assets/documents/28926-823833.current-state-of-integrated-aquacultur.

Iwama, G.K., Tautz, A.F., 1981. A simple growth model for Salmonids in Hatcheries. Can. J. Fish. Aquat. Sci. 38 (6), 649–656.

Jiang, Z.J., Fang, J.G., Mao, Y.Z., Wang, W., 2010. Eutrophication assessment and bioremediation strategy in a marine fish cage culture area in Nansha Bay. J. Appl. Phycol. 22, 421–426.

Jobling, M., 2003. The thermal growth coefficient (TGC) model of fish growth: a cautionary note. Aquacult. Res. 34, 581–584.

Kelly, M.S., Brodie, C.C., McKenzie, J.D., 1998. Somatic and gonadal growth of the sea urchin *Psammechinus miliaris* (Gmelin) maintained in polyculture with the Atlantic salmon. J. Shellfish Res. 17, 1557–1562.

Kooijman, S.A.L.M., 1986. Energy budgets can explain body size relations. J. Theor. Biol. 121, 269–282.

Kooijman, S.A.L.M., 2008. Dynamic Energy Budget Theory for Metabolic Organization, third ed. CUP, Cambridge.

Kooijman, S.A.L.M., 2014. Add_my_pet: Paracentrotus lividus. URL: http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/html/Paracentrotus_lividus.html (accessed 21.05.14.).

Lapointe, B.E., Tenore, K.R., 1981. Experimental outdoor studies with *Ulva fasciata Delile I*. Interaction of light and nitrogen on nutrient uptake, growth and biochemical composition. J. Exp. Mar. Biol. Ecol. 92, 135–152.

Lobban, C.S., Harrison, P.J., 1994. Seaweed Ecology and Physiology. CUP, Cambridge.

Luo, M.B., Liu, F., Xu, Z.L., 2012. Growth and nutrient uptake capacity of two co-occurring species, *Ulva prolifera* and *Ulva linza*. Aquat. Bot. 100, 18–24.

Marine Harvest, 2012. Salmon Farming Industry Handbook. http://www.marineharvest.com/PageFiles/1296/2012%20Salmon%20Handbook%2018.juli_h%C3%B8y%20tl.pdf (accessed 30.04.14).

Marine Scotland, 2013. Draft Seaweed Policy Statement Consultation Paper. http://www.scotland.gov.uk/Publications/2013/08/6786 (accessed 01.06.14).

Neori, A., Cohen, I., Gordin, H., 1991. Ulva lactuca biofilters for marine fishpond effluents. II. Growth rate, yield and C: N ratio. Bot. Mar. 34, 483–489.

Neori, A., Chopin, T., Troell, M., Buschmann, A.H., Kraemer, G.P., Halling, C., Shipgel, M., Yarish, C., 2004. Integrated aquaculture: rationale, evolution and state of the art emphasizing seaweed biofiltration in modern mariculture. Aquaculture 231, 361–391.

Nizzolli, D., Welsh, D.T., Bartoli, M., Viaroli, P., 2005. Impacts of mussel (Mytilus galloprovincialis) farming on oxygen consumption and nutrient cycling in a eutrophic coastal lagoon. Hydrobioligia 550, 183–198.

Nunes, J.P., Ferreira, J.G., Gazeau, F., Lencart-Silva, J., Zhang, X.L., Zhu, M.Y., Fang, J.G., 2003. A model for sustainable management of shellfish polyculture in coastal bays. Aquaculture 219, 257–277.

Perrot, T., Rossi, N., Ménesguen, A., Dumas, F., 2014. Modelling green macroalgal blooms on the coasts of Brittany, France to enhance water quality management. J. Mar. Syst. 132, 38–53.

Pietrak, M.R., Molloy, S.D., Bouchard, D.A., 2012. Potential role of *Mytilus edulis* in modulating the infectious pressure of *Vibrio anguillarum* on an integrated multi-trophic aquaculture farm. Aquaculture 326–29, 36–39.

