Assessing the biotechnical feasibility of *Ulva* (seaweed) integration with *Tripneustes gratilla* (sea urchin) in a commercial-scale recirculating IMTA system: a farm-scale model approach

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Abstract

This study evaluated the environmental, production, and economic benefits of integrating the seaweed *Ulva* with the sea urchin *Tripneustes gratilla* in a commercial-scale recirculating IMTA (integrated multitrophic aquaculture) system. Key benefits include *Ulva*'s biofiltration of urchin farm effluent and its potential as feed for *T. gratilla*. A farm-scale model was developed to explore these benefits where a system consisting of 42 urchin tanks (8.5 m^3 each) and a 300 m^2 *Ulva* raceway under different feeding scenarios (fresh *Ulva*, formulated feed and a mix) was simulated. The model predicted that the urchin system emits an average of 28 g total ammonia nitrogen (TAN) per day. While the *Ulva* raceway could remove 100% of the TAN emitted, this quantity of TAN is insufficient to sustain *Ulva* growth leading to a net reduction of *Ulva* biomass. However, with design or management adjustments the nitrogen provided in the urchin feed, which is lost in the settled solids (sludge), could be utilized through mineralization for Ulva production, creating a highly circular and efficient IMTA system. The model also indicated that ammonia toxicity is unlikely to limit *T. gratilla* production, with predicted TAN levels below 0.018 mg/L. The system's projected productivity is substantial, with an estimated annual yield of 323 t WW/ha for whole urchins and 72 t WW/ha for gonads, outperforming other high-value invertebrate species. This productivity suggests that *T. gratilla* aquaculture could become a viable and profitable industry, with this model offering critical insights for its sustainable development.

Keywords: IMTA, biofiltration, aquaculture, *Ulva*, sea urchins, circularity, recirculating

1 Introduction

The promotion of sustainable aquaculture development, treating and valorising farm effluent (wastewater), is essential to minimize environmental impact and optimize nutrient use. One effective approach is the development of co-culture or integrated multi-trophic aquaculture (IMTA) systems (Granada et al., 2016; Hossain et al., 2022; Khanjani et al., 2022; Troell et al., 2009). Aquaculture farm effluents when released into the ecosystems may induce potential environmental impact such as eutrophication. These nutrients can be assimilated and thus bioremediated by primary producers such as macroalgae. Numerous studies have demonstrated the benefits of integrating algae in IMTA systems in open water, flow-through, or recirculating systems (Aníbal et al., 2014; Bartoli et al., 2005; Ben-Ari et al., 2014; Bolton et al., 2016; Grosso et al., 2021; Shpigel et al., 2018).

In South Africa, commercial success has been achieved with *Haliotis midae* (abalone) and *Ulva lacinulata (*green macroalgae) large-scale recirculating IMTA farms (Bolton et al., 2009; Nobre et al., 2010; Robertson-Andersson, 2003). In this setup, effluent from abalone tanks is directed into adjacent *Ulva* raceways, where the macroalgae assimilate dissolved nutrients, allowing bioremediated water (50-75%) to be recirculated back to the abalone tanks. The *Ulva* grows rapidly in the high-nutrient effluent and can be used as feed for the abalone. Additionally, *Ulva* has been found to improve the bacteria microbiome of abalone farms (de Jager et al., 2024). This approach directly addresses the key economic and environmental challenges of land-based aquaculture: wastewater management, feed requirements and disease.

The success of abalone-*Ulva* IMTA farms in South Africa has subsequently inspired similar systems with different species, such as the urchin-*Ulva* system assessed in this study. *Tripneustes gratilla* has been identified as a very promising candidate for aquaculture due to its fast growth rates and high economic value for the "uni" (sea urchin gonad) trade (Toha et al., 2017). *Tripneustes gratilla* inhabits shallow reef areas and seagrass beds across tropical and subtropical regions of the Indo-Pacific, where it is commercially harvested in the Philippines, Indonesia, and Japan (Toha et al., 2017). Furthermore, it has been shown to be a suitable candidate for co-culture with *Ulva* in a land-based IMTA system (Cyrus, 2013; Shpigel et al., 2018). Producing *Ulva* on-site to directly feed the urchins could substantially reduce the need for expensive artificial pellet feeds, made using a large proportion of wild-caught fish meal, thereby reducing operational costs and off-site environmental impacts. Fresh *Ulva* has been found to be an adequate feed to increase diameter and height of *T. gratilla* during grow-out, however, gonad quality and quantity are maximised when *T. gratilla* is fed a specific formulated feed known as "20U" (Cyrus, 2015). This feed incorporates 20% dried *Ulva lacinulata* to promote palatability and maintain optimal colouration of gonads during this enhancement phase, hence its name "20U". Beyond feed provision, the co-culture of *Ulva* with sea urchin can provide environmental benefits through the bioremediation of urchin effluent, potentially outperforming conventional filtration systems (Copertino et al., 2009). This biofiltration and recirculation strategy also reduces electricity costs related to pumping (Nobre et al., 2010) and heating or cooling, depending on climatic requirements. While pilot-scale *T. gratilla-Ulva* IMTA systems have been built and operated successfully in South Africa and Israel (personal observation, 2021, Shpigel *et al.*, 2018), it has not yet occurred on a commercial-scale.

While recirculating IMTA systems in general are more efficient than traditional monoculture aquaculture systems, they have not yet been widely adopted (Troell *et al.*, 2009; Hossain et al., 2022). This lack of uptake is partly because of recirculating IMTA systems' level of complexity (Hughes and Black, 2016; Kleitou *et al.*, 2018), where a fine balance between the various organisms cultured within the system is required to achieve functionality. This balance is most fundamentally an equilibrium between the nutrient emissions from the fed organisms and the nutrient assimilation of the extractive organism. The performance and feasibility of IMTA systems depend on the adequate biomass ratio among co-farmed species (Reid et al. 2012). For example, if the degree of biofiltration of the extractive organism, recirculation and/or flow rates are not sufficient, nutrients will accumulate in the system and could reach toxic levels. On the contrary, if the fed organism does not provide sufficient nutrients to sustain the population of extractive organisms, then this population can crash, leading to issues such as severely reduced biofiltration or increased eutrophication. To establish this equilibrium, conditions such as flow rates, system design, and the biomass ratio of fed to extractive organisms need to be carefully managed.

Determining these optimal culture conditions to achieve this equilibrium is fundamental to the success of a recirculating IMTA system. Typically, these conditions are established via a trial-and-error method, where a physical IMTA system is constructed, conditions are implemented and adapted, and/or the system is reconstructed until equilibrium is observed. This can be highly inefficient in terms of resources, time and livestock. A considerably more efficient, replicable, and scalable method to determine optimal conditions that balance species of varying trophic levels is through mathematical farm-scale simulation modelling (Chary *et al.*, 2022; Duarte *et al.*, 2003; Jiménez del Río *et al.*, 1996; Ren *et al.*, 2012). In engineered and controllable ecosystems, such as land-based recirculating aquaculture systems, simulation models can provide a wide variety of additional uses (Cacho, 1997), offering valuable insight into the functional, environmental and economic feasibility of the proposed systems. Simulation models offer an opportunity for in-depth optimisation, all without having to build a physical pilot system.

The foundation of an IMTA farm-scale model should be based on the primary resource exchanged between the fed and extractive organisms. In many aquaculture systems, this resource is nitrogen, specifically total ammonia nitrogen (TAN), which is generally the first waste product from the fed organism to become toxic (Hargreaves, 1998). TAN, along with other dissolved nitrogen species, is often the first nutrient to limit algal growth in aquaculture (Neori et al., 1991). A simulation of TAN exchange between these reactors forms a TAN mass balance model, which helps identify where production limitations occur for both the fed and extractive organisms. This model could then be extended into a broader system framework which simulates the production processes and therefore becomes a farm-scale model (Chary et al, 2022). Economic parameters, such as the monetary value of urchins and the substitution of wild-caught fish with *Ulva* as feed, could also be integrated, creating a comprehensive bioeconomic model.

The main goal of this study is to use farm-scale modelling to determine the biotechnical feasibility of the proposed *T. gratilla*-*Ulva* IMTA system. Specifically, the study considers whether an *Ulva* raceway could provide complete biofiltration of TAN and produce a sufficient feed for production of *T. gratilla* in a land-based recirculating IMTA system, thereby replicating the success of integrated abalone-*Ulva* production systems in South Africa.

Explicitly, the objectives of this study were to determine:

1. The feasibility of the *Ulva* raceway as a biofilter for *T. gratilla* TAN emissions;
2. The feasibility of the *Ulva* raceway as a feed source for *T. gratilla*;
3. Potential for TAN accumulation within the *T. gratilla* system to reduce urchin production; and
4. The production of marketable product (urchin gonad).

