Ecological Modelling 484 (2023) 110486

Contents lists available at ScienceDirect

Ecological Modelling

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

Can seaweeds feed the world? Modelling world offshore seaweed production potential

P.A.J. van Oort [*], A. Verhagen, A.K. van der Werf

Wageningen University & Research, Agrosystems Research, P.O. box 16, Wageningen 6700AA, The Netherlands

ARTICLE INFO

Keywords:
Food security
Seaweed
Model
Nutrients
Wave height

ABSTRACT

Pressure on the terrestrial ecosystems is large and big concerns exist regarding whether a growing world population can be fed from the land. Little is known about if and how much these concerns could be alleviated by harvesting more from the oceans. We modelled the biophysical production potential of seaweeds, and their current and possible future contribution to world food supply. We estimate seaweeds currently provide up to 0.13% of global food energy supply. Seaweed production is increasing more rapidly than terrestrial production. At current rates of increase we estimate seaweed energy contribution of 0.25% in 2050. Production potential of seaweeds could contribute up to 2 to 14% of global food supply if farming 1% of the modelled suitable space within the Exclusive Economic Zone. We show this large potential contribution to world food supply will only be achieved with unprecedented increases in seaweed production, while offshore seaweed cultivation is still in its infancy. The study shows large uncertainties that warrant further research. Modelling shows vast areas of world oceans are unsuitable because of being too far out of shore, having too low nutrient concentrations or having too high waves. Only 2–9% of world oceans and 6–25% of the Exclusive Economic Zone (EEZ) was shown to be suitable for seaweed production. Identifying suitable sites for offshore seaweed cultivation is therefore important. Site suitability maps reported for the 3 model species can be useful for private companies and policy makers expanding seaweed in new high potential production areas around the world.

1. Introduction

Pressure on the terrestrial ecosystems is large and big concerns exist regarding whether a growing world population can be fed from the land (Fischer et al., 2014; Garnett et al., 2013; Godfray et al., 2010; Spillias et al., 2023; van Ittersum et al., 2016). In this context the question has been raised whether oceans will help feed humanity (Buschmann et al., 2017; Duarte et al., 2022, 2009; Godfray et al., 2010; Spillias et al., 2023). Furthermore, concerns about excessive fisheries impact on marine ecosystems are widely acknowledged, while any form of animal production, whether from land or sea is subject to energy loss in conversion from plant to animal biomass (Fresán and Sabaté, 2019; Van Zanten et al., 2018). Production of seaweed has been put forward as a possible solution to both pressure on the land and as a more energy efficient alternative to fisheries (Duarte et al., 2009). Oceans cover about 70% of the earth surface and the potential seems largely untapped. While the logic is evident, to date we know very little about seaweed production potential of the world oceans.

Seaweed cultivation can contribute to a range of sustainable development goals, the focus here is on sustainable development goal (SDG) 2, Zero Hunger. The main questions addressed are (1) how much seaweed can potentially be produced within economic and ecological boundaries and (2) if achieved, how much could seaweeds contribute to global food supply. Intensive large scale seaweed cultivation can potentially cause harmful marine ecosystem effects, because seaweed competes with phytoplankton for carbon, light and nutrients. Mass cultivation of seaweed could theoretically lead to excessive competition with phytoplankton, and the whole marine ecosystem that feeds (directly or indirectly) on phytoplankton (Aldridge et al., 2021; Campbell et al., 2019; van der Meer et al., 2022). In this context a case is to be made for confining seaweed cultivation to sites and parts of the year when ample nutrients are available and competition therefore less. A precautionary approach could be to use only 1% of a designated high nutrient part of the ocean for seaweed cultivation – the choice of this number 1% is rather arbitrary but is so low we would hardly expect negative ecosystems effects. This assumption requires further testing. From the seaweed production perspective, the assumption of cultivating 5% rather than 1% would lead to a 5 fold increase in production. In the

---

[*] Corresponding author.
E-mail address: pepijn.vanoort@wur.nl (P.A.J. van Oort).

https://doi.org/10.1016/j.ecolmodel.2023.110486
Received 1 February 2023; Received in revised form 8 August 2023; Accepted 10 August 2023

discussion section we reflect on how model outcomes are sensitive to such assumptions and we identify key uncertainties.

Seaweeds are sometimes thought of as poorly digestible for human beings. A recent study shows humans, with aid of human gut bacteria, can digest seaweed polysaccharides (Pudlo et al., 2022). Seaweeds can be used as a food source (Bruhn et al., 2019; Forster and Radulovich, 2015; Mahadevan, 2015; Rajauria et al., 2015). According to van den Burg et al. (2021) between 75 and 85% of worldwide seaweed production is used for direct human consumption in Asia. This being said, seaweeds currently represent only a tiny part of the human diet. A large consumer market does not exist at the time of writing (FAO, 2018, 2021; van den Burg et al., 2021), but such a market may well grow in the above context of challenges of feeding future world population and growing challenges in terrestrial production. Before investing heavily in developing supply chains, processing industry and marketing it is relevant to know whether the oceans can actually deliver. From the bio-physical perspective, how much scope is there for increasing seaweed production? In this context we present an exploratory study of how much food energy seaweeds might theoretically provide.

The objective of this paper is to present estimates of global seaweed production potential from the biophysical perspective. After quantifying this production potential, we address how likely it is for this potential to be realised by 2050 and if so, how much could it contribute to world food supply?

2. Materials and methods

We first present the scope of the model (§2.1), followed by a model overview (§2.2). Source data are described in Section 2.4, parameters and methods and equations in Sections 2.3 and 2.5. Scenarios for sensitivity analysis and for contribution of seaweed to future food supply (in 2050) are defined in Section 2.6.

2.1. Scope: offshore within the Exclusive Economic Zone (EEZ)

Distance to shore is important from the economic perspective. Production costs for harvesting and planting increase with distance from shore and cultivation too far out of shore may not be economically viable (Kapetsky et al., 2013; Lehahn et al., 2016). In the short term expansion of seaweed in the nearshore environment seems more likely (Spillias et al., 2023). But human pressures on the nearshore environment are increasing and from this perspective, it is relevant also to explore production potential further offshore (Gentry et al., 2017). Marine governance is much less developed than terrestrial governance (Lovatelli et al., 2013; Zaucha and Gee, 2018). One commonly used legal concept is the so-called “Exclusive Economic Zone” (EEZ), a zone of 200 nautical miles (~370 km) in which sovereign states have special rights regarding the exploration and use of marine resources. Imagine a fish trailer or bulk carrier ship cruising through (and in the process destroying) a seaweed farm. Inside the EEZ one may have some form of marine spatial planning of shipping traffic lanes and some form of legal protection of a seaweed farm. Outside the EEZ spatial planning and legal protection is much less. We limit our analysis of global seaweed production potential to this EEZ because (1) one may expect exceedingly higher production costs further out into the oceans and (2) operating under the umbrella of the nations associated with a particular EEZ can offer some legal protection.

Agronomy is important. Any seaweed farmer would want to cultivate only in suitable sites and (in case of seasonality) during months suitable for cultivation. For a new and expanding industry, scientific identification of suitable sites and months can be relevant. In the high latitudes (towards the North and South poles) strong seasonality in environmental variables, in combination with temperature niches of seaweed species, may render parts of the year unsuitable for cultivation, hence intra-annual variability in site suitability is for these higher latitudes a factor to be considered – something which has been done in regional modelling studies (Broch et al., 2019; van der Molen et al., 2018) but to date not in global studies (Froehlich et al., 2019; Spillias et al., 2023). The scenario of fertilising seaweed farms in open ocean seems very unlikely, hence marine nutrient concentrations are important. Some studies modelled effects of nutrient concentrations on growth (Broch et al., 2019; van der Molen et al., 2018). Others used relative terms such as favourable N:P ratios (Froehlich et al., 2019), which raises the question whether equally high production levels can be attained for a site with favourable N:P ratios, yet with very low concentrations – our premise is production potential would be low in such an environment. Spillias et al. (2023) modelled probability of species occurrence partially dependent on marine nitrate concentrations, but production estimates were made independently of nutrient concentrations, thus not lower at lower concentrations. Here we present an approach where production levels are lower at lower nutrient concentrations and an approach where seasonality in environmental variables is explicitly modelled.

2.2. Model overview

The new model developed here is named World Offshore Macro Algae Production Potential (WOMAPP). WOMAPP follows a four-step approach to calculating seaweed production potential. First site suitability is calculated. We define site suitability as a number between 0 = unsuitable to 1 = perfectly suitable. Site suitability is calculated per pixel x per month m, first separately for six environmental variables. Overall monthly Seaweed Site Suitability $SSS_{s,m,x}$ for model species s in month m in pixel x is the minimum of the individual suitabilities per environmental variable (Eq. (1)):

$$SSS_{s,m,x} = min\left(f\left(T_{m,x},s\right),f\left(I_{m,x},s\right),f\left(N_{m,x},s\right),f\left(P_{m,x},s\right),f\left(S_{m,x},s\right),f\left(SWH_{m,x},s\right)\right) \tag{1}$$

where, $T_{m,x}$ is the temperature T in month m in pixel x derived from 12 global (monthly) temperature maps. $f(T_{m,x}, s)$ is the site suitability for species s in terms of its sensitivity to temperatures. Likewise, species specific functions $f(X_{m,x}, s)$ are defined for all environmental variables X: Temperature (T), Irradiance (I), Nitrogen (N), Phosphorous (P), salinity (S) and Significant Wave Height (SWH). $SSS_{s,m,x}$ values were calculated for the entire world oceans, they can be visualised for the world oceans or showing only pixels within the EEZ.

The actual absolute rate of growth $AARG$ (ton dry ha^{-1} month^{-1}) is calculated as the product of the potential growth rate (PGR) and site suitability. Thus, actual growth will be less in unfavourable conditions (low SSS). The derivation of the PGR parameter is presented in Section 2.3.2.

$$AARG_{s,m,x} = SSS_{s,m,x} * PGR \tag{2}$$

In step 2 WOMAPP calculates yield potential (tonnes dry ha^{-1} year^{-1}). Binary variable $C_{s,m,x}$ indicates whether (1) or not (0) seaweed s is cultivated in a particular site and month. We set $C_{s,m,x}$ to 1 based on two agronomic criteria: (1) minimum overall monthly Seaweed Site Suitability $SSS_{s,m,x} > 0.5$ and (2) $C_{s,m,x}$ is only set to 1 if the pixel has 4 or more suitable months (i.e. 4 or more months with $SSS_{s,m,x} > 0.5$). The binary EEZ_x is 1 for pixels inside the EEZ and otherwise zero. Thus per pixel x, annual yield $Y_{s,x}$ (tonnes dry ha^{-1} year^{-1}) can be calculated as:

$$Y_{s,x} = \int_{m=1}^{m=12} EEZ_x \times C_{s,m,x} \times AARG_{s,m,x} \tag{3}$$

In step 3, production (tonnes dry species^{-1} pixel^{-1} year^{-1}) is calculated by summing over the cultivated area. The spatial resolution of our environmental data is 1° x 1°. A 1° pixel is around 12,000 km^2 at the equator, around 6000 km^2 along the Norwegian coast and near zero towards the North & South pole. Such a pixel will never be completely cultivated. Let fC be the fraction cultivated and A_x be the area in km^2 of a pixel x at a given latitude. For each pixel potential production for seaweed *s*, $P_{s,x}$ (tonnes dry species^{-1} pixel^{-1} year^{-1}), can be calculated as:

$$P_{s,x} = Y_{s,x} \times A_x \times fC \times \ 100 \tag{4}$$

where, the 100 is for unit conversion from hectare to km^2. Production can be expressed in fresh matter, in dry matter, in nutritional energy (Joules) or other nutritional metrics. Comparing production of food products with very different energy or dry matter content would be comparing apples with oranges. For example 1 kg fresh seaweed may contain only 150 g of dry matter whereas 1 kg of rice grains will contain 860 g of dry matter. Comparing fresh weights would lead to overestimation of the importance of seaweed. Here for more standardised comparisons of seaweed production with global food production we will compare the two in terms of energy for food consumption.