Reid, G.K., Chopin, T., Robinson, S.M.C., Azevedo, P., Quinton, M., Belyea, E., 2013. Weight ratios of the kelps, Alaria esculenta and Saccharina latissima, required to sequester dissolved inorganic nutrients and supply oxygen for Atlantic salmon, *Salmo salar*, in integrated multi-trophic aquaculture systems. Aquaculture 408/409, 34–46.

Ren, J.S., Stenton-Dozey, J., Plew, D.R., Fang, J., Gall, M., 2012. An ecosystem model for optimising production in integrated multitrophic aquaculture systems. Ecol. Modell. 246, 34–46.

Sanderson, J.C., Dring, M.J., Davidson, K., Kelly, M.S., 2012. Culture, yield and bioremediation potential of *Palmaria palmata* (Linnaeus) Weber & Mohr and *Saccharina latissima* (Linnaeus) C. E. Lane, C. Mayes, Druehl & G. W. Saunders adjacent to fish farm cages in northwest Scotland. Aquaculture 354/355, 128–135.

Schuenhoff, A., Shpigel, M., Lupatsch, I., Ashkenazi, A., Msuya, F.E., Neori, A., 2003. A semi-recirculating, integrated system for the culture of fish and seaweed. Aquaculture 221, 167–181.

Shi, J., Wei, H., Zhao, L., Yuan, Y., Fang, J., Zhang, J., 2011. A physical-biological

coupled aquaculture model for a suspended aquaculture area of China. Aquaculture 318 (3–4), 412–424.
Skretting, 2015. Sustainable Economic Aquafeeds. http://www.skretting.com/Internet/SkrettingGlobal/webInternet.nsf/wprid/9EE28C6A30408348C125749500466A75/$file/10_05_06_SEA_eng.pdf (accessed 04.05.15).
Solidoro, C., Pecenik, G., Pastres, R., Franco, D., Dejak, C., 1997. Modelling macroalgae (*Ulva rigida*) in the Venice lagoon: model structure identification and first parameters estimation. Ecol. Modell. 94 (2–3), 191–206.
Soto, D., Aguilar-Manjarrez, J., Hishamunda, N., 2008. Building an ecosystem approach to aquaculture. In: FAO/Universitat de les Illes Balears Expert Workshop. 7–11 May 2007, Palma de Mallorca, Spain. FAO Fisheries and Aquaculture Proceedings. No. 14. Rome, FAO.
Steele, J.H., 1962. Environmental control of photosynthesis in the sea. Limnol. Oceanogr. 7, 137–150.
Tomas, F., Romero, X., Turon, X., 2005. Experimental evidence that intra-specific competition in seagrass meadows reduces reproductive potential in the sea urchin *Paracentrotus lividus* (Lamarck). Sci. Mar. 69, 475–484.
Troell, M., Halling, C., Neoric, A., Chopind, T., Buschmanne, A.H., Kautskya, N., Yarishf, C., 2003. Integrated mariculture: asking the right questions. Aquaculture 226, 69–90.
Turon, X., Giribet, G., López, S., Palacín, C., 1995. Growth and population structure of Paracentrotus lividus (Echinodermata: Echinoidea) in two contrasting habitats. Mar. Ecol. Prog. Ser. 122, 193–204.
Wang, X., Olsen, L.M., Reitan, K.I., Olsen, Y., 2012. Discharge of nutrient wastes from salmon farms: environmental effects, and potential for integrated multi-trophic aquaculture. Aquacult. Environ. Interact. 2, 267–283.
Wang, X., Broch, O.J., Forbord, S., Handå, A., Skjermo, J., Reitan, K.I., Vadstein, O., Olsen, Y., 2013. Assimilation of inorganic nutrients from salmon (*Salmo salar*) farming by the macroalgae (*Saccharina latissima*) in an exposed coastal environment: implications for integrated multi-trophic aquaculture. J. Appl. Phycol. 26 (4), 1869–1878.