While it has been found that fresh *Ulva* and the 20U formulated feed promote similar somatic growth rates of *T. gratilla*, the 20U feeds result in greater gonad quantity, therefore it has been suggested to feed the formulated feed for at least the last three months of the production cycle (Cyrus et al, 2015). However, the ideal feeding regime in terms of balancing nitrogen, feed requirements, economics and gonad production are not definitely known, thus three feeding scenarios were tested and compared:

A) fresh *Ulva* for the entire culture period,

B) an artificial feed specifically formulated for *T. gratilla* known as “20U” due to its 20% dried *Ulva* inclusion (fully described in Cyrus et al., (2014)) for the entire culture period, and

C) fresh *Ulva* for the grow-out period (four months) and the 20U formulated feed for the gonad enhancement period (three months).

2 Material and Methods

2.1 Conceptual farm design

The conceptual recirculating urchin-*Ulva* system used as a basis for developing the model in this study is based on the design of one of the commercial integrated abalone-*Ulva* 'clusters' at Sea Harvest Aquaculture's Buffeljags Abalone Farm in South Africa (Figure 1; www.vikingaquaculture.co.za). This is due to this system being commercially validated and accessible. In the abalone-*Ulva* and urchin-*Ulva* systems, the fed organisms (urchins or abalone) are the primary product of the farm, whereas the *Ulva* does not have any direct economic value but has indirect value as a feed, biofilter and promotes improved system health (Bolton et al., 2009; de Jager et al., 2024; Nobre et al., 2009; Robertson-Andersson, 2003). The conceptual system incorporates 42 fibreglass abalone tanks (6 × 1.8 × 0.8 m) to hold the urchins in baskets (20 baskets per tank) and an *Ulva* raceway (30 × 10 × 0.5 m). In the *Ulva* raceway, most of the water movement is driven by a large rotating paddle wheel.

[Figure 1]

Bioremediated water from the *Ulva* raceway flows is pumped directly into each urchin tank. Effluent water exits each urchin tank, from the opposite side of each tank inlet, and returns directly to the *Ulva* raceway, bypassing other tanks within the cluster. The flow rate of each urchin tank is 4 250 $l.h^{-1}$ (i.e., 0.5 full tank water turnovers per hour). This will result in the *Ulva* raceway receiving 178 500 $l.h^{-1}$ (i.e., 1.19 full raceway water turnovers per hour). These rates were chosen based on the minimum values that support high urchin survival in trials on the pilot scale urchin-*Ulva* IMTA system constructed at Buffeljags Abalone Farm (Checa

2024 et al.) and findings from other experiments (de Vos et al., 2024a, 2024b; Mos et al., 2012).

2.2 Overview of the urchin-*Ulva* farm-scale model

The urchin-*Ulva* farm-scale model is a simplified dynamic IMTA model composed of two modules, representing the simulated processes for each species (Figure 2):

Urchin module: an individual *T. gratilla* growth submodel is combined with a simple population dynamic submodel to predict population size and biomass at cohort and farm level. This allows for estimation of gonad production, feed requirements and TAN emissions; and

***Ulva* module**: estimates *Ulva* nitrogen assimilation and biomass production, given the light levels and TAN input from the urchin system.

[Figure 2]

The primary assumptions of this model are summarised in Table 1 and elaborated on in the Supplementary Material A.

Table 1. Outline of the primary assumptions made in the model, including values, concise descriptions, and corresponding references supporting each assumption. Further information can be found in Supplementary Material A.

Assumption	Value	Description/reason	Reference
Oxygen supply	Not limiting	*Tripneustes gratilla* have low oxygen consumption and high tolerance to low oxygen conditions	Mos et al., 2012
Temperature	25°C	Typical for equatorial/tropical regions suited for *T. gratilla* culture.	Dworjanyn et al., 2007
Salinity	35 ppm	Assumed not limiting for *Ulva* production.	Bews et al., 2021; Xiao et al., 2016
Light irradiance	2,500 µmol photons m^{-2} s^{-1}	Typical for equatorial regions.	Lüning, 1991
Photoperiod	12/12 hr	Typical for equatorial regions	
Initial *Ulva* stocking density	1 kg/m²	Optimal for *Ulva* protein content and production.	Neori et al., 1991

Seawater inflowing TAN concentration	0 mg/l	Negligible oligotrophic tropical waters, TAN derived from urchins and feed only.	Rees et al., 1999
Nitrate & phosphate influence	Not significant	For *Ulva* nitrate uptake inhibited by ammonia and phosphate not limiting. For urchins production of nitrate and phosphate is low.	de Vos et al., 2024b; Hadley et al., 2015; Ale et al., 2011; Björnsäter and Wheeler, 1990

2.3 Urchin module

2.3.1 Urchin individual growth submodel

Johnson's differential growth equation (Ricker, 1979) was applied to predict the growth of urchins (*T. gratilla*):

$$dS = \mathrm{k} * S_t * \mathrm{d}T(\mathrm{In}S_\infty - \mathrm{In}S_t)^2 \quad (1)$$

Where:

dS = urchin growth (test diameter, mm)

k = constant

S_t = initial urchin diameter (test diameter, mm)

dT = time (days)

S_∞ = asymptotic urchin test diameter

Parameters k (2.92) and S_∞ (90) were obtained from Dafni (1992), who fed *T. gratilla* under similar aquaculture conditions to those simulated in this study, i.e. at a temperature ranging from 20.7°C to 26.7°C and urchins were fed with *Ulva lactuca* (Dafni, 1992). As mentioned, feed types are not forcing variables of the Johnson's equation, therefore this same growth model was applied to the urchins, regardless of the feeding scenario.

The predictions of test diameter (S, mm) were then converted to mass (M, grams) using the following power function (Equation 2; Balisco, 2015):

$$M = 0.07334\left(\frac{s}{10}\right)^{2.6725} \quad (2)$$

2.3.2 Urchin population dynamics and biomass

To the best of our knowledge, no commercial urchin-*Ulva* IMTA systems are currently operational, therefore a production cycle had to be conceptualised for this study. This cycle is based on experience, findings and observations from the newly constructed urchin (*T. gratilla*)-*Ulva* pilot IMTA system at Buffeljags, laboratory trials at the Department of Fisheries, Forestry and Environment (DFFE) Marine Research Aquarium, and abalone-*Ulva* IMTA farms in South Africa (Checa et al., 2024).

The urchin population in each tank depends on the stocking density, mortality, and harvesting. The growth model suggests urchins (*T. gratilla)* will take seven months to reach market size (approximately 56 mm test diameter) from weaning (approximately 10 mm test diameter). If a cohort of weaned urchins is added each month and the seven-month-old cohort is harvested, there will be a total of seven cohorts in the production system at any given time. The number of tanks allocated to each cohort (Supplementary Material B) was determined through back calculation based on maximising the quantity of harvestable adult urchins given the total number tanks available (42), not exceeding a stocking density of 20% coverage of the internal surface area of the basket (de Vos et al., 2024a) and a mortality/culling rate of 36% over the culture cycle. This mortality rate was set to simplify the allocation of tanks per cohort. Lower mortality rates were observed in previous trials (de Vos et al., 2024a), but the higher rate used in this study also accounts for the culling of smallest individuals after grading.

Urchin biomass in each tank was estimated by multiplying the number of individuals by the average individual mass predicted. To ensure simplicity, it was assumed that there was no inter-individual variability of growth between urchins within a cohort. This greatly reduces the complexity of the model and its computation time (Chary *et al.*, 2022). Accounting for inter-individual variability is not necessary for the scope of this model.

The gonad production was estimated by multiplying the gonadosomatic index (GSI) by the total mass of the harvest urchin cohort. Two different average (± standard deviation) GSIs were assumed depending on the feed urchins were provided (Table 3).

2.3.3 Urchin feed requirements

The quantity of feed required per feeding event was determined by multiplying the total urchin biomass by the recommended percentage of the specific feed type. The amount and frequency of feeding were based on the maximum values for urchin feeding observed in earlier studies and on experience from the pilot farm (Cyrus et al., 2015; Shpigel et al., 2018; Shpigel and Erez, 2020, de Vos et al., 2024a). While the biomass of the growth model increases in a daily timestep, feed requirements were calculated on a weekly basis to reflect a more realistic and practical adjustment of feeding rations for a commercial farm.

2.3.4 *T. gratilla* total ammonia nitrogen (TAN) emission submodel

Generalised Additive Models (GAMs) were applied to describe and predict the TAN emission of *T. gratilla* culture systems for reasons explained in section 4.5. To construct and train the GAM model, data were collected from an experiment where 18 tanks were stocked with *T. gratilla* exposed to various feed types (fresh *Ulva* or pellets), feed quantity, exchange rates (turnover/h), stocking densities, size of urchins and number of urchins, as fully described in de Vos et al. (2024b).