At a 1° spatial resolution a world map has $180\times360 = 64{,}800$ pixels, of which around 70% is oceans. Global biophysical production potential P_s in tonnes per species *s* per year is calculated as the sum over all pixels:

$$P_s = \int_{x=1}^{64800} P_{s,x} \tag{5}$$

Finally in step 4, global production per species P_s is converted from kilograms to energy content, this final step is a simple unit conversion and is explained in Section 2.6.2. An example calculation of the first three steps of the WOMAPP model is presented in Fig. 1.

2.3. Photosynthesis and potential growth rate

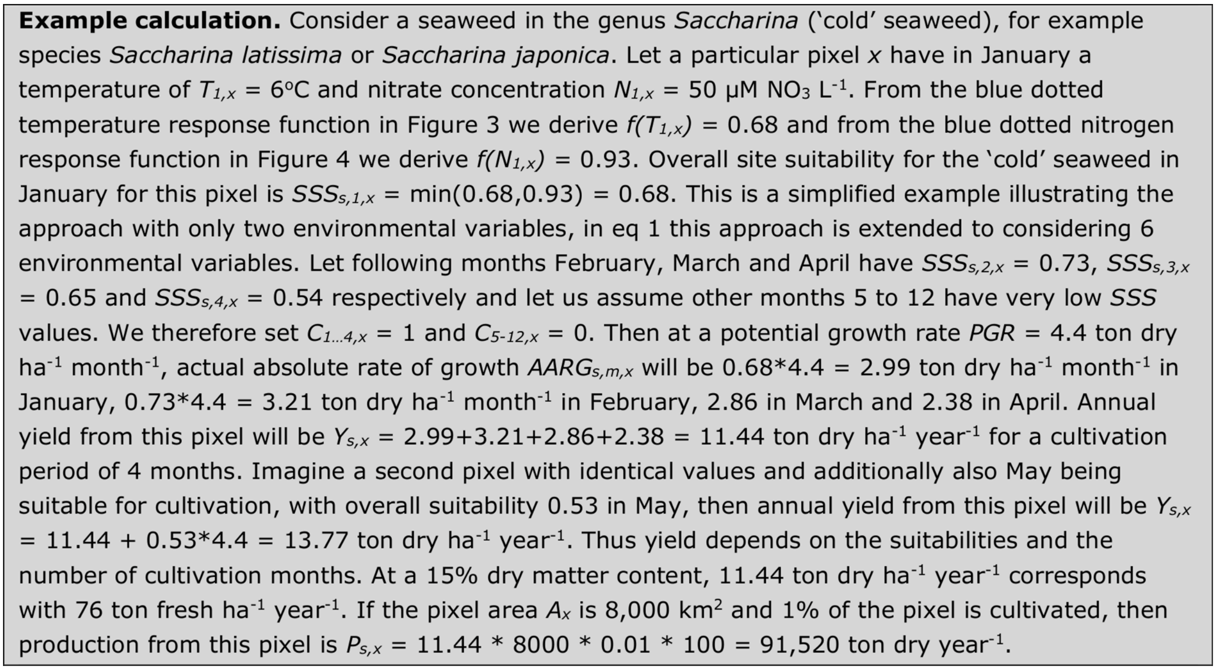
2.3.1. Photosynthesis models

Two approaches to modelling growth in seaweeds are (1) the more mechanistic approach of dynamically modelling the processes of light interception, photosynthesis, respiration, reserve mobilization and conversion of assimilates into structural and reserve biomass (Borlongan et al., 2017a, 2017b, 2017c; Borlongan et al., 2017d; Broch and Slagstad, 2012; Duarte and Ferreira, 1997; Lavaud et al., 2020; Lehahn et al., 2016; Venolia et al., 2020; Wang et al., 2019). Advances are being made in seaweed modelling leading to seaweed growth models developed and tested for individual species and tested in a limited number of sites. At the time of writing these more mechanistic models are hard to generalise to the global level. These models require more input data which are not available at a global level. We lack many of the necessary input data that would be needed for running these models and we lack validation data on a larger scale that would allow for testing how well these models can be applied outside the domain for which they were tested and developed. Therefore we opt for a simpler approach, the *PGR* approach to modelling growth.

2.3.2. Potential growth rate

We developed the simpler approach outlined in Eq. (2), with a fixed potential growth rate parameter *PGR*, which we estimate at 4.42 ton dry ha^{-1} month^{-1}, see the derivation in the supplementary material S1. This *PGR* approach is a compromise in balancing model complexity and data availability. In line with limited data availability the *PGR* approach is less complex than the mechanistic dynamic models referred to above. Yet the *PGR* approach is more complex than previous global modelling studies in which estimated production potential was not directly dependent on environmental conditions .

Growth of seaweeds during its cultivation period is often sigmoid (Broch and Slagstad, 2012; van Oort et al., 2022) or expo-linear (Lavaud et al., 2020; Venolia et al., 2020) if the seaweed is harvested before growth flattening off. Through site suitabilities $SSS_{s,m,x}$ our model often produces similar sigmoid patterns. Planting is often at a time when environmental conditions are only just good enough (e.g. kelp species planted in autumn), in which case $SSS_{s,m,x}$ is only just above 0.5 and the actual absolute rate of growth $AARG_{s,m,x}$ is still relatively low. Growth then proceeds into the more favourable part of the season with higher $SSS_{s,m,x}$ and $AARG_{s,m,x}$. And finally growth flattens of as environmental conditions become less good towards the end of the growing season. Another process that may cause growth flattening off is sporulation, in which seaweed mobilise their reserves to produce spores for reproduction. This process is not modelled here because generally seaweed farmers will seek to harvest before this process occurs and they will select strains that will not sporulate within the designated cultivation period.



Example calculation. Consider a seaweed in the genus *Saccharina* ('cold' seaweed), for example species *Saccharina latissima* or *Saccharina japonica*. Let a particular pixel *x* have in January a temperature of $T_{1,x}$ = 6°C and nitrate concentration $N_{1,x}$ = 50 μM NO_3 L^{-1}. From the blue dotted temperature response function in Figure 3 we derive $f(T_{1,x})$ = 0.68 and from the blue dotted nitrogen response function in Figure 4 we derive $f(N_{1,x})$ = 0.93. Overall site suitability for the 'cold' seaweed in January for this pixel is $SSS_{s,1,x}$ = min(0.68,0.93) = 0.68. This is a simplified example illustrating the approach with only two environmental variables, in eq 1 this approach is extended to considering 6 environmental variables. Let following months February, March and April have $SSS_{s,2,x}$ = 0.73, $SSS_{s,3,x}$ = 0.65 and $SSS_{s,4,x}$ = 0.54 respectively and let us assume other months 5 to 12 have very low *SSS* values. We therefore set $C_{1\ldots4,x}$ = 1 and $C_{5\text{-}12,x}$ = 0. Then at a potential growth rate *PGR* = 4.4 ton dry ha^{-1} month^{-1}, actual absolute rate of growth $AARG_{s,m,x}$ will be 0.68*4.4 = 2.99 ton dry ha^{-1} month^{-1} in January, 0.73*4.4 = 3.21 ton dry ha^{-1} month^{-1} in February, 2.86 in March and 2.38 in April. Annual yield from this pixel will be $Y_{s,x}$ = 2.99+3.21+2.86+2.38 = 11.44 ton dry ha^{-1} year^{-1} for a cultivation period of 4 months. Imagine a second pixel with identical values and additionally also May being suitable for cultivation, with overall suitability 0.53 in May, then annual yield from this pixel will be $Y_{s,x}$ = 11.44 + 0.53*4.4 = 13.77 ton dry ha^{-1} year^{-1}. Thus yield depends on the suitabilities and the number of cultivation months. At a 15% dry matter content, 11.44 ton dry ha^{-1} year^{-1} corresponds with 76 ton fresh ha^{-1} year^{-1}. If the pixel area A_x is 8,000 km^2 and 1% of the pixel is cultivated, then production from this pixel is $P_{s,x}$ = 11.44 * 8000 * 0.01 * 100 = 91,520 ton dry year^{-1}.

Fig. 1. Example calculation.

2.4. Ocean data

The two most widely used datasets for global mariculture studies are (1) the World Ocean Atlas (WOA, 2018), see Froehlich et al. (2019) and Lehahn et al. (2016) and (2) the Bio-Oracle dataset (Assis et al., 2018) used by Spillias et al. (2023). Figs. S 1–S 4 in the supplementary material S2 present comparisons of the two datasets. A choice between these two datasets is a choice between high spatial resolution and high temporal resolution: WOA2018 provides environmental data at a finer (monthly) temporal resolution yet with a with a course spatial resolution (1°, around 110 × 110 km at the equator); Bio-Oracle has a coarser temporal resolution (annual average, min max and range) and a finer spatial resolution (0.08°, 9 km at the equator). The high temporal resolution of WOA2018 is relevant when considering strong seasonality in environmental variables for the higher latitudes (closer to the North and South pole. The high spatial resolution of Bio-Oracle is important considering steep gradients that can be found in nutrient concentrations, declining exponentially as one moves from estuaries towards open sea shore (Flo et al., 2011; van Oort et al., 2022). A 110 km spatial average nutrient concentration (WOA2018) will always be lower than the nutrient concentration in the 0–5 km just near the shore and even in Bio-Oracle, a 9 km average may not be representative of nutrient concentrations at say 100 m from shore. Further out of shore spatial variability in nutrient concentrations is much smaller and the WOA therefore provides a fair representation of the offshore marine environment. Hence the WOA can be used for offshore modelling, but it may be underestimating nutrient concentrations and seaweed potential just near the shore. Moreover, WOA2018 also provides incomplete coverage of the near-shore, with no data available for parts of the near shore (see supplementary material S2).

For each environmental variable we used 12 maps, one per month to assess monthly site suitability. From the World Ocean Atlas (WOA, 2018) we extracted temperature (°C), nitrate (μmol N per liter), phosphate (μmol P per liter) and salinity maps (psu). WOA2018 has temperature at 0.25° resolution and the other variables at 1° resolution. We used the 1° spatial resolution and monthly temporal resolution data. For nitrate and phosphate WOA2018 only contains long term averages. For temperature and salinity we used monthly average calculated over the most recent period available in WOA2018, that is 2005–2017. For all biophysical variables we used surface concentrations, consistent with the fact that future offshore commercial seaweed cultivation will most likely be from manmade floating structures (Whiting et al., 2020). Surface irradiance data (MJ m^{-2} d^{-1}) were derived from the NASA-POWER Global Climatology (NASA, 2020) and aggregated to the same 1° monthly resolution as the WOA2018. Monthly Significant Wave Height (*SWH*) data (m.) were obtained from the ERA5 dataset (Hersbach et al., 2019). The ERA5 dataset contains monthly data from 1959 onwards at 0.5° spatial resolution. For consistency with WOA data we calculated monthly averages over the period 2005–2017 and we spatially aggregated to the same 1° monthly resolution as the WOA2018. Delineation of the Exclusive Economic Zone (EEZ) was obtained from www.marineregions.org (Flanders_Marine_Institute, 2020).

