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ARTICLE

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Exergy efficiency of light conversion into biomass in the macroalga *Ulva* sp. (*Chlorophyta*) cultivated under the pulsed light in a photobioreactor

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Abstract

Marine macroalgae are a potential feedstock for biorefineries that can reduce dependence on fossil fuels and contribute to bioeconomy. New knowledge and technologies for efficient conversion of solar energy into macroalgae biomass are needed to increase biomass yields and energy conversion efficiency. In this work, we show that the green macroalgae from *Ulva* sp. can grow under the pulsed light in a photobioreactor with higher exergy conversion efficiency in comparison to cultivation under constant light with the same intensity. In the tested frequencies, 1–40 Hz and duty cycles (DC) 1–100%, DC has a stronger impact on the growth rate than frequency. The efficiency of light transformation into biomass increased with decreasing DC. Pulsating with DC 20% led to 60% of the biomass chemical energy yield for the respective constant light (DC 100%). Models of *Ulva* sp. growth rate and exergy conversion efficiency as a function of pulsating light parameters were developed. These results open new directions to enhance solar to chemical energy conversion through macroalgae by controlling the light distribution in the macroalgal biomass.

KEYWORDS
energy conversion efficiency, flashing light, macroalgae, photobioreactor, pulsed light, *Ulva*

1 | INTRODUCTION

Offshore biomass production could play a significant role in the development of economy by reducing the use of fossil fuels, slowing the growth of land conversion to agriculture, providing food, platform chemicals, and fuels (Buschmann et al., 2017; Lehahn, Ingle, & Golberg, 2016; Zilberman, 2013). Therefore, the potential of macroalgae feedstock for such sustainable biorefinery is under intensive investigation in laboratory and pilot scales (Bikker et al., 2016; Camus, Infante, & Buschmann, 2016; van et al., 2013). A critical step in the use of macroalgae for industrial-scale biorefinery is the sustainability of biomass production. Current technology for offshore marine biomass cultivation includes systems for kelp growth (Bird, 1987), tidal flat farms, floating cultivation (Bird, 1987), ring cultivation (Buck, & Buchholz, 2004), wind-farm integrated systems, bottom plantation (Aitken, Bulboa, Godoy-Faundez, Turrion-Gomez, & Antizar-Ladislao, 2014), reviewed in (Fernand et al., 2016). However, future expansion of the biomass production in the sea will need shifting the cultivation infrastructure to more exposed environments where operation with current technologies would require complex logistics and high costs (Troell et al., 2009, 2011). Clearly, new knowledge on solar energy to chemical energy conversion in macroalgae biomass is needed; new technologies to use this knowledge for effective offshore cultivation will increase the biomass yields per unit of installation area that currently restraining by the production costs.

A key factor in the production of biomass refers to biomass yield (kg dry matter [DM]) per unit of installation area (m^2). Low yields

require larger areas to supply the total biomass, thus more fuel is needed for boat transportation (Lehahn et al., 2016). Higher yields per unit area would lead to lower environmental impacts, low sea areas footprint of the large-scale systems, and would drive the cost reduction because of the smaller transportation costs (Lehahn et al., 2016). Yields are limited by multiple factors, such as nutrients availability, diseases, physical environment (waves), and biological environment (grazing) (Fernand et al., 2016; Polikovsky, Chemodanov, & Golberg, 2018). The major energy input for biomass growth is the solar energy. One of the limitations of solar energy conversion into biomass is the time limit of photosynthetic receptors to capture photons and regenerate in the light reactions of photosynthesis (Kok, Forbush, & McGloin, 1970). This is in addition to restrictions caused by the activity of key enzymes involved in the biochemistry of dark reactions when CO_2 is being reduced to simple sugars (Miranda, Baker, & Long, 1981). While plants and algae have the ability to harvest almost 100% of the incident PAR (i.e., the arriving photons), the total photosynthetic efficiency is only around 6% due to the low conversion of this energy into biochemical products in the cell, together with a significant loss of energy as heat and fluorescence (Zhu, Long, & Ort, 2010). Therefore, in a continuously sun illuminated outdoor seaweed cultivation system, the rate of photosynthesis is not limited by the number of incident photons during the daytime (Farquhar & Sharkey, 1982; Marcus, Altman-Gueta, Wolff, & Gurevitz, 2011; Stitt, 1986).

Photosynthetic rates are, in addition, significantly affected by several other factors including a number of physiological processes limited by temperature, CO_2, and nutrients diffusion, and carbon fixation enzymes (León-Sánchez, Nicolás, Nortes, Maestre