An ensemble supervised learning method known as random forest analysis (Breiman, 2001) was applied to determine the extent of influence that the six explanatory variables (listed above) had on the TAN production in the training data, allowing for variable selection when creating the GAM model. Model selection utilised various tools including Akaike's Information Criterion, deviance explained, and the importance of individual variables determined by both the random forest analysis and biological understanding (Supplementary Material C). Based on this, the model used the following predictor variables:

- Time since the last feeding (in hours), differentiated by feed type (pellets or *Ulva*);
- The quantity of feed supplied relative to tank volume, which is a function of urchin stocking density (kg.m^{-3}); and
- Exchange rate of the urchin aquaculture system (turnovers per hour).

The GAM model operates on an hourly time step to estimate TAN concentration per tank as a function of time from feeding. This hourly time step is necessary as the TAN emissions vary greatly in the first few hours after feeding and therefore the model can be used to ensure

TAN concentration will not reduce *T. gratilla* production. A further description of the GAM can be found in Supplementary Material D.

2.3.5 External validation of *T. gratilla* submodels

Data from Cyrus et al. (2015a) was used to validate the individual growth model. This dataset included observed size (n = 282) from urchins with an approximate test diameter of 30 to 80 mm over 32 weeks, while being fed 20U pellets, fresh *Ulva* or a combination of the two diets. A dataset containing 2 987 paired urchin mass and test diameter measurements collected over the various urchin trials discussed in de Vos et al., (2024b) was used to validate the size to mass relationship.

TAN emission submodel was validated using data from an experimental trial which closely resembled the train data experiment but with larger scale systems (Supplementary Material E). Criteria used for model validation included the mean absolute percentage error (MAPE) and root-mean-square error (RMSE). Additionally, a regression method of model validation was applied to all the urchin submodels. The observed and predicted results were plotted against each other, and a straight line of best fit was created via ordinary least squares (OLS). A good model, where the predicted and observed values are similar, will result in the line of best fit having:

- A slope very near 1 (as the observed and predicted values would be directly proportional);
- the intercept would be near 0, as there would be no bias; and
- the coefficient of determination (R^2) value would be near 1, due to high correlation.

The coefficients and their associated standard errors are applied in a T-test or Wald-test to determine whether they differ significantly from their expected values (Jusup *et al.*, 2009). Based on this, the performance of models can be classified into one of the categories; “poor”, “fair”, “good” and “very good” (Supplementary Material F, Portilla and Tett, 2007).

2.4 *Ulva* module

The *Ulva* growth and nitrogen assimilation submodels described here are largely based on the model described by Solidoro *et al.* (1997). The specific growth rate of *Ulva* (μ_{growth}) is predicted using a basic multiplicative model (Equation 5), where the maximum observed specific growth rate (μ_{max}) is multiplied by the factor that is most limiting (Lehahn *et al.*, 2016; Martins and Marques, 2002; Solidoro *et al.*, 1997; Zollmann *et al.*, 2021). These limiting factors could be internal concentration of nutrients ($\mathrm{g(N)}$), light ($\mathrm{g(I)}$), temperature and/or salinity. This model assumes temperature and salinity to not be restrictive (Supplementary Material A). The parameter descriptions and the values used can be seen in Table 2 with equations and further description in Supplementary Material G.

Table 2. Parameters used in the *Ulva* growth and nitrogen assimilation submodels model and their sources.

Parameter	Description	Value	Source
μ_max	Observed maximum specific growth rate	0.416 $\mathrm{day^{-1}}$	Oca et al., 2019, Bendoricchio et al., 1994; de Guimaraens et al., 2005; Duke et al., 1989; Hadley et al., 2015; Menesguen and Salomon, 1988; Parker, 1981
λ	Specific rate of natural biomass loss (mortality and fragmentation)	0.066 $\mathrm{day^{-1}}$	Oca et al., 2019
K_I	Half-light saturation constant	20 µmol photons $\mathrm{m^{-2}\ s^{-1}}$	Chemodanov et al., 2019; Zollmann et al., 2021
PAR	Photosynthetically active radiation (ratio of sunlight suitable for photosynthesis)	0.43	Mõttus et al., 2013
K_0	Water light extinction coefficient	1.5 $\mathrm{m^{-1}}$	Oca et al., 2019

K_a	*Ulva* light extinction coefficient	0.01 m^2 gDW^{-1}	Oca et al., 2019
N_{min}	Minimum nitrogen content in *Ulva*	10 mg N g^{-1} DW	Cohen and Neori, 1991; Sfriso et al., 1987
N_{crit}	Critical nitrogen content in *Ulva*	20 mg N g^{-1} DW	Fujita, 1985
k_c	Growth constant	8	Solidoro et al., 1997
V_{max}	Maximum TAN uptake rate by *Ulva*	5.2 mg N g DW^{-1} h^{-1}	Solidoro et al., 1997
N_{max}	Maximum nitrogen content in *Ulva*	45 mg N g^{-1} DW	Cohen and Neori, 1991; Sfriso et al., 1987
K_{TAN}	Half-saturation constant for TAN	0.7 mg L^{-1}	Fujita, 1985; Solidoro et al., 1997

2.5 Scenarios for urchin feeding:

This study models three different feeding scenarios to evaluate the impact of feed type, frequency, and gonadosomatic index (GSI) on urchin growth and production. The following scenarios vary in the type of feed provided (*Ulva* or formulated pellets), the feeding schedule, and the resulting GSI (Table 3).

Table 3. Feeding scenarios (type and frequency) with corresponding gonadosomatic index (GSI) for *Tripneustes gratilla* that were tested in the urchin-*Ulva* farm scale model.

Scenario	Feed Type	Feeding Schedule	GSI	Description
A) *Ulva* only	Fresh *Ulva*	*Ulva* provided daily at a rate of 6% of the total urchin body mass in the given tank/basket	13.11 ±3.42% (de Vos et al., 2024a)	Urchins are fed only *Ulva* throughout the production cycle. GSI for *Ulva*-fed urchins is generally lower.
B) Pellets only	Formulated pellets	1.5% of urchin body mass four times per week	22.57 ±4.8% (Cyrus, 2015a; de Vos, unpublished)	Urchins are fed only formulated pellets for the entire production cycle, resulting in a higher GSI.
C) *Ulva* and pellet combination	*Ulva* for the first four months; pellets for the last three months	*Ulva*: 6% of urchin body mass daily (first four months); Pellets: 1.5% four times a week (last three months)	22.57 ±4.8% (Cyrus, 2015a; de Vos, unpublished)	Combines fresh *Ulva* for somatic growth early and pellets for gonad enhancement later, aiming to achieve a high GSI.

3 Results

3.1 Validation of models

3.1.1 Validation of urchin growth and diameter to mass sub-models

The predictions derived from the Johnson's differential growth equation (Dafni, 1992) were found to be on average 13.61% lower (i.e., 7.71 mm) than the observed values of *T. gratilla* growth from an external data source (n = 281), indicating underestimation of the predicted size. According to the slope (0.62), standard error (13.743), and R^2 (0.762) coefficients, Johnson's growth equation can be categorised as a fair model (further information at Supplementary Material H). The MAPE was 18.31%.

The predicted values for the diameter to mass conversion model underpredicted the mass by on average 0.67% (i.e., 0.87 g) when compared to the external data set. The MAPE was 0.1%. It should be noted that this data set was considerably larger (n = 2987). When the coefficients of the OLS fitted line were tested, it was similarly found that the slope (0.800), intercept (24.986) and R^2 (0.850) coefficients differ significantly from their null hypotheses and therefore this model is also classified as "fair" (Supplementary Material H). This concludes that the urchin production model therefore generally underestimates growth.

3.1.2 Validation of urchin TAN emission model

A comparison between observed and predicted values from an external data set provided evidence that the GAM model can provide accurate predictions of TAN emissions from *T.*

gratilla aquaculture systems of various sizes. RMSE was low (0.006). Regression between predicted and observed values indicated high correlation between these values ($R^2 = 0.713$, Supplementary Material H). The corresponding tests for the slope (0.961) and intercept (0.004) coefficients of the line of best fit resulted in it being categorised as a “very good” model (Supplementary Material H).

3.2 Model use

3.2.1 Urchin biomass production

At the beginning of each month, there would be nearly 9.5 t (364 000 individuals) of urchin in the system. By the end of each month, these urchins would have increased to a total biomass of 13,2 t (Figure 3). At this point, every cohort would need to be stocked down to retain the stocking density below 20% ISA coverage, aside from cohort seven (that would have been in the production cycle for seven months), which would be harvested. The minimum volumetric stocking density, 2.9 kg.m^{-3}, was on day zero of cohort one. This density gradually increased to reach a maximum on day 30 in cohort seven, which had a density of 42 kg.m^{-3}. At the end of each month there would be 3.22 t of harvestable whole urchin regardless of feeding scenario. Therefore, the annual whole urchin harvest would be 38.64 t.

[Figure 3]

3.2.2 Scenario comparison: urchin gonad production, feed requirements and TAN emissions

At the end of each month there are 3.22 t of harvestable whole urchin regardless of feeding scenario. Therefore, the annual whole urchin harvest will be 38.64 t. In the scenario A (*Ulva* only), gonad production per month (±standard deviation) yielded 0.42± 0.1 t while in scenario B or C (pellets as finishing diets) it yielded 0.73± 0.15 t. The feed requirements for each scenario are demonstrated in Table 4.