2.5. Seaweed site suitability functions

2.5.1. Seaweeds

Typical cold temperature species are *Saccharina latissima* (kelp) and *Saccharina japonica* (formerly classified as *Laminaria japonica*). Intermediate temperature species are *Undaria pinnatifida* (Japanese wakame) and species of the genus *Porphyra* (Japanese nori) and *Ulva lactuca* (sea lettuce). Commercially important seaweeds in the tropics are of the genera *Euchema, Kappaphycus and Gracilaria*. More species and their application are discussed in FAO (2018).

We derived from the literature environmental response functions for these species for 6 environmental variables. For the intermediate temperature species, particularly little was found on species of the genera *Undaria* and *Porphyra* hence most of the literature on the intermediate temperature species was from measurements made on species of the genera *Ulva*, mainly *Ulva lactuca*. Still relatively little is known on seaweeds and often the literature is scattered. Studies on different species and from different regions in the world were combined to obtain for each seaweed species group with different temperature niches ('Cold', 'Intermediate', 'Warm') a set of seaweed group specific environmental suitability functions.

2.5.2. Irradiance

A range of studies model gross photosynthesis, respiration and net photosynthesis as a function of irradiance, temperature and light interception by frond area (Borlongan et al., 2017a, 2017b, 2017c; Borlongan et al., 2017d; Broch and Slagstad, 2012; Duarte and Ferreira, 1997; Lavaud et al., 2020; Venolia et al., 2020). Although these studies all use different equations for modelling light saturation, all equations result in similarly shaped saturation functions and all show saturation at around 7.6 MJ m^{-2} d^{-1}. Hence we modelled Irradiance Suitability with just this one function. The function shown in Fig. 2 was derived from equations and parameters for gross photosynthesis as reported in Broch and Slagstad (2012), modelled at a temperature of 20 °C. A suitability value in the range of 0 to 1 was obtained by dividing gross photosynthesis (g C m^{-2} d^{-1}) by maximum gross photosynthesis (at the saturation point of 7.6 MJ m^{-2} d^{-1}). Absolute gross photosynthesis (in g C m^{-2} d^{-1}) is higher at optimum temperatures (Fig. 3), but across studies the saturation point is 7.6 MJ m^{-2} d^{-1} regardless of temperature. In the Supporting Material S3, Fig. S 5 shows monthly global surface irradiance levels, Fig. S 6 shows resulting monthly Irradiance Suitability.

2.5.3. Temperature

Fig. 3 shows blue lines for 'cold' species with a temperature optimum at around 10 °C, green for intermediate temperatures (optimum around 20 °C) and red lines for 'warm' species (optimum around 30 °C). The multiple lines shown reflect differences between studies, the dotted lines were used for modelling site suitability in our model. Temperature response functions have also been reported for *Pyropia* and *Undaria* (Watanabe et al., 2014a, 2014b, 2016) but the plotted temperature range is so wide we considered those too uncertain to be used for modelling. For modelling global seaweed potential we used the functions with the solid dots in Fig. 3: for the cold seaweeds: (Broch and Slagstad, 2012) equation for blade area growth; for the intermediate temperature species: (Lavaud et al., 2020) and for the warm seaweeds (Borlongan et al., 2017a). Parameters and equations for the functions shown are available in the model code (van Oort, 2023).

2.5.4. Nutrients

The most widely used approach to modelling nutrient uptake is using the Michaelis–Menten equation (Eq. (6)) where uptake *V* (μmol N or P per m^2 or gram seaweed per day) increases with marine nutrient concentration *X* (μmol N or P per liter) up to a maximum daily uptake *Vmax*.

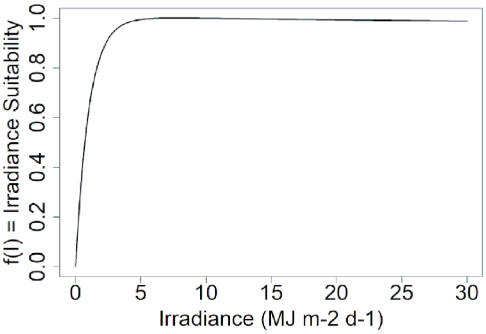


Fig. 2. Irradiance suitability function (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.).

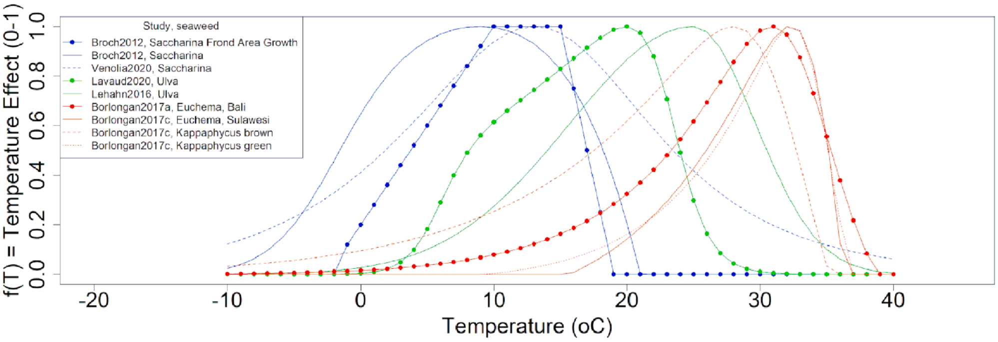


Fig. 3. Temperature response functions. Colours refer to seaweeds with different temperature niches: cold (blue), intermediate (green) and warm (red). Lines marked with solid dots were used for global modelling (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

Not multiplying with *Vmax* yields a response function scaled to 0 to 1 (Eq. (7)):

$$V(X) = Vmax * X / (X + k) \tag{6}$$

$$f(X) = X / (X + k) \tag{7}$$

where, k is the half saturation constant, which we will refer to as k_N and k_P, for nitrate and phosphate respectively. We know by now that three important additional factors have big impact on k values found:

1. Lower k values for starved seaweeds, i.e. with low internal nutrient reserves (Fujita, 1985; Lubsch and Timmermans, 2018, 2020; Smit, 2002).
2. Lower k values at higher temperatures (Espinoza and Chapman, 1983; Smit, 2002).
3. Higher k values when water motion is very slow (Gonen et al., 1995; Hurd, 2000).

Experimental conditions varying along the three variables above may well cause large variation in k values found, this is often difficult to tell as water motion and seaweed reserves are often not reported in experimental studies. Ideally a model would consider all these processes simultaneously, but to date large experiments with factorial design of a range of nutrient concentrations, water flow velocities and temperatures have not been conducted. In the few studies cited above the number of treatments was limited (e.g. a larger range of nutrient concentrations at only two temperatures) which makes interpolation and extrapolations quite uncertain. In controlled conditions one may first cultivate seaweed in high and low nutrient conditions to obtain specimen with high and low reserves, but measurement of which part of total seaweed biomass is reserves and which part structural biomass remains a challenge. Just a few mechanistic dynamic simulation models can simulate nutrient uptake dynamics and seaweed nutrient reserves simultaneously (Broch and Slagstad, 2012; Lavaud et al., 2020; Venolia et al., 2020), but at a global level and for other species, we are still far from having such knowledge on interaction effects between reserves and nutrient uptake. Therefore, despite these caveats, the best we can do for now is use these Michaelis–Menten functions.

Figs. 4 and 5 show results that seem in contradiction with previous experimental findings of lower k values at higher temperatures (Espinoza and Chapman, 1983; Smit, 2002). Instead, Figs. 4 and 5 show lowest k values for the cold temperature species and highest k values for the warmer temperature species, except in the study by Wang et al. (2019). Fig. 4 shows for the (red) warm species curves drawn with k_N values of 10 μM N L^{-1} or higher. While in the tropical offshore environment, surface water N concentrations are mostly in the range of 0–3 μM N L^{-1}. Thus using any of these functions with $k_N \geq 10$ would result in showing offshore cultivation in the tropics is impossible. Fig. 4 shows for the (green) intermediate temperature species curves drawn with k_N values ranging from 1.46 to 40.7 μM N L^{-1}. Also here, if the higher k_N values were true, offshore cultivation of intermediate temperature species would be impossible. To quantify the uncertainty in global seaweed production potential we therefore simulated two scenarios:

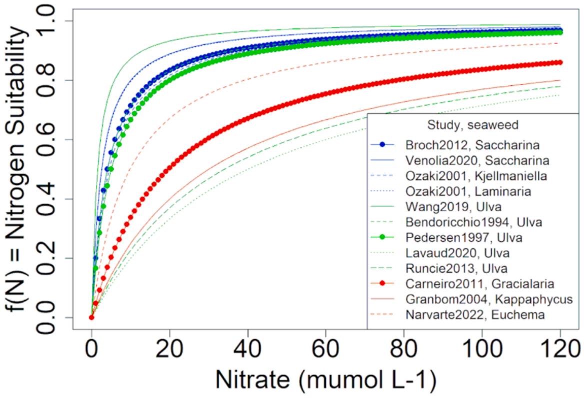


Fig. 4. Michaelis–Menten functions for nitrogen. Colours refer to seaweeds with different temperature niches: cold (blue), intermediate (green) and warm (red). Lines marked with solid dots were used for global modelling in the pessimistic scenario (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

1. Optimistic scenario with low $k_N = 1.46$ μM N L^{-1} and $k_P = 0.06$ μM P L^{-1} for the intermediate (green) and warm (red) seaweed species based on Wang et al. (2019).
2. Pessimistic scenario with for the intermediate (green) species $k_N = 5$ μM N L^{-1} (Pedersen and Borum, 1997) and $k_P = 1.97$ μM P L^{-1} (Douglas et al., 2014) and for the warm seaweed species $k_N = 19.6$ μM N L^{-1} and $k_P = 5.0$ μM P L^{-1} (Carneiro et al., 2011).

In both scenarios we used for the cold seaweeds species $k_N = 4.0$ μM N L^{-1} (Broch and Slagstad, 2012) and $k_P = 0.135$ μM P L^{-1} (Ozaki et al., 2001). The Ozaki k_P value was calculated as the average of two k_P values (0.09 and 0.18) reported by Ozaki for species *Laminaria japonica*.

2.5.5. Salinity

For salinity, a saturating response function *f(S)* is reported for *Saccharina latissima* by Broch et al. (2019), with reduced growth at low salinity S (Fig. 6). Including such a function is important when modelling kelp in Norwegian fjords with high sweet water influx and when modelling site suitability of poorly disclosed seas fed with large sweet water volumes from rivers, such as the Baltic sea. For *Ulva lactuca* (Lehahn et al., 2016) report a bell shaped function with an optimal salinity level of around 18. With world ocean salinity of 33–37 psu using this function would render almost all of the world oceans unsuitable. Therefore we did not use the (Lehahn et al., 2016) salinity function in the current study. Hayashi et al. (2011) cultivated the tropical seaweed *Kappaphycus alvarezii in vitro* at a wide range of salinity levels (psu 25, 35, 45 and 55), which showed the highest daily growth *DGR* rate at 35 psu and lower at the other salinities. A parabola was fitted through the Hayashi data (*DGR* vs salinity) with negative values set to 0 to obtain an *f(S)* function scaled from 0 to 1.

2.5.6. *Significant wave height*

Evidently a rough sea can be detrimental to seaweed cultivation. Man-made structures on which seaweed is growing can be physically damaged in a rough sea. Parts or the whole body of the seaweed may break off due to wave action or strong current. Methodologically quantification of roughness of the sea is challenging, both in terms of practicalities of measurement and because wave height constantly changes. A commonly used metric is the Significant Wave Height (*SWH*). Technically, we used the variable “Significant height of combined wind waves and swell” provided by ERA5 (Hersbach et al., 2019) and briefly defined as “the average height of the highest third of surface ocean/sea waves generated by wind and swell”. In the Supporting Material S3, Fig. S 7 shows maps of monthly wave heights, Fig. S 8 shows maps of resulting monthly wave heights suitability calculated with Fig. 7.

A few studies have attempted to establish effects of rough sea on seaweeds and floating structures for cultivation (Azevedo et al., 2019; Bak et al., 2018; Buck and Buchholz, 2004, 2005) but none of these provides readily useable response functions that use as input wave maps such as available from ERA5 or other sources. Here we made our own estimate, using the function shown in Fig. 7, in which *SWH* below 2 m is considered a calm complete suitable ocean/sea and *SWH* above 4 m is considered too wild for seaweed cultivation. Bak et al. (2018) report offshore cultivation was possible in an exposed area with occasional significant wave heights of 3–6 m, this study suggests possibly Fig. 5 is too pessimistic. To account for this uncertainty we also simulated a scenario with the *SWH* function switched off.

2.6. *Scenarios*

2.6.1. *Seaweed production scenarios*

We present calculations of biophysical production potential of seaweed. Scenarios are used for sensitivity analysis (on nutrient requirement and wave height) and for exploration of possible future trends in seaweed production. Common assumptions in all scenarios are that:

1 Cultivation is only in the EEZ (parameter EEZ_x in Eq. (3)).

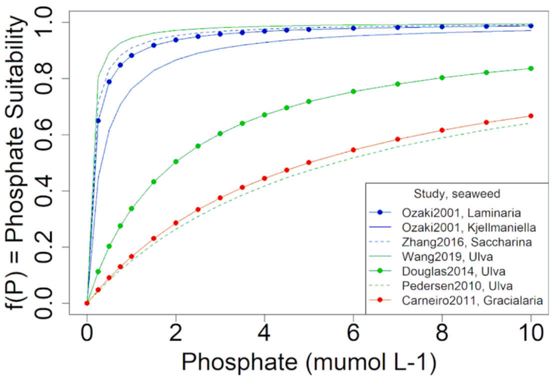


Fig. 5. Michaelis–Menten functions for phosphorous. Colours refer to seaweeds with different temperature niches: cold (blue), intermediate (green) and warm (red). Lines marked with solid dots were used for global modelling in the pessimistic scenario (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

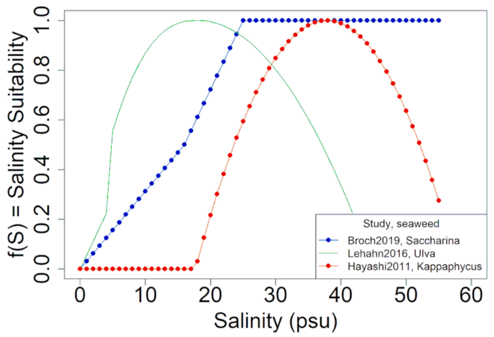


Fig. 6. Salinity response function. Colours refer to seaweeds with different temperature niches: cold (blue), intermediate (green) and warm (red). Lines marked with solid dots were used for global modelling (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

2 Cultivation is only in suitable sites and months, i.e. with minimum site suitability of 0.5 during at least 4 months (parameter $C_{s,m,x}$ in Eq. (3)). Note this implicitly leads to selection of pixels with high nutrient concentrations, thus where competition with phytoplankton will be limited. With this criterion a pixel with 8 suitable months will be cultivated for 8 months, a pixel with 4 suitable months will be cultivated 4 months and a pixel with 3 suitable months will not be cultivated;

3 Of each suitable pixel x, only 1% (parameter fC in Eq. (4)) will be cultivated.

2.6.1.1. *Distribution of 1% within a pixel.*

We are not making assumptions on distribution of the 1% seaweed within large ~10,000 km^2 pixels. Most likely seaweed cultivation will be concentrated in parts of pixels closest to the shore, where nutrient concentrations are often higher and transportation costs from land to seaweed farm are lower. If the 1% seaweed is concentrated within a cultivation zone of 100 km long and 2 km wide along the shore, then within this narrow strip seaweed density would be 100 / 200 = 50% and the 1% would be a weighted average of (200×50% + 9800×0%) / 10,000 = 1%. Seaweed densities up to 50% have been reported in the literature (Jin et al., 2023). In the absence of strict regulations, it seems more likely seaweed farming would develop in such highly suitable areas with a pixel, and possibly more than only 1% of the pixel. This all the more calls for further research into ecosystem effects of offshore seaweed cultivation.

2.6.1.2. *Environmental and economic concerns.*

The above set of assumptions accommodates economic concerns about production costs increasing with distance from shore and it partially accommodates ecological concerns over competition between seaweed and phytoplankton (and the entire marine food web that feeds on phytoplankton, van der Meer et al. 2022). Further research is needed on ecosystems effects and on regulations enforcing maximum percentage area use within designated production areas.

2.6.1.3. *Uncertainties.*

One of the main uncertainties identified above is regarding nutrient requirements of the intermediate and warm temperature seaweeds. We model this uncertainty by considering an optimistic scenario and a pessimistic scenario as defined above. A second uncertainty is in the sensitivity to high waves. For the ‘cold’ seaweeds the optimistic scenario is with the wave suitability function (Fig. 7) switched off and the pessimistic scenario is with sensitivity to high waves. Additional sensitivity analyses are presented in the Supporting Material S4.

2.6.1.4. *Transition pathway.*

The pathway towards achieving potential

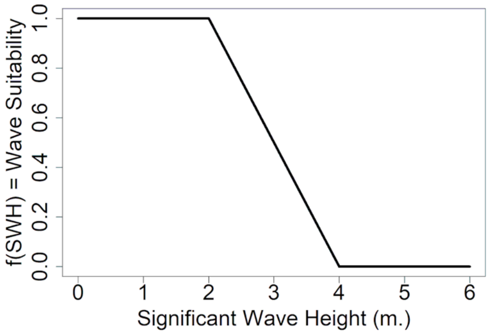


Fig. 7. Effect of wave height on site suitability for seaweed cultivation. Source: authors' estimate.

production (in tonnes annually) matters. It is nice to imagine a future world with large scale sustainable seaweed cultivation, but are we currently on track towards this ideal world? To assess this we extrapolated the current trend in seaweed production and we modelled what acceleration in production would be needed to achieve modelled potential production levels (optimistic and pessimistic) by the year 2050.

2.6.2. *Contribution to world food supply*

From FAOSTAT food balance sheets (FAO, 2023), global daily food supply including losses in households and losses in retail in 2019 was 2963 kcal capita^{-1} day^{-1}. With world population 7.652×10^{9} in 2019 and a conversion factor 1 kcal = 4.184 kJ, total world food supply in terms of energy is 34.6 × 10^{12} J year^{-1}. Projected population in 2050 is 9.735×10^{9} (United Nations, 2022), estimated food supply in 2050, assuming no change in diets, is 34.6 × 10^{12} * (9.735 / 7.652) = 44.1 × 10^{12} Jyear^{-1}. We are aware that with wealth of Asian countries increasing per capita intake may also increase, while at the same time concerns about limits to growth might force us into scenarios of lower per capita intake.

To assess the potential contribution of seaweeds to current and future food energy supply for food we converted from seaweed weight to energy. According to Olsson et al. (2020), seaweeds contain 273–557 g carbohydrates kg^{-1} dry seaweed and 59–201 g protein kg^{-1} dry seaweed). Similarly, Kraan (2013) reports seaweeds dry mass consisting for about 60% of carbohydrates. Energy content of carbohydrates and proteins in the same, 4 kcal g^{-1} dry. We thus estimate 1 kg of dried seaweed can provide 1×(0.6×1000)×4×4.184 = 8.4 MJ of energy. For reference, Table 1 compares energy content (MJ kg^{-1}) of seaweed with that of rice grains. The conversion factor of 8.4 MJ kg^{-1} dry was used to assess the current and future energy supply from seaweed compared with global food energy supply.

3. Results

3.1. *Global suitability for the three model species*

For the cold temperature species group, Fig. 8 shows the number months with overall monthly suitability's $SSS_{s,m,x}$ greater than 0.5, within the EEZ and with sensitivity to high waves. Supplementary material S4 shows for the cold temperature species group, site suitability is strongly sensitive to whether or not the significant wave height is taken into account: the area suitable for the cold temperature species group is far larger without than with the taking into account the *SWH* suitability function (Fig. S 19). Table 2 shows the production potential for the cold seaweeds within the EEZ is three times as large (370 vs 124 MT dry year^{-1}) in the optimistic scenario (not sensitive to waves) than in the pessimistic scenario (sensitive to waves). The main high potential region for cold seaweeds identified from Fig. 8 is the region of the coast of Southern Argentina. A vast suitable area further offshore in Southern Argentina (Fig. S 12, supporting material) is not considered here because it is outside the EEZ. The second largest suitable region identified from Fig. 8 is a northern belt in the Pacific (Alaska, Japan, Soviet Union). Small suitable regions are Greenland, parts of the North Sea (United Kingdom, Netherlands and other surrounding countries), Namibia (due to upwelling of cold nutrient rich water) and New Zealand.

Table 1
Energy content of seaweed and rice grains.

	Seaweed unprocessed	Brown rice uncooked
kg fresh	1	1
kg dry	0.15	0.86
MJ kg^{-1} fresh	1.3	14.1
MJ kg^{-1} dry	8.4	16.4

Table 2 shows in the pessimistic nutrient uptake parameter scenario, world oceans were found completely unsuitable for offshore cultivation of intermediate and warm temperature species. This may seem at odds with large tropical seaweed production in a number of tropical countries (Langford et al., 2021; McHugh, 2003; Valderrama et al., 2013, 2015). Our hypothesis is this is due to higher nutrient concentrations in the nearshore environment due to nutrient rich influx from estuaries and the fact that the course spatial resolution of the data used here (§2.4, supplementary material S2) does not represent well the higher nutrient concentrations often found just near the shore. We reflect on this uncertainty in the discussion section.

Fig. 9 shows for the intermediate temperature species for the optimistic nutrient uptake parameter scenario the number of suitable months. In this optimistic scenario large suitable regions are in nutrient upwelling regions along the coasts of South America and the South Western coasty of Africa. Suitable regions for intermediate temperature seaweeds are found in between the high latitudes (too cold) and low latitudes (to warm).

Suitable sites for the 'warm' seaweed species are found closer to the equator (Fig. 10), with a large suitable area in the central Pacific and two other much smaller suitable regions are in middle America (The Caribbean and Pacific coast of Nicaragua) and the Arabic peninsula. Supporting material also shows a vast suitable region in the central Pacific outside the EEZ (Fig. S 14, supporting material), which is here not included in seaweed production scenarios because our scenarios are limited to seaweed production within the EEZ.

More background information is presented in the supporting material. Figs. S9–S11 show monthly suitabilities for the entire oceans, showing which parts of the year are suitable for cultivation. Figs. S12–S14 are similar to Figs. 8–10, showing number of suitable months. The difference is Figs. S12–S14 show suitabilities for the whole world before clipping out the EEZ. Only suitable regions within the EEZ (Figs. 8–10) were subsequently used for production estimates discussed in following sections.