Table 4. Monthly dry weight (DW) urchin feed requirements for the conceptual urchin-*Ulva* IMTA system for the three different feed scenarios. While Scenario A and C require fresh *Ulva*, it has been converted into dry mass, so values are more comparable. The pellets contain 20% dried *Ulva* (Cyrus 2015a).

Feeding scenario	Pellets (t DW, 20% *Ulva* inclusion)	Total *Ulva* (t DW)
A (Fresh *Ulva* only)	0.00	2.43
B (Pellets only)	2.57	0.51
C (*Ulva* then pellets)	1.33	0.98

The urchin production and TAN emission models show that, for all feeding scenarios, TAN concentrations in the combined water from all urchin tanks (into the *Ulva* raceway) fluctuate daily based on the time since the last feeding (Figure 4). The weekly increase reflects the increasing amount of feed, and this cycle repeats each month.

For Scenario A, where fresh *Ulva* is fed to all urchin cohorts, the average TAN concentration over the production cycle from the urchin system into the *Ulva* raceway is 0.012 mg/l. The minimum TAN concentration is 0.008 mg/l, observed an hour prior to each feeding in the first week of the production cycle (Figure 4). The maximum TAN concentration is 0.017 mg/l, observed 10 hours after feed is provided in the last week of the production cycle. The daily average nitrogen production from this urchin system, derived from TAN, was 41.51 g. The greatest TAN concentration within a single tank for this scenario was 0.018 mg/l.

When pellets are provided to all urchin cohorts (Scenario B), the TAN emission from the entire urchin system was on average 0.006 mg/l. While this average value is considerably lower than that of Scenario A, the fluctuations in TAN emission were considerably higher with total system maximum of 0.023 mg/l and minimum of -0.005 mg/l. The maximum value was observed an hour after feeding and is depicted as a spike on top of the crest (Figure 4). A maximum TAN concentration within a single tank for this scenario was 0.027 mg/l, from cohort seven, one hour after feeding and in the last week of the production cycle. The average daily TAN derived nitrogen production of the urchin system effluent when fed pellets was 20.708 g per day. The TAN concentration of Scenario C, where a combination of fresh *Ulva* and pellets are fed, shows a similar pattern and values to that of Scenario B.

[Figure 4]

3.2.3 *Ulva* nitrogen assimilation and growth

The results of the *Ulva* assimilation and growth model indicated that the 300 m^2 raceway is more than sufficient to remove all the TAN emitted from the urchin system. Scenario A, which has effectively double the TAN input of Scenarios B and C (0.012 mg/l and 0.06 mg/l average respectively), also has effectively double the nitrogen uptake (Figure 5). The spatial TAN assimilation rate for Scenario A ranges between 0.187 to 0.390 g.m^{-2}.d^{-1}, while for Scenarios B and C, this metric ranges between 0.088 and 0.193 g.m^{-2}.d^{-1}. To sustain these values, the total nitrogen uptake for the entire raceway of all scenarios is equal to or exceeds the TAN emission from the urchin for approximately the first 11 days of the production cycle, where, for example, *Ulva* total N uptake on day 11 for Scenario A is 57g, while the urchins only provide 42g of N. This discrepancy in nitrogen uptake of the *Ulva* and nitrogen supply from the urchins is made up by the internal nitrogen stores within the *Ulva*.

[Figure 5]

The urchin production system does not provide enough TAN to support *Ulva* growth in a 300 m^2 *Ulva* raceway, regardless of feeding scenario. The total *Ulva* biomass increases for the first 11 days for Scenario A and 10 days for Scenarios B and C (Figure 6). Both achieve a total biomass of approximately 57 kg DW, which translates to a stocking density of about 1.4 $kg.m^{-2}$ WW. However, this growth is not sustained and, after 20 days into the production cycle, the *Ulva* biomass is below the initial stocking density. This means that by the end of the production cycle there will be a net loss of *Ulva*. The corresponding curve of the *Ulva*'s internal nitrogen composition (N_{int}; Figure 6) largely explains the rise and decline in *Ulva* growth. This model assumed the initial nitrogen composition of *Ulva* is 20 mg N. g^{-1} DW, and therefore has internal nitrogen stores that can support growth. This changes on day 11 or 10 (for Scenarios A or B and C respectively), where the internal nitrogen content reaches the minimum value of 10 mg N. g^{-1} DW, at which point growth is not supported and the natural biomass loss results in a net decline in biomass (Figure 6).

[Figure 6]

To indicate the maximum potential of this *Ulva* raceway, the light limited growth was calculated. If a 300 m² *Ulva* raceway is stocked to 1 kg WW.m^{-2} with light levels typical of a tropical region and is not nitrogen limited (only light limited), this would result in a constant specific growth rate (SGR) of 0.299. Under these conditions, the raceway would yield 362 kg DW per production cycle (month) if harvested daily to maintain the *Ulva* at the density of 1 kg.m^{-2}. The amount of feed that a 300 m^2 *Ulva* raceway could produce relative to the *Ulva* requirements of the three different feed ratios are 14.91%, 71.05% and 36.98% for scenarios A, B and C, respectively.

4 Discussion

4.1 The feasibility of the *Ulva* raceway as a biofilter for urchin TAN emissions

TAN emissions predicted from urchins were the highest in the Scenario A (average of 0.138 g TAN.m^{-2}.day^{-1}), however this is below assimilation capacity of the *Ulva* raceway. TAN removal capacity of *Ulva* can range from 0.4 to 7.4 g m^{-2}.day^{-1} (Msuya and Neori, 2008). Thus, this model indicates that while a 300 m^2 *Ulva* raceway would be capable of removing all urchin emitted TAN from this urchin production system, a smaller unit would be sufficient and could allow more farm area to be dedicated to urchin production.

Reducing the size of the *Ulva* raceway may, however, be technically unfeasible. If a conservative TAN removal rate of 2 g m^{-2}.d^{-1} is assumed (Ben-Ari *et al.*, 2014), a raceway of about 21 m^2 would be capable of removing the TAN from Scenario A. This is unlikely to be practical because if other variables, specifically flow rates in the urchin tanks, remain constant the turnover rate of the raceway would be 17.2 h^{-1}. The turbulence would be severe and, while not tested, it seems unlikely that the *Ulva* would be productive in this environment.

Reducing exchange rates and/or increasing urchin stocking densities could justify the size of the *Ulva* raceway. This suggests that sea urchin production could be higher or require lower pumping costs, without the risk of TAN toxicity. These changes could potentially enhance farmers' profits. However, further experimentation is necessary before implementing these adjustments, as other factors, such as the system’s carbonate chemistry (Mos et al., 2015; Shpigel and Erez, 2020), may negatively affect production. While the *Ulva* raceway can remove all the TAN produced by the urchins, modifications to the system would be required to optimize efficiency.

4.2 The feasibility of the *Ulva* raceway as a feed source for urchin production

The model predicted a net loss of *Ulva* biomass over the monthly production cycle without harvesting, due to the mismatch between the TAN supplied by the urchins and the *Ulva's* nitrogen requirements. This decline in *Ulva* biomass suggests that no *Ulva* would be available to feed the urchins under the current system configuration. Consequently, the model indicates that the *Ulva* raceway, as it stands, would not be a feasible food source for the urchins. However, the following basic mass-balance calculations show that the urchins can provide sufficient nitrogen, suggesting that with modifications to the system, the *Ulva* raceway could potentially supply a significant amount of feed for the urchins and be a suitable biofilter.

If nitrogen was not limited, the 300m^2 raceway could produce substantial amount of *Ulva.* The light-limited *Ulva* production submodel indicated the production could be 0.362 t DW per month. This production rate (43g DW m^{-2} d^{-1}) is very similar to what is observed in real systems (Ben-Ari *et al.*, 2014; Mata *et al.*, 2010; Mata and Santos, 2003; Msuya and Neori, 2008; Neori *et al.*, 1991) and likely could still be increased with stocking density and harvesting optimisation. While this light-limited *Ulva* production would not completely fulfil the *Ulva* demand for any of the feeding scenarios, it would still supply relatively substantial amounts, up to 71.05% (for Scenario B), thus providing economic and environmental benefits mentioned in the introduction. This implies the most practical feeding scenario is Scenario B, where only the formulated feed (with 20% *Ulva* inclusion) is supplied to all urchin cohorts. Alternatively, if the 0.362 t DW *Ulva* per month (light-limited *Ulva* production) was formulated into pellets, they would have an *Ulva* inclusion level of 14%, instead of the recommended 20%. There is evidence that this 14% inclusion would not reduce urchin production compared to the 20% inclusion (Cyrus *et al.*, 2014). This indicates the *Ulva* raceway does have the ability to provide a substantial feed source for the urchins, if nitrogen is not limited.

To produce 0.362 t DW *Ulva* per month would require at least 7.24kg of nitrogen per month (where $N_{int} = N_{crit}$). This is considerably more nitrogen (in the form of TAN) than the nitrogen emission model predicted (1.16, 0.58 and 0.64 kg TAN month^{-1} for Scenarios A, B, and C respectively). However, the monthly nitrogen inputs of each urchin feeding scenario (48.71, 105.84, and 74.2 kg N month^{-1} for Scenarios A, B, and C respectively) well exceeds the nitrogen required to sustain this light-limited *Ulva* production. Therefore, the TAN derived nitrogen predicted to be emitted from the urchin system only accounts for 2.39, 0.55 and

0.86% of the inputted feed nitrogen for Scenarios A, B, and C respectively. As intended, the urchins will retain some of this nitrogen. It is not known how much will be retained by *T. gratilla*, but another species of urchin, *Paracentrotus lividus,* has a nitrogen retention rate ranging from 3.14% to 10.53% (Lourenço *et al.*, 2020). This implies that at least 85% of the inputted nitrogen not retained by the urchins or excreted as TAN thus currently unaccounted for in the system.

The potential remaining pathways of the inputted nitrogen are other dissolved nitrogen species (nitrate *etc.*), nitrogen loss (effectively *in situ* biofiltration) and particulate nitrogen (sludge). De Vos et al. (2024b) found no evidence of nitrate emissions from urchins fed pellets, but those fed *Ulva* did emit nitrate. As a crude calculation, urchins fed *Ulva* emitted nitrate-nitrogen at a rate of 0.00365 mg N-NO_3 per g urchin WW per day, resulting in a maximum system-wide emission of 48.18 g N-NO_3 per day in the final week of production (Scenario A). While slightly higher than TAN-N emissions, this is only 19% of the nitrogen required for light-limited *Ulva* production. Despite *Ulva*'s ability to assimilate both TAN and NO_3, there is a lack of evidence that *T. gratilla* effluent can support significant Ulva production in this farm design. Removal of nitrogen within the urchin tank is possible and has been observed to various degrees in other aquaculture systems via the microbial community (Fu *et al.*, 2015) along with/or denitrification (Hargreaves, 1998; van Rijn *et al.*, 2006). However, de Vos et al., (2024b) did not provide clear evidence of any nitrogen removal by the tank, suggesting if the urchin tank does remove nitrogen, it may not be to a great extent.

The most apparent sink for the unaccounted feed-derived nitrogen of this system is via settled or suspended particulates. While further research should be conducted to confirm this, this seems most likely as there is does not seem to be another major pathway (for reasons described above) and the accumulation of settled particulates (sludge) has been shown to have a strong influence on nitrogen emissions (de Vos et al., 2024b). *Ulva* cannot assimilate solids, such as organic nitrogen. Therefore, nitrogen in this state cannot be utilised and, if dealt with incorrectly, could negatively impact the environment. Overall, while the *Ulva*-urchin farm-scale model predicts that the current system configuration does not provide sufficient TAN for sustainable *Ulva* production, there is clear indication there is sufficient nitrogen within the system's nitrogen budget to support substantial *Ulva* production. However, the system design will need to be adjusted to include a means of mineralizing the particulate nitrogen into a dissolved form which can be assimilated by the *Ulva*. This has been achieved in freshwater aquaponic systems and there has been development in applying this to marine systems (Goddek et al., 2018). If this enhanced circularity is achieved, the *Ulva* raceway could be an adequate feed source for the sea urchins yet still provides sufficient biofiltration.

4.3 Potential for TAN toxicity within the *Urchin* system

There is evidence that TAN levels would not negatively impact urchin production on the conceptual farm. The maximum predicted TAN concentration in an urchin tank across all feed scenarios was 0.018 mg/l. To estimate a worst-case scenario, one could assume this maximum TAN concentration occurred concurrently with a high pH 8.5. These environmental conditions would result in a free (un-ionised) ammonia nitrogen (FAN) concentration of 0.002 mg/l. This level is well below the FAN level (0.016 mg/l) that reduced growth (but with no mortalities) *of Strongylocentrotus droebachiensis* (Siikavuopio et al., 2004), which is the best indication available of ammonia toxicity of urchins. Therefore, it can be concluded that there is no evidence *T. gratilla* will be negatively affected by ammonia levels in this aquaculture system.

It is important to note that while nitrogen accumulation is unlikely to reduce urchin production, there are other water quality parameters, beyond the scope of this model, that may negatively affect urchin growth. Carbon dioxide specifically is most likely to be limiting for urchin production due to its negative impact on shell calcification (Mos *et al.*, 2015; Shpigel and Erez, 2020). The extent of this limitation could be modelled, and various strategies could be taken to reduce its effects. One of these strategies could be the biofiltration of *Ulva*. Regardless of the carbon chemistry, there is evidence the production of urchins in this conceptual farm is realistic because these specific conditions (stocking densities, flow rates *etc*) have been tested empirically (de Vos et al, 2024a, de Vos et al 2024b).

4.4 Estimation of *Tripneustes gratilla* production

This *T. gratilla-Ulva* IMTA system is estimated to produce 0.42 and 0.73 t of urchin gonad per month if fed *Ulva* and formulated feed as a finishing diet respectively. When compared to the aquaculture of other benthic species, production of *T. gratilla* with in this system appears high. This conceptual IMTA farm occupies 1 200 m^2 of land area (including the *Ulva* raceway and spaces between tanks) and the spatial gonad production would be ca. 42 and 73 t WW.ha^{-1}.$year^{-1}$ for the finishing diets of *Ulva* (Scenario A) and pellets (Scenario B and C) respectively. This yield of marketable product is high when compared to sea cucumber farming. Sea cucumbers cultured in ponds are reported to yield 3 t DW.ha^{-1} .year^{-1} (Brown and Eddy, 2015) and sea cucumber ranching beneath mussel beds is expected to yield 0.75 t DW.ha^{-1}.year^{-1} (Brown and Eddy, 2015). A more direct comparison can be made with abalone, which are cultured in effectively the same (intensive) system. The predicted production of whole urchins per water surface area (farm area occupied by urchin tanks) is 323.26 t WW.ha^{-1} while whole abalone production is calculated to be 135.29 t WW.ha^{-1}.year^{-1} based on values from Cloete (2009). This suggests *T. gratilla* farm in intensive systems could achieve much greater yields relative to other high value invertebrates. However, market research and economic feasibility analysis is required before this species can be deemed financially sustainable.

4.5 Regression model to predict TAN emissions

The production of TAN by fed organisms in aquaculture is frequently predicted using mechanistic models such as nitrogen retention or bioenergetic models (Chary *et al.*, 2022). These models rely on understanding, describing and formalising the underlying processes that influence the outcome. There are two reasons this approach is not used in this study. As *T. gratilla* is a new aquaculture candidate species there is data scarcity and thus the required parameters for these mechanistic models are largely not available. For the retention model specifically, two important parameters could not be determined. The digested nitrogen (nitrogen retained by the urchin for growth) and nitrogen retention apparent digestibility coefficient (ADC) for *Ulva* has not been clarified in the literature. Furthermore, these input variables could not be determined during the data collection period of this study for various reasons, including unavailability of juveniles. The second reason this family of models, and specifically nitrogen retention, is not utilized is due to difficulties of creating an accurate model. This is demonstrated by TAN production rates, based on nitrogen emission models, for the same species differing by a factor of 10 in the literature (Wheaton *et al.*, 1994). This is not surprising as there are numerous highly complex factors which have non-linear and interacting effects on TAN emission (de Vos et al., 2024b; Yu et al., 2021). Therefore, to get accurate TAN emission predictions using a mechanistic approach would likely require separating, quantifying, understanding and accurately predicting the influence of each factor (such as microbial communities), as well as the interactions between all factors.

TAN emissions of *T. gratilla* were predicted with generalised additive models (GAMs). GAMS are a “black box” approach that uses an empirical regression model. While countless factors influence TAN, the designer and manager of the aquaculture facility only has control of relatively few factors (such as stocking density, flow rate, feed quantity, sludge removal *etc*). Therefore, these controllable factors are examined as dependent variables in a regression model with the independent variable being TAN emissions. GAMs create a response variable which is dependent linearly on smoothing functions of the predictor variables (Hastie, 1992). The linearity of the model allows for easy interpretation, while the ability to regularize the predictor functions reduces the probability of overfitting (Wood, 2006). A similar approach has been shown to accurately predict TAN concentration in *Ctenopharyngodon idellus* (grass carp) pond aquaculture (Yu *et al.*, 2021) and nitrogen emissions from cage aquaculture of various finfish species (Islam, 2005). The close alignment between observed and predicted TAN levels in this study demonstrates the model's effectiveness and suggests its suitability for similar applications in future research.