3.2. *Global production potential*

Table 2 shows global biophysical production potential according to the optimistic and pessimistic scenario. Suitable area is between 8 and 34 million km^{2} (777–3398 Mha), 6–25% of global EEZ area (138 million km^{2}) and 2–9% of world ocean area (362 million km^{2}). Thus vast areas of world oceans are unsuitable either due to biophysical constraints or being too far out of shore (outside the EEZ). In the pessimistic nutrient uptake parameter scenario only 'cold' seaweeds can be cultivated offshore, with annual potential production of 828 MT fresh (124 MT dry). In the more optimistic nutrient uptake scenario potential annual production levels are be 4878 MT Fresh and 732 MT dry. The large difference between the optimistic 732 and pessimistic 124 MT dry (6x smaller) shows the strong sensitivity of potential production estimates to uncertainties about impact of high waves and uncertainties about tropical seaweed nutrient requirements.

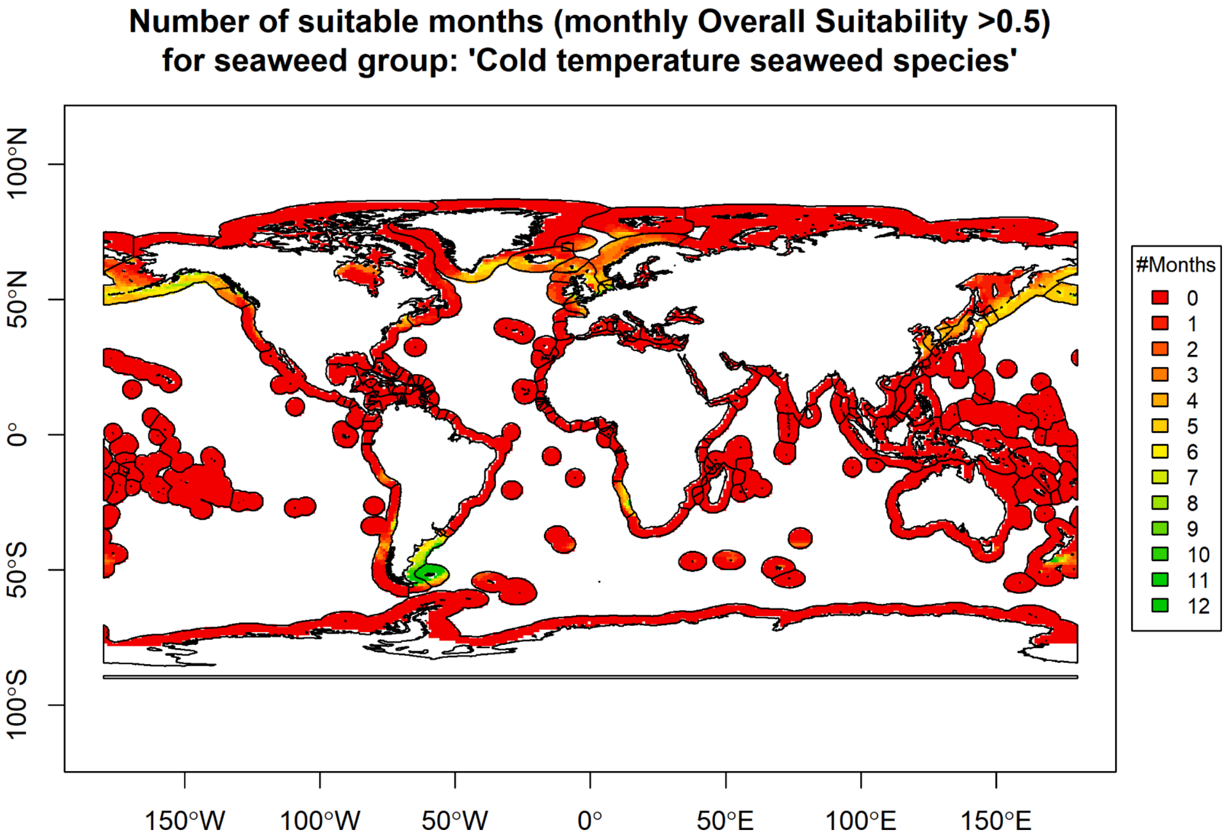


Fig. 8. Months with overall monthly suitability > 0.5 for the cold temperature seaweeds group inside the EEZ. Scenario with suitability dependent on Significant Wage height.

Table 2
Scenario calculations for biophysical seaweed production potential.

Scenario[1]	Model species temperature niche	Suitable (km^2)	Planted (km^2)	Production (MT Fresh)	Production (MT Dry)
optimistic	Cold – excl waves	15,387,403	153,874	2465	370
	Intermediate	11,413,047	114,130	1405	211
	Warm	7,180,667	71,807	1009	151
	Total	33,981,117	339,811	4878	732
pessimistic	Cold – incl waves	7,770,050	77,701	828	124
	Intermediate	0	0	0	0
	Warm	0	0	0	0
	Total	7,770,050	77,701	828	124

[1] Optimistic and pessimistic refers to large uncertainty about sensitivity to high waves (Section 2.5.6) in the cold species and large uncertainty in nutrient requirements of seaweeds in the mid-latitudes (intermediate temperatures) and in tropics (warm) as discussed in Section 2.5.4 of this paper.

3.3. Scenarios of production growth

Fig. 11 shows current trends in seaweed fresh production. FAO (2021) reports global fresh seaweed production increasing linearly from 20.2 MT fresh in 2010 to 34.7 MT fresh in 2019 (see also Fig. S11 in Supplementary material S3). The average annual increase is 1.6 MT fresh year^{-1} Seaweed production extrapolated to 2023 is 42.4 MT. To achieve the optimistic potential of 4878 MT fresh (Table 2) in 2050, seaweed production would have to increase by (4878–42.4)/(2050–2023) = 179 MT fresh year^{-1}, an annual rate of increase in production that is 179 / 1.6 = 111x higher than experienced in the past 2 decades. To achieve the pessimistic potential of 828 MT fresh (Table 2) in 2050, seaweed production would have to increase by (828–42.4)/(2050–2023) = 29 MT fresh year^{-1}, an annual rate of increase in production that is 29 / 1.6 = 18x higher than experienced in the past 2 decades. Even the most pessimistic estimate of global production potential will only be achieved with unprecedented acceleration of the current trend of global annual seaweed production increase.

3.4. Contribution to world food supply

Estimated global annual production of 34.7 MT fresh seaweed per year in 2019 can provide 43.7 × 10^{15} J year^{-1} of energy, compared with total annual world food supply of 34.6 × 10^{18} J year^{-1} in 2019 (Table 3). We thus estimate seaweeds currently provide only a fraction of 0.13% of food energy supply. The number is even less when considering not all seaweed is used as food, part of global seaweed production is used for biofuel energy production (Kerrison et al., 2015; Kraan, 2013). Our future scenarios show this number could rise to 0.25% if current seaweed production trend is continued (bottom thin line in Fig. 11). The number increases because the trend of increase in seaweed production is stronger than the trend for terrestrial food production (see Duarte et al. 2009 and see Table S 1 & Fig. S 15 in Supplementary material S3). Should the biophysical potential be fully realised (Table 2; upper two

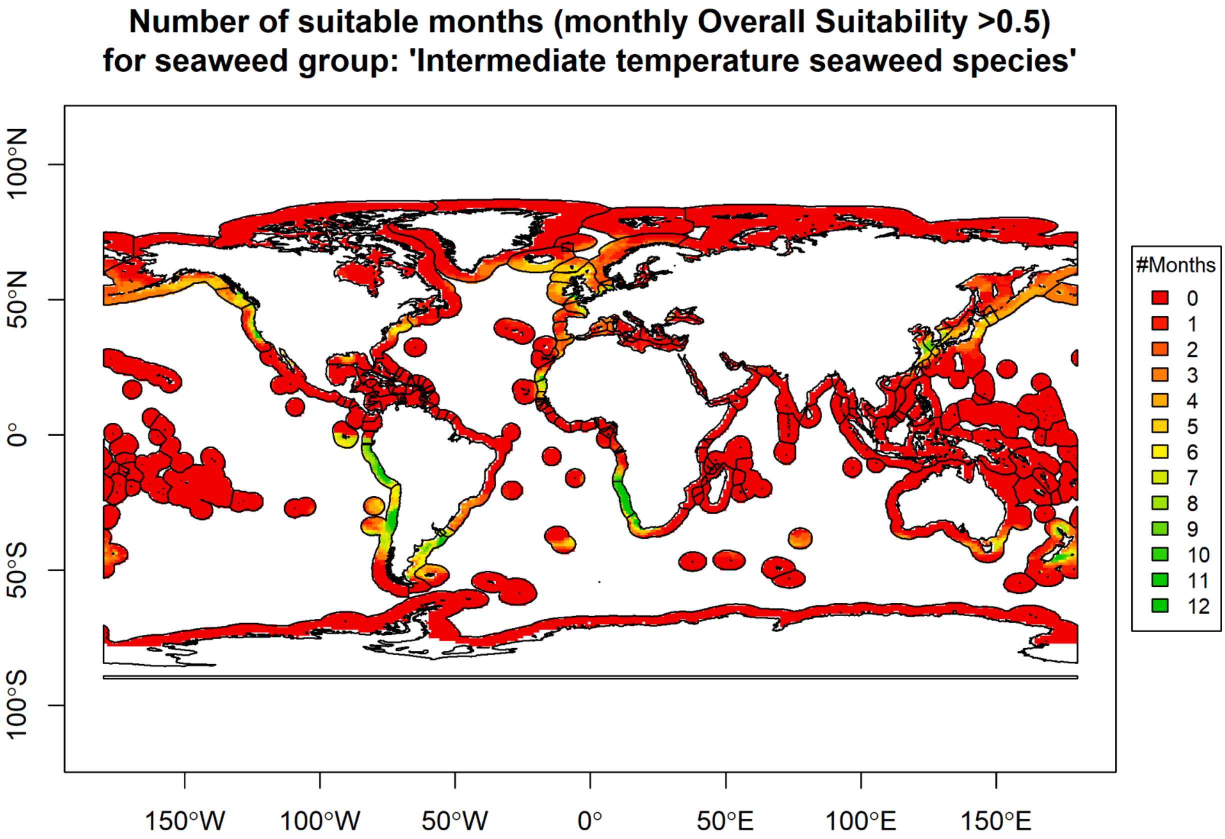


Fig. 9. Months with overall monthly suitability > 0.5 for the intermediate temperature seaweeds group. Optimistic nutrient uptake scenario. The black line 200 nautical miles out of shore is the EEZ.

lines in Fig. 11), contribution of seaweeds to total world food production in 2050 could increase to up to 2 to 14%.

4. Discussion

4.1. Main findings

We estimated, within ecological and economic boundaries, the global biophysical production potential of seaweeds cultivated offshore. For the scientific community the current study highlights the large knowledge gaps that still exist in seaweed research and quantifies the implications of these uncertainties for global production potential estimates. We reflect on these uncertainties in the following sections. For the policy making environment it is useful to have a ballpark estimate of the global production potential of seaweeds, even if (as we showed) such estimates are highly uncertain.

Our study is relevant in a context of growing population and growing pressure on terrestrial production, in which context it is relevant to explore how much human food energy seaweeds could potentially contribute to feeding the future world population. Our calculations show seaweed production can provide for up to a substantial number of 2 to 14% of global food energy supply. However at current rate of increase in seaweed production, projected energy supply from seaweeds in 2050 is projected to become only 0.25% of global food energy supply. A 2 to 14% contribution to global food energy supply will only be achieved with unprecedented acceleration of seaweed production.

Our studies show only 6–25% of the Exclusive Economic Zone (EEZ) and only 2–9% of world oceans is suitable for seaweed cultivation. With such limited area being suitable (according to our model), it is useful to identify suitable areas and suitable months, so development of new seaweed farms can target these high potential areas. Maps presented in the current study may be useful for this purpose.