4.6 Improvements of the urchin-*Ulva* farm-scale model

As might be argued in the case of all models, this model could be more sophisticated. Also applicable to the model is the statement, “the key to a model's usefulness is leaving out the unimportant factors and capturing the interactions between the important factors” (Ford and Ford, 1999). Importantly, the model has achieved its goal and objectives with a majority of the submodels being validated within this study (in the case of the urchin module) or in other studies (for the *Ulva* module). It appears very unlikely that a more sophisticated and/or accurate model would change the general conclusions drawn here.

However, if this model was used for different objectives, particularly those related to production optimisation, the following improvements are recommended:

- As mentioned, the carbonate chemistry is most likely the first parameter to limit *T. gratilla* production. If a model was developed to predict the increase of $C0_2$ and decrease of bicarbonates in a *T. gratilla* aquaculture system it could greatly assist with determining optimal flow rates (volumetric), stocking density and necessary mitigation strategies (such as *Ulva* biofiltration).
- Microbial communities have been shown to have a strong influence of nutrient loads in aquaculture (Bentzon-Tilia *et al.*, 2016) and there is evidence IMTA can modulate the microbiome in a manner which will enhance production (de Jager, 2021; Macey et al., 2022). The impact of the microbiome has important potential benefits in IMTA and could be modelled to quantify them (Fu *et al.*, 2015).
- There is evidence that the regression model provides accurate predictions of TAN emissions, even from tanks of a considerably larger scale. However, it is still advised

to continuously validate this model with external scale-appropriate data, especially if these data can be sourced from a functioning *T. gratilla* farm. Furthermore, additional training data can be added to this GAM model to further increase its accuracy and applicability.

- Net underprediction of this growth model suggests true stocking densities may be greater than predicted. While this may result in greater than expected production, this could also have detrimental effects if it was used for system optimisation because TAN levels could be greater than expected and more biofiltration could be required. This contribution has not focused on optimisation but rather feasibility, where even if the stocking density was 13.11% higher, it would still not support considerable *Ulva* growth. Thus, for these objectives it does not appear necessary to reinvent the wheel with new production models as none of the major conclusions would differ.

4.7 Conclusion

. In conclusion, this study demonstrates the potential feasibility of integrating *Ulva* with *Tripneustes gratilla* in a commercial-scale IMTA system. The model predicts that an *Ulva* raceway can effectively remove TAN emissions from sea urchin farming but as the system is currently configured, it would not sustain *Ulva* biomass growth. With design adjustments to improve nitrogen availability, such as enhanced mineralization of settled solids, this integrated system could not only achieve efficient biofiltration but also produce substantial amounts of seaweed feed, making it a circular and self-sustaining system.

The low predicted TAN levels across feeding scenarios indicate that the risk of ammonia toxicity to urchins is minimal. Furthermore, the model suggests that the productivity of *T. gratilla* in this system could exceed that of other high-value invertebrates, offering a promising economic opportunity for sea urchin aquaculture.

By consolidating extensive data, this farm-scale model provides not only valuable insight into the design requirements for this urchin-*Ulva* system, but it can also serve as a foundation for more specific economic and environmental analyses, lifecycle assessments, and the development of tailored IMTA systems. Modelling tools such as this play an essential role in guiding decision-making, optimizing system design, and promoting sustainable aquaculture practices, ultimately supporting the establishment and expansion of an environmentally friendly and economically viable sea urchin industry.

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6 Data statement

The data supporting the findings of this study are available upon request. Due to the context-specific nature of the data, direct access through a repository is not provided the authors would like to directly explain the data. However, access will be granted to interested researchers upon reasonable request.

7 Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the corresponding author used ChatGPT 4 to improve readability and language. After using this tool, the author reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Figure 6. The total biomass of *Ulva* present in the raceway over the culture period is shown on the primary (left) y-axis while the internal nitrogen composition of *Ulva* (N_{int}) is shown on the secondary (right) y-axis. The change in N_{int} over time for all scenarios is the same

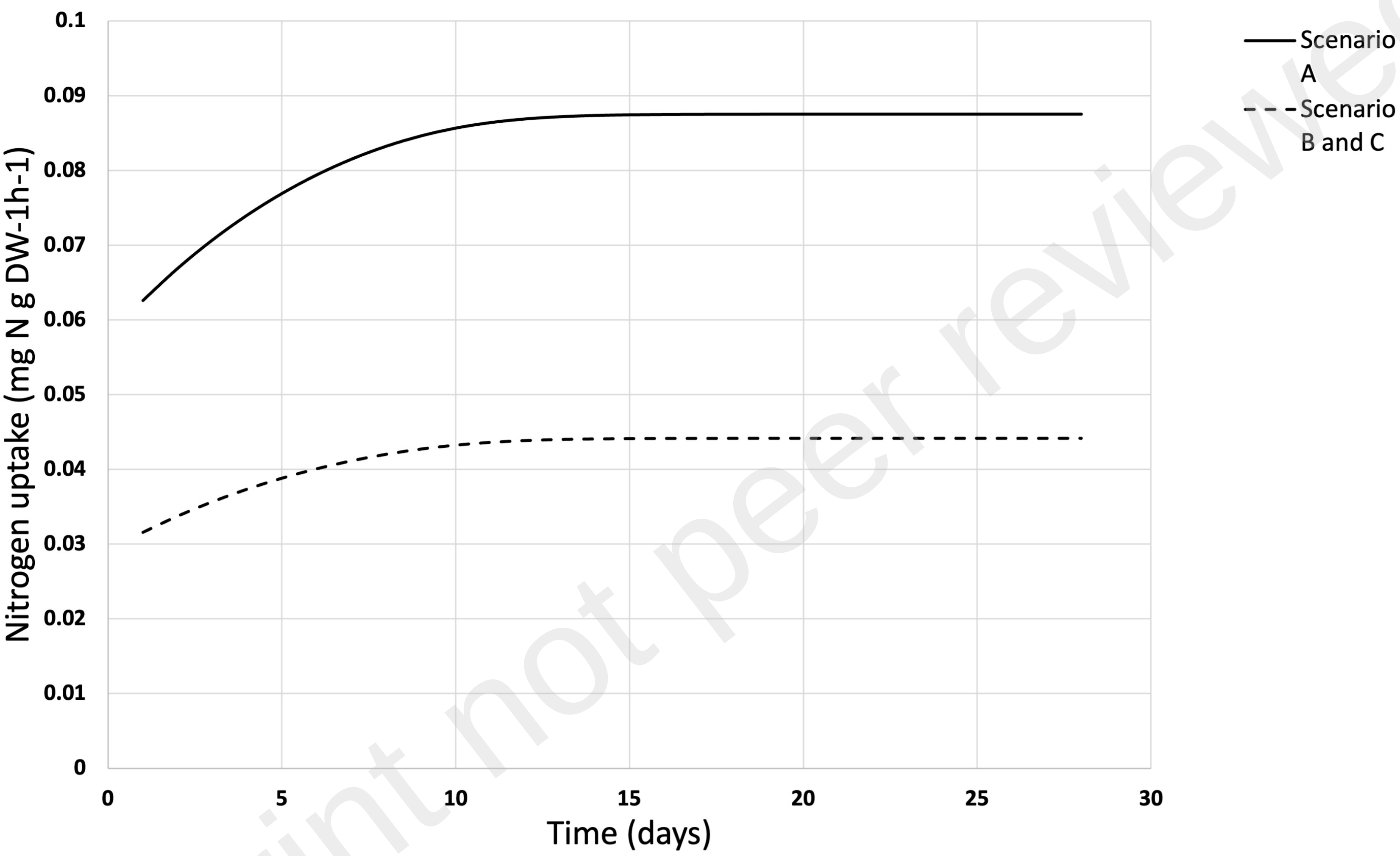
Figure 5. The nitrogen uptake of the *Ulva* in the raceway over the production cycle for the various urchin feeding scenarios. Scenarios B and C are shown as a single curve as they have effectively the same average TAN input.

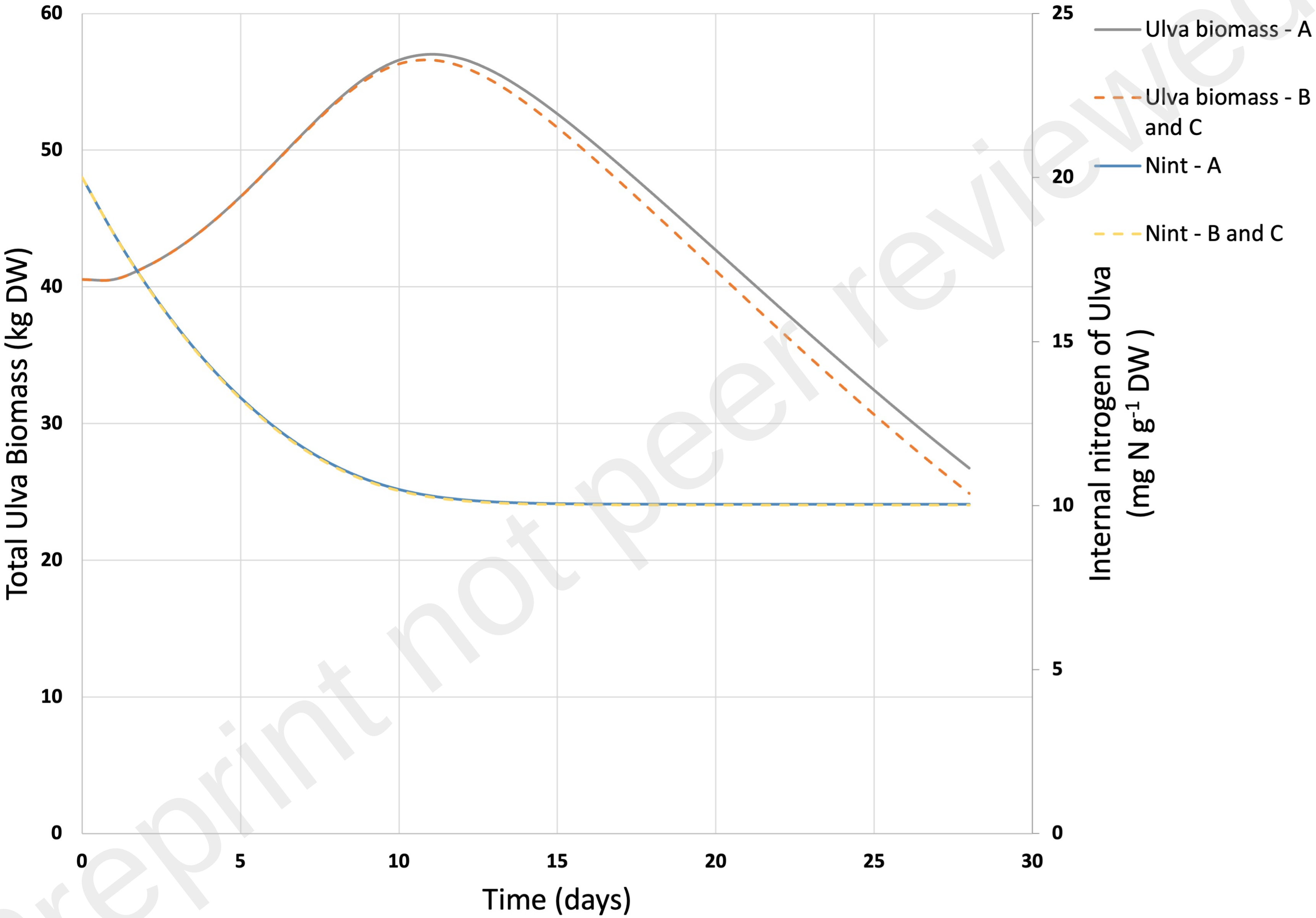
Figure 4. The graphs depict the total ammonia nitrogen (TAN) concentrations of the water flowing from all the urchin tanks into the *Ulva* raceway over the 28-day production cycle across three feeding scenarios. In Scenario A, fresh *Ulva* is the sole feed for all cohorts. In Scenario B, urchins are fed with 20U pellets (containing 20% *Ulva*, Cyrus 2015a), the spikes in TAN represent the leaching as pellets are added into the system. The sharper spikes on days 7, 14 and 21 represent the change of weekly feeding regimes and the need to feed two days in a row, instead of every second day. Scenario C illustrates TAN concentrations when fresh *Ulva* is provided to urchin cohorts 1–4, while cohorts 5–7 receive only 20U pelleted feed to enhance gonad size.

Figure 3. The increase in total urchin biomass within each cohort over the monthly production cycle. Each colour represents a different cohort, starting with cohort one being the juvenile (*ca.* 10 mm) urchins, which have been in the production cycle for a month or less. It ends with the cohort that has been in the system for seven months (cohort seven), which will be harvested at the end of the cycle.

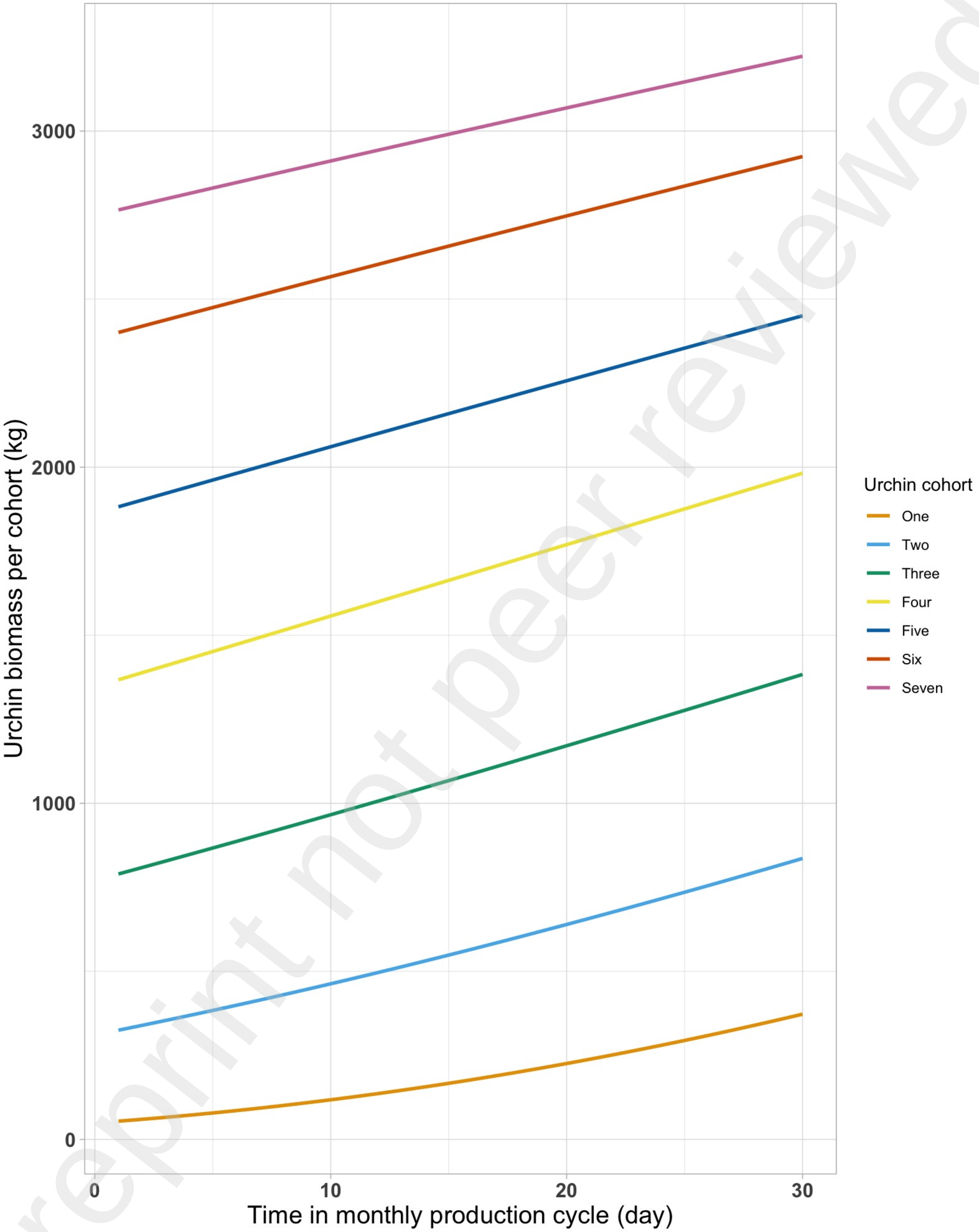
Figure 2. Schematic description of the **urchin-*Ulva*** farm-scale integrated multitrophic aquaculture (IMTA) model. The urchin module uses Johnson's differential growth equation on an individual scale to estimate population dynamics. This population dynamic provides biomass predictions, which are used to estimate feed requirements, gonad production and total ammonia nitrogen (TAN) emissions. The TAN emitted from the urchins, light availability and size of the *Ulva* raceway are the primary inputs for the *Ulva* module. This module uses the relationship between the internal nitrogen composition of *Ulva* (N_{int}), the nitrogen uptake and the daily growth to estimate the TAN assimilation and biomass dynamics. The biomass dynamics can be used to estimate the monthly production of *Ulva*, which can be used for urchin feed.