4.2. Offshore & nearshore cultivation

The current paper complements recent work by Spillias et al. (2023) which also provided global production estimates. Surprisingly, both studies arrive at a similar contribution of seaweed to global food supply (Spillias et al. estimate a contribution of 10% to world food supply), but the production is obtained from different environments. Our study explores the offshore environment within the EEZ, up to around 370 km out of shore and we presumed for ecological concerns only 1% of each suitable site would be cultivated.

We used an environmental dataset with higher temporal resolution yet with poor representation of the near coastal environment (supplementary material S2). Spillias et al. (2023) considered the nearshore environment with cultivation confined to the narrow coastal zone up to 200 seafloor depth. In the study by Spillias et al. (2023), for each suitable pixel 50% of the pixel area was cultivated.

The two studies used different approaches to simulating production, but since these approaches were applied to different cultivated regions, one to one comparisons are not possible. What is clear from the comparison is that the two studies identify different highly suitable regions. According to Spillias et al. (2023), much of the highly suitable areas for nearshore seaweed cultivation are in Indonesia, which is consistent with current practice (FAO, 2021) and which is consistent with a modelling approach that does not consider absolute numbers for marine nutrient concentrations as a factor influencing yield potential. On the contrary our approach which does consider absolute numbers for marine nutrient concentrations suggests marine nutrient concentrations in Indonesia in the offshore environment are generally too low (Fig. S 3) and points to middle America, the central Pacific and the Arabic peninsula as the most suitable regions for tropical seaweed cultivation (Fig. 10). These interesting differences in identified suitable regions follow from differences in methods and differences in environmental input data. These disparate

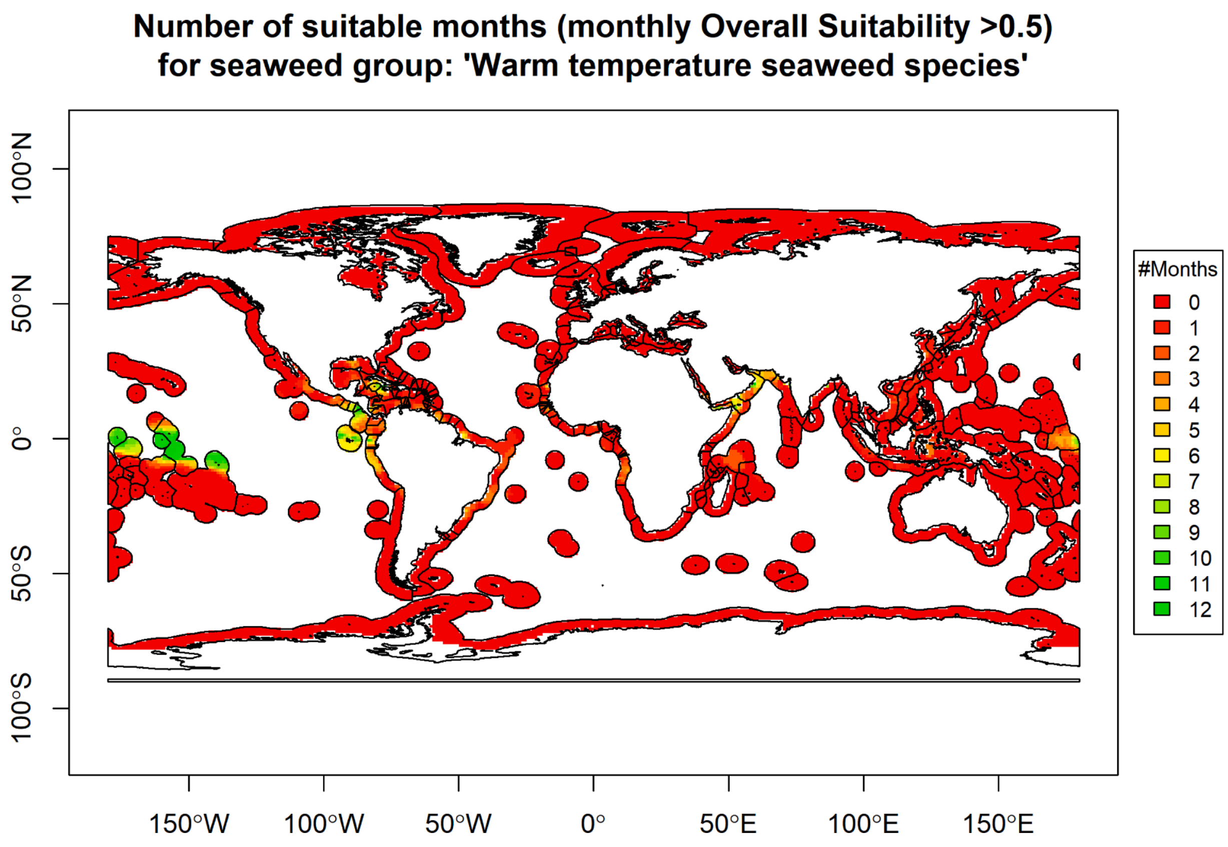


Fig. 10. Months with overall monthly suitability > 0.5 for the warm temperature seaweeds group. Optimistic nutrient uptake scenario. The black line 200 nautical miles out of shore is the EEZ.

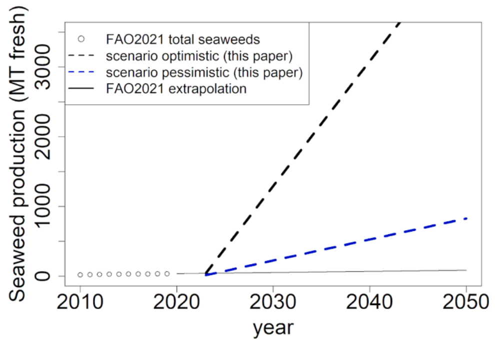


Fig. 11. Projections of future seaweed production: current trend and scenario realizing the biophysical production potential.

results help highlight implications of model assumptions and indicate a need for further research.

To date seaweed cultivation is often concentrated in sheltered bays or sheltered coastlines (Bak et al., 2018; Broch et al., 2019; Langford et al., 2021; Setyawidati et al., 2018). Our study targets the offshore environment which is generally less crowded with shipping and other marine sea uses. Offshore seaweed cultivation is showing first promising results but is also still in its infancy (Bak et al., 2018; Kerrison et al., 2015; Kraan, 2013; Solvang et al., 2021; Whiting et al., 2020). Much is still unknown about up to how far out of shore cultivation remains cost effective (Buschmann et al., 2017; Kapetsky et al., 2013; Lehahn et al., 2016). Oceans tend to be rougher further out of shore and much is still unknown about the engineering aspect of how to design floating structures for seaweed cultivation that can withstand high waves (Broch et al., 2019; Buck and Buchholz, 2004, 2005; Kapetsky et al., 2013; Kerrison et al., 2015; Kraan, 2013; Lehahn et al., 2016; Lovatelli et al., 2013; Solvang et al., 2021; van der Molen et al., 2018; Whiting et al., 2020).

Table 3
Seaweed potential contribution to world food supply expressed in energy.

	2019	2050
World food supply (TJ year^{-1})[1]	34,626,884	44,050,786
Seaweeds (TJ year^{-1})		
Current trend	43,767	108,139
Pessimistic[2]		1,043,115
Optimistic		6,146,811
Seaweeds / Total food supply		
Current trend	0.13%	0.25%
Pessimistic		2%
Optimistic		14%

[1] 1 Tera Joule (TJ) is 10^{12} J.

[2] Optimistic and pessimistic refers to large uncertainty about sensitivity to high waves (Section 2.5.6) in the cold species and large uncertainty in nutrient requirements of seaweeds in the mid-latitudes (intermediate temperatures) and in tropics (warm) as discussed in Section 2.5.4 of this paper.

4.3. *Validation*

Validating a model such as presented here is a challenge. Offshore seaweed cultivation is still in its infancy, therefore for vast areas of the world oceans, simply no seaweed data are available at all. No global maps exist of where and when seaweed is successfully cultivated offshore, let alone maps showing where seaweed cultivation was tried and failed. One may find an occasional study located within a 1° x 1° pixel (110 × 110 km at the equator). Even if available, such a site would represent only a sample out of a total of approximately 45,360 marine 1° x 1° pixels[1]. Thus observations from within 1 or few out of 45 thousand observations are hardly useful to validate or invalidate the maps reported here. Even within a 1° x 1° pixel spatial variability can exist in environmental conditions, especially as discussed above for pixels close to the shore, where the nearshore environment is not representative of environmental conditions and site suitability of the larger 1° pixel. Therefore multiple samplings may be needed per pixel to obtain a pixel average yield observation for model validation.

There are also differences in growth of different strains of the same species (e.g. see Jansen et al. 2022). Implicitly the model presented in this paper presumes farmers cultivate well performing strains, which implies validation should also be with well performing strains. In a context where selection and propagation of highly productive seaweed strains is still an emerging business (Ask and Azanza, 2002; Buschmann et al., 2001) one may need a number of months of experimentation with different strains to identify per site the most productive strains, and only after that cultivation and sampling for validation could commence. It should be clear model validation at a global scale is at the time of writing practically impossible. Which is why we refer to the current study as exploratory. For future validation, we recommend a stratified sampling scheme in which per species, cultivation is monitored in sites and months ranging from highly suitable to highly unsuitable (according to our model), and with validation sites in different parts of the world and for different species.

4.4. Uncertainties

Parameter uncertainty related to wave sensitivity of cold seaweeds led to a difference in suitable area of 15.4 vs 7.8 million km^2 (Table 2), a factor 2 difference and production potential ranging from 370 to 124 MT dry $year^{-1}$, a factor 3 difference. Parameter uncertainty related to nutrient requirements of intermediate and warm temperature species led to a difference in suitable area of 18.6 vs 0 million km^2 (Table 2) and production potential in the range of 0 to 211+151=362 MT dry $year^{-1}$. Uncertainty arises from our choice to confine production to the EEZ (about 370 km out of shore). In comparison in an assessment of offshore mariculture potential, Kapetsky et al. (2013) considered a much narrower zone of 46 km around ports as a cost-effectiveness suitability criterion. If 46 rather than 370 km out of shore were used as an criterion, potential seaweed production would be much less. A simple estimate is (46/370) times 2 to 14% is 0.29% to 1.73%, possibly higher due to higher nutrient concentrations and potential yields in the narrow coastal zone, possibly lower because the number of ports is limited (there may be biophysically suitable areas without a port present within 46 km). A similar uncertainty is in our choice to allocate only 1% of each suitable pixel for cultivation, accommodating for ecological concerns. Very little is known about potential competition between seaweed and the natural marine food web (Aldridge et al., 2021; Campbell et al., 2019; van der Meer et al., 2022) and therefore our 1% is a rather arbitrary choice. Should we raise this number to e.g. 5%, potential contribution of seaweed to global food energy production would increase by a factor 5 from 2–14% to 12–70%. A dietary shift towards such high percentages of seaweed consumption does not seem very likely. Rather, all of these order of magnitude calculations serve to quantitatively illustrate the large uncertainties that exist and that require further research.

A different category of uncertainty is outside the model domain and related to the transition pathway. It is relatively easy to model production potential, but quantifying the potential does not guarantee it will also be achieved. We showed that if current trends continue, estimated seaweed to human food energy in 2050 would be only 0.25%, much less than the simulated potential of 2–14%. Thus this potential will only by achieved with significant acceleration of growth of the seaweed sector, while here in the discussion section we showed offshore cultivation is still in its infancy. A major uncertainty is therefore also the question if and how much the offshore seaweed sector can grow in coming decades.

The current study did not consider possible implications of climate change. Sea surface temperatures are increasing and this will lead to shifts in which areas are suitable for which species. Suitable area for the cold temperature species will decrease (Murcia et al., 2020) and may be replaced with species of the intermediate temperature group. The situation is most worrying for the warm temperature species group (Du et al., 2022; Kim et al., 2021), where, if temperature functions as shown in Fig. 3 are correct, sites may become too hot for cultivation. Further research on climate change impact on seaweed cultivation potential is needed.

The qualitative conclusion that can be drawn from our research, regardless of all the uncertainties discussed above, is that the potential contribution of seaweed to feeding the world is substantial. The current exploratory study showing worldwide production potential may give impetus to continued R&D investments in advancing the offshore seaweed sector.

5. Conclusions

The current study is one of the first to estimate, within ecological and economic boundaries, the global biophysical production potential of offshore seaweeds cultivation. Within large uncertainty boundaries it shows seaweeds could contribute up to 2 to 14% of global food supply, a substantial contribution that will only be achieved with unprecedented increases in seaweed production.

Data & code availability

The data used in the current study are available from public sources. At the time of writing:

- WOA2018: https://www.ncei.noaa.gov/access/world-ocean-atlas-2018/.
- ERA5: https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels-monthly-means?tab=overview.
- EEZ: https://doi.org/10.14284/312.
- NASA-POWER agroclimatology: https://power.larc.nasa.gov/.

WOMAPP code: https://doi.org/10.5281/zenodo.7598570.
WOMAPP output files: https://doi.org/10.5281/zenodo.8016286.

CRediT authorship contribution statement

P.A.J. van Oort: Visualization, Conceptualization, Methodology, Formal analysis, Data curation, Writing – review & editing. **A. Verhagen:** Visualization, Conceptualization, Methodology, Writing – review & editing. **A.K. van der Werf:** Visualization, Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

van Oort, P.A.J. (2023). World Offshore Macro Algae Production Potential (WOMAPP) code. Zenodo. https://doi.org/10.5281/zenodo.7598570; van Oort, P.A.J. (2023). World Offshore Macro Algae Production Potential (WOMAPP) netcdf output data (1.0) [Data set].

---

[1] World is covered by 180 x 360 = 64,800 pixels with 1° x 1° resolution of which approximately 70% is marine, thus 86,400x0.7 = 45,360.

Zenodo. https://doi.org/10.5281/zenodo.8016286

Acknowledgments

We thank both anonymous reviewers for their thoughtful comments. Funding: the authors would like to acknowledge funding from the Wageningen University & Research Programme on "Food Security and Valuing Water" (project code KB-35-004-001) that is supported by the Dutch Ministry of Agriculture, Nature and Food Quality with grant number KB-35-004-001.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2023.110486.

References

Aldridge, J.N., Mooney, K., Dabrowski, T., Capuzzo, E., 2021. Modelling effects of seaweed aquaculture on phytoplankton and mussel production. Application to Strangford Lough (Northern Ireland). Aquaculture 536, 736400.

Ask, E.I., Azanza, R.V., 2002. Advances in cultivation technology of commercial eucheumatoid species: a review with suggestions for future research. Aquaculture 206, 257–277.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Global Ecol. Biogeogr. 27, 277–284.

Azevedo, I.C., Duarte, P.M., Marinho, G.S., Neumann, F., Sousa-Pinto, I., 2019. Growth of Saccharina latissima (Laminariales, Phaeophyceae) cultivated offshore under exposed conditions. Phycologia 58, 504–515.

Bak, U.G., Mols-Mortensen, A., Gregersen, O., 2018. Production method and cost of commercial-scale offshore cultivation of kelp in the Faroe Islands using multiple partial harvesting. Algal Res. 33, 36–47.

Borlongan, I.A., Gerung, G.S., Kawaguchi, S., Nishihara, G.N., Terada, R., 2017a. Thermal and PAR effects on the photosynthesis of Eucheuma denticulatum and Kappaphycus striatus (so-called Sacol strain) cultivated in shallow bottom of Bali, Indonesia. J. Appl. Phycol. 29, 395–404.

Borlongan, I.A., Nishihara, G.N., Shimada, S., Terada, R., 2017b. Effects of temperature and PAR on the photosynthesis of Kappaphycus sp. (Solieriaceae, Rhodophyta) from Okinawa, Japan, at the northern limit of native Kappaphycus distribution in the western Pacific. Phycologia 56, 444–453.

Borlongan, I.A., Nishihara, G.N., Shimada, S., Terada, R., 2017c. Photosynthetic performance of the red alga Solieria pacifica (Solieriaceae) from two different depths in the sublittoral waters of Kagoshima, Japan. J. Appl. Phycol. 29, 3077–3088.

Borlongan, I.A.G., Gerung, G.S., Nishihara, G.N., Terada, R., 2017d. Light and temperature effects on photosynthetic activity of E ucheuma denticulatum and K appaphycus alvarezii (brown and green color morphotypes) from Sulawesi Utara, Indonesia. Phycol. Res. 65, 69–79.

Broch, O.J., Alver, M.O., Bekkby, T., Gundersen, H., Forbord, S., Handå, A., Skjermo, J., Hancke, K., 2019. The kelp cultivation potential in coastal and offshore regions of Norway. Front. Mar. Sci. 5, 529.

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

Bruhn, A., Brynning, G., Johansen, A., Lindegaard, M.S., Sveigaard, H.H., Aarup, B., Fonager, L., Andersen, L.L., Rasmussen, M.B., Larsen, M.M., Elsser-Gravesen, D., Borsting, M.E., 2019. Fermentation of sugar kelp (Saccharina latissima)-effects on sensory properties, and content of minerals and metals. J. Appl. Phycol. 31, 3175–3187.

Buck, B.H., Buchholz, C.M., 2004. The offshore-ring: a new system design for the open ocean aquaculture of macroalgae. J. Appl. Phycol. 16, 355–368.

Buck, B.H., Buchholz, C.M., 2005. Response of offshore cultivated Laminaria saccharina to hydrodynamic forcing in the North Sea. Aquaculture 250, 674–691.

Buschmann, A.H., Camus, C., Infante, J., Neori, A., Israel, A., Hernandez-Gonzalez, M.C., Pereda, S.V., Gomez-Pinchetti, J.L., Golberg, A., Tadmor-Shalev, N., Critchley, A.T., 2017. Seaweed production: overview of the global state of exploitation, farming and emerging research activity. Eur. J. Phycol. 52, 391–406.

Buschmann, A.H., Correa, J.A., Westermeier, R., Hernández-González, M.D.C., Norambuena, R., 2001. Red algal farming in Chile: a review. Aquaculture 194, 203–220.

Campbell, I., Macleod, A., Sahlmann, C., Neves, L., Funderud, J., Øverland, M., Hughes, A.D., Stanley, M., 2019. The environmental risks associated with the development of seaweed farming in Europe - prioritizing key knowledge gaps. Front. Mar. Sci. 6, 107.

Carneiro, M.A.A., de Freire, F.A.M., Marinho-Soriano, E., 2011. Study on biofiltration capacity and kinetics of nutrient uptake by Gracilaria cervicornis (Turner) J. Agardh (Rhodophyta, gracilariaceae). Revista Brasileira de Farmacognosia 21, 329–333.

Douglas, E.J., Haggitt, T.R., Rees, T.A.V., 2014. Supply- and demand-driven phosphate uptake and tissue phosphorus in temperate seaweeds. Aquat. Biol. 23, 49–60.

Du, Y., Zhang, J., Jueterbock, A., Duan, D., 2022. Prediction of the dynamic distribution for Eucheuma denticulatum (Rhodophyta, Solieriaceae) under climate change in the Indo-Pacific Ocean. Mar. Environ. Res. 180, 105730.

Duarte, C.M., Bruhn, A., Krause-Jensen, D., 2022. A seaweed aquaculture imperative to meet global sustainability targets. Nat. Sustain. 5, 185–193.

Duarte, C.M., Holmer, M., Olsen, Y., Soto, D., Marbà, N., Guiu, J., Black, K., Karakassis, I., 2009. Will the oceans help feed humanity? Bioscience 59, 967–976.

Duarte, P., Ferreira, J.G., 1997. A model for the simulation of macroalgal population dynamics and productivity. Ecol. Modell. 98, 199–214.

Espinoza, J., Chapman, A.R.O., 1983. Ecotypic differentiation of Laminaria longicruris in relation to seawater nitrate concentration. Mar. Biol. 74, 213–218.

FAO, 2018. The Global Status of Seaweed production, Trade and Utilization. FAO Globefish Research Programme Volume 124. Rome, 120 pp.

FAO, 2021. FAO Yearbook. Fishery and Aquaculture Statistics 2019, Rome.

FAO, 2023. Food balances (2010).https://www.fao.org/faostat/en/#data/FBS [accessed online 2023-06-02].

Fischer, T., Byerlee, D., Edmeades, G., 2014. Crop Yields and Global Food Security: Will Yield Increase Continue to Feed the World? Australian Centre for International Agricultural Research (ACIAR), Australia, Canberra. ACT.

Flanders_Marine_Institute, 2020. Union of the ESRI country shapefile and the Exclusive Economic Zones (version 3).

Flo, E., Garcés, E., Manzanera, M., Camp, J., 2011. Coastal inshore waters in the NW Mediterranean: physicochemical and biological characterization and management implications. Estuar. Coast. Shelf. Sci. 93, 279–289.

Forster, J., Radulovich, R., Tiwari, B.K., Troy, D.J., 2015. Chapter 11 - seaweed and food security. Seaweed Sustainability. Academic Press, San Diego, pp. 289–313.

Fresán, U., Sabaté, J., 2019. Vegetarian diets: planetary health and its alignment with human health. Adv. Nutr. 10, S380–S388.

Froehlich, H.E., Afflerbach, J.C., Frazier, M., Halpern, B.S., 2019. Blue growth potential to mitigate climate change through seaweed offsetting. Curr. Biol. 29, 3087–3093 e3083.

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.

Garnett, T., Appleby, M.C., Balmford, A., Bateman, I.J., Benton, T.G., Bloomer, P., Burlingame, B., Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P.K., Toulmin, C., Vermeulen, S.J., Godfray, H.C.J., 2013. Sustainable intensification in agriculture: premises and policies. Science 341, 33–34.

Gentry, R.R., Froehlich, H.E., Grimm, D., Kareiva, P., Parke, M., Rust, M., Gaines, S.D., Halpern, B.S., 2017. Mapping the global potential for marine aquaculture. Nat. Ecol. Evol. 1, 1317–1324.

Godfray, H.C.J., Beddington, J.R., Crute, I.R., Haddad, L., Lawrence, D., Muir, J.F., Pretty, J., Robinson, S., Thomas, S.M., Toulmin, C., 2010. Food security: the challenge of feeding 9 billion people. Science 327, 812–818.

Gonen, Y., Kimmel, E., Friedlander, M., 1995. Diffusion boundary layer transport in gracilaria conferta (rhodophyta). J. Phycol. 31, 768–773.

Hayashi, L., Faria, G.S.M., Nunes, B.G., Zitta, C.S., Scariot, L.A., Rover, T., Felix, M.R.L., Bouzon, Z.L., 2011. Effects of salinity on the growth rate, carrageenan yield, and cellular structure of Kappaphycus alvarezii (Rhodophyta, Gigartinales) cultured *in vitro*. J. Appl. Phycol. 23, 439–447.

Hersbach, H., Bell, B., Berrisford, P., Biavati, G., Horányi, A., Muñoz Sabater, J., Nicolas, J., Peubey, C., Radu, R., Rozum, I., Schepers, D., Simmons, A., Soci, C., Dee, D., Thépaut, J.N., 2019. ERA5 monthly averaged data on single levels from 1979 to present. Copernicus Climate Change Service (C3S) Climate Data Store (CDS). (Accessed on 11-Feb-2021), doi: 10.24381/cds.f17050d7.

Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. J. Phycol. 36, 453–472.

Jansen, H.M., Bernard, M.S., Nederlof, M.A.J., van der Meer, I.M., van der Werf, A., 2022. Seasonal variation in productivity, chemical composition and nutrient uptake of Ulva spp. (Chlorophyta) strains. J. Appl. Phycol. 34, 1649–1660.

Jin, R., Ye, Z., Chen, S., Gu, J., He, J., Huang, L., Christakos, G., Agusti, S., Duarte, C.M., Wu, J., 2023. Accurate mapping of seaweed farms with high-resolution imagery in China. Geocarto. Int. 38, 2203114.

Kapetsky, J.M., Aguilar-Manjarrez, J., Jenness, J., 2013. A Global Assessment of Offshore Mariculture Potential from a Spatial Perspective. FAO Fisheries and Aquaculture Technical Paper No. 549. Rome, FAO. 181 pp.

Kerrison, P.D., Stanley, M.S., Edwards, M.D., Black, K.D., Hughes, A.D., 2015. The cultivation of European kelp for bioenergy: site and species selection. Biomass Bioenergy 80, 229–242.

Kim, B.T., Han, I.S., Lee, J.S., Kim, D.H., 2021. Impact of seawater temperature on Korean aquaculture under representative concentration pathways (RCPs) scenarios. Aquaculture 542, 736893.

Kraan, S., 2013. Mass-cultivation of carbohydrate rich macroalgae, a possible solution for sustainable biofuel production. Mitig. Adapt. Strateg. Global Change 18, 27–46.

Langford, A., Waldron, S., Sulfahri, Saleh, H., 2021. Monitoring the COVID-19-affected Indonesian seaweed industry using remote sensing data. Mar. Policy 127, 104431.

Lavaud, R., Filgueira, R., Nadeau, A., Steeves, L., Guyondet, T., 2020. A dynamic energy budget model for the macroalga Ulva lactuca. Ecol. Modell. 418, 108922.

Lehahn, Y., Ingle, K.N., Golberg, A., 2016. Global potential of offshore and shallow waters macroalgal biorefineries to provide for food, chemicals and energy: feasibility and sustainability. Algal Res. 17, 150–160.

Lovatelli, A., Aguilar-Manjarrez, J., Soto, D., 2013. Expanding mariculture farther offshore. Technical, environmental, spatial and governance challenges. FAO Fisher. Aquac. Proc. 24, 85.

Lubsch, A., Timmermans, K., 2018. Uptake kinetics and storage capacity of dissolved inorganic phosphorus and corresponding N:P dynamics in Ulva lactuca (Chlorophyta). J. Phycol. 54, 215–223.

Lubsch, A., Timmermans, K.R., 2020. Phosphate and nitrate uptake dynamics in Palmaria palmata (Rhodophyceae): ecological and physiological aspects of nutrient availability. J. Phycol. 54, 215–223.

Mahadevan, K., Tiwari, B.K., Troy, D.J., 2015. Chapter 13 - seaweeds: a sustainable food source. Seaweed Sustainability. Academic Press, San Diego, pp. 347–364.

McHugh, D.J., 2003. A guide to the seaweed industry. FAO Fisheries Technical Paper 441.

Murcia, S., Riul, P., Mendez, F., Rodriguez, J.P., Rosenfeld, S., Ojeda, J., Marambio, J., Mansilla, A., 2020. Predicting distributional shifts of commercially important seaweed species in the Subantarctic tip of South America under future environmental changes. J. Appl. Phycol. 32, 2105–2114.

NASA, 2020. Prediction Of Worldwide Energy Resources (POWER). https://power.larc.nasa.gov/ [accessed online 2023-06-02].

Olsson, J., Toth, G.B., Albers, E., 2020. Biochemical composition of red, green and brown seaweeds on the Swedish west coast. J. Appl. Phycol. 32, 3305–3317.

Ozaki, A., Mizuta, H., Yamamoto, H., 2001. Physiological differences between the nutrient uptakes of Kjellmaniella crassifolia and Laminaria japonica (Phaeophyceae). Fish. Sci. 67, 415–419.

Pedersen, M.F., Borum, J., 1997. Nutrient control of estuarine macroalgae: growth strategy and the balance between nitrogen requirements and uptake. Mar. Ecol. Prog. Ser. 161, 155–163.

Pudlo, N.A., Pereira, G.V., Parnami, J., Cid, M., Markert, S., Tingley, J.P., Unfried, F., Ali, A., Varghese, N.J., Kim, K.S., Campbell, A., Urs, K., Xiao, Y., Adams, R., Martin, D., Bolam, D.N., Becher, D., Eloe-Fadrosh, E.A., Schmidt, T.M., Abbott, D.W., Schweder, T., Hehemann, J.H., Martens, E.C., 2022. Diverse events have transferred genes for edible seaweed digestion from marine to human gut bacteria. Cell Host Microbe 30, 314–328 e311.

Rajauria, G., Cornish, L., Ometto, F., Msuya, F.E., Villa, R., Tiwari, B.K., Troy, D.J., 2015. Chapter 12 - Identification and selection of algae for food, feed, and fuel applications. Seaweed Sustainability. Academic Press, San Diego, pp. 315–345.

Setyawidati, N.A.R., Puspita, M., Kaimuddin, A.H., Widowati, I., Deslandes, E., Bourgougnon, N., Stiger-Pouvreau, V., 2018. Seasonal biomass and alginate stock assessment of three abundant genera of brown macroalgae using multispectral high resolution satellite remote sensing: a case study at Ekas Bay (Lombok, Indonesia). Mar. Pollut. Bull. 131, 40–48.

Smit, A.J., 2002. Nitrogen uptake by Gracilaria gracilis (Rhodophyta): adaptations to a temporally variable nitrogen environment. Bot. Mar. 45, 196–209.

Solvang, T., Bale, E.S., Broch, O.J., Handå, A., Alver, M.O., 2021. Automation concepts for industrial-scale production of seaweed. Front. Mar. Sci. 8, 613093.

Spillias, S., Valin, H., Batka, M., Sperling, F., Havlík, P., Leclère, D., Cottrell, R.S., O'Brien, K.R., McDonald-Madden, E., 2023. Reducing global land-use pressures with seaweed farming. Nat. Sustain. 6, 380–390.

United Nations, D., Population Division, 2022. World Population Prospects.

Valderrama, D., Cai, J., Hishamunda, N., Ridler, N., 2013. Social and Economic Dimensions of Carrageenan Seaweed Farming. Fisheries and Aquaculture Technical Paper No. 580. Rome, FAO. 204 pp.

Valderrama, D., Cai, J., Hishamunda, N., Ridler, N., Neish, I.C., Hurtado, A.Q., Msuya, F.E., Krishnan, M., Narayanakumar, R., Kronen, M., Robledo, D., Gasca-Leyva, E., Fraga, J., 2015. The economics of Kappaphycus seaweed cultivation in developing countries: a comparative analysis of farming systems. Aquac. Econ. Manag. 19, 251–277.

van den Burg, S.W.K., Dagevos, H., Helmes, R.J.K., 2021. Towards sustainable European seaweed value chains: a triple P perspective. ICES J. Mar. Sci. 78, 443–450.

van der Meer, J., Hin, V., van Oort, P.A.J., van de Wolfshaar, K.E., 2022. A simple DEB-based ecosystem model. Conserv. Physiol. 10, coac057.

van der Molen, J., Ruardij, P., Mooney, K., Kerrison, P., O'Connor, N.E., Gorman, E., Timmermans, K., Wright, S., Kelly, M., Hughes, A.D., Capuzzo, E., 2018. Modelling potential production of macroalgae farms in UK and Dutch coastal waters. Biogeosciences 15, 1123–1147.

van Ittersum, M.K., van Bussel, L.G.J., Wolf, J., Grassini, P., van Wart, J., Guilpart, N., Claessens, L., De Groot, H., Wiebe, K., Mason-D'Croz, D., Yang, H., Boogaard, H., van Oort, P.A.J., van Loon, M.P., Saito, K., Adimo, O., Adjei-Nsiah, S., Agali, A., Bala, A., Chikowo, R., Kaizzi, K., Kouressy, M., Makoi, J.H.J.R., Ouattara, K., Tesfaye, K., Cassman, K.G., 2016. Can sub-Saharan Africa feed itself? Proc. Natl. Acad. Sci. USA 113, 14964–14969.

van Oort, P.A.J.. World Offshore Macro Algae Production Potential (WOMAPP) code. Zenodo. https://doi.org/10.5281/zenodo.7598570.

van Oort, P.A.J., Rukminasari, N., Latama, G., Verhagen, A., van der Werf, A.K., 2022. The Bio Economic Seaweed Model (BESeM) for modelling tropical seaweed cultivation – experimentation and modelling. J. Appl. Phycol. 34, 2627–2644.

Van Zanten, H.H.E., Herrero, M., Van Hal, O., Röös, E., Muller, A., Garnett, T., Gerber, P.J., Schader, C., De Boer, I.J.M., 2018. Defining a land boundary for sustainable livestock consumption. Global Change Biol. 24, 4185–4194.

Venolia, C.T., Lavaud, R., Green-Gavrielidis, L.A., Thornber, C., Humphries, A.T., 2020. Modeling the growth of Sugar Kelp (Saccharina latissima) in aquaculture systems using dynamic energy budget theory. Ecol. Modell. 430, 109151.

Wang, C., Su, R., Guo, L., Yang, B., Zhang, Y., Zhang, L., Xu, H., Shi, W., Wei, L., 2019. Nutrient absorption by Ulva prolifera and the growth mechanism leading to green-tides. Estuar. Coast. Shelf. Sci. 227, 106329.

Watanabe, Y., Nishihara, G.N., Tokunaga, S., Terada, R., 2014a. Effect of irradiance and temperature on the photosynthesis of a cultivated red alga, Pyropia tenera (= Porphyra tenera), at the southern limit of distribution in Japan. Phycol. Res. 62, 187–196.

Watanabe, Y., Nishihara, G.N., Tokunaga, S., Terada, R., 2014b. The effect of irradiance and temperature responses and the phenology of a native alga, Undaria pinnatifida (Laminariales), at the southern limit of its natural distribution in Japan. J. Appl. Phycol. 26, 2405–2415.

Watanabe, Y., Yamada, H., Mine, T., Kawamura, Y., Nishihara, G.N., Terada, R., 2016. Photosynthetic responses of Pyropia yezoensis f. narawaensis (Bangiales, Rhodophyta) to a thermal and PAR gradient vary with the life-history stage. Phycologia 55, 665–672.

Whiting, J.M., Wang, T., Yang, Z., Huesemann, M.H., Wolfram, P.J., Mumford, T.F., Righi, D., 2020. Simulating the trajectory and biomass growth of free-floating macroalgal cultivation platforms along the U.S. west coast. J. Mar. Sci. Eng. 8, 1–19.

WOA, 2018. World Ocean Atlas 2018.

Zaucha, J., Gee, K., 2018. Maritime Spatial Planning: Past, Present, Future. Palgrave Macmillan, Basingstoke, Hampshire.