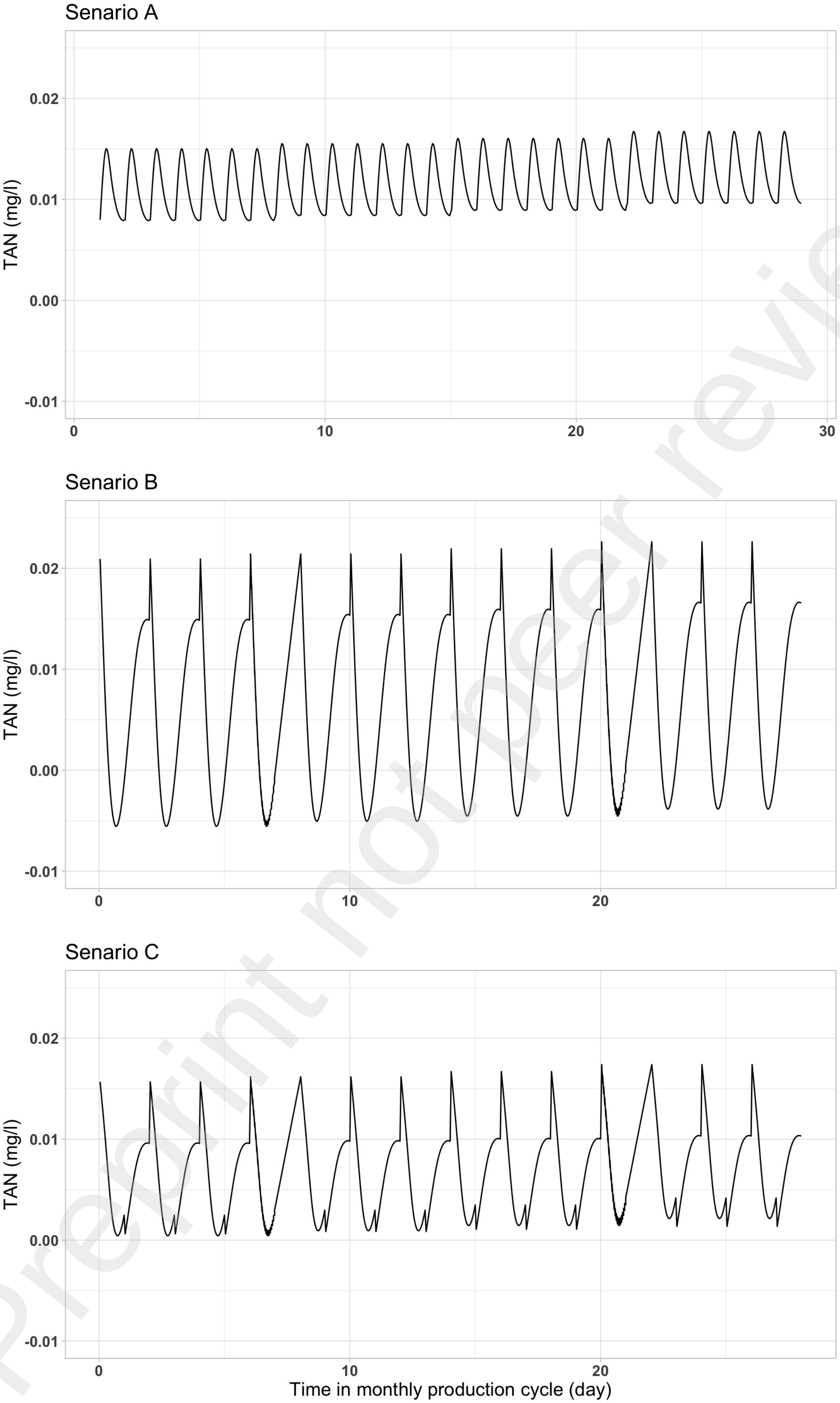
Figure 1. Aerial view of one of the 28 existing abalone-*Ulva* commercial recirculating integrated multitrophic aquaculture (IMTA) systems or clusters at Sea Harvest Aquaculture's Buffeljags Abalone Farm. The cluster consists of 42 abalone tanks (each 8.5m^3) and one Ulva raceway. This design has been replicated in this study for the conceptual *Tripneustes gratilla*-*Ulva* IMTA system. Labels indicate the primary components. The sump is not incorporated into the model.

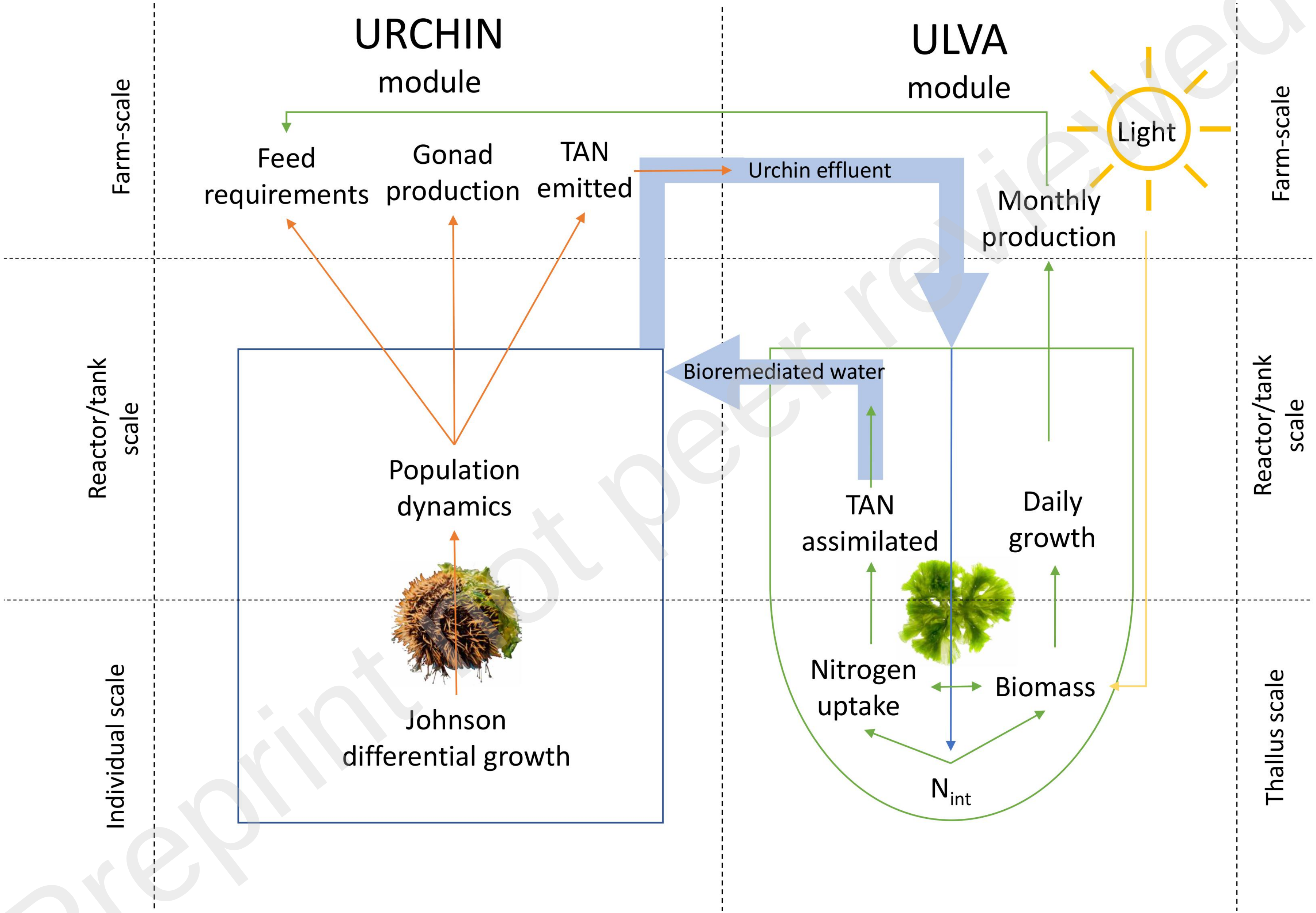

Nitrogen uptake (mg N g DW-1h-1)
0.1
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
0
5
10
15
20
25
30
Time (days)
Scenario A
Scenario B and C



60
50
40
30
20
10
0
Total Ulva Biomass (kg DW)
25
20
15
10
5
0
Internal nitrogen of Ulva (mg N g^{-1} DW)
0
5
10
15
20
25
30
Time (days)
Ulva biomass - A
Ulva biomass - B and C
Nint - A
Nint - B and C


3000
2000
1000
0
0
10
20
30
Time in monthly production cycle (day)
Urchin biomass per cohort (kg)
Urchin cohort
One
Two
Three
Four
Five
Six
Seven


Senario A
TAN (mg/l)
0.02
0.01
0.00
-0.01
0
10
20
30
Senario B
TAN (mg/l)
0.02
0.01
0.00
-0.01
0
10
20
Senario C
TAN (mg/l)
0.02
0.01
0.00
-0.01
0
10
20
Time in monthly production cycle (day)


URCHIN
module
ULVA
module
Farm-scale
Farm-scale
Feed requirements
Gonad production
TAN emitted
Urchin effluent
Light
Monthly production
Reactor/tank scale
Reactor/tank scale
Bioremediated water
Population dynamics
TAN assimilated
Daily growth
Individual scale
Thallus scale
Nitrogen uptake
Biomass
Johnson differential growth
N_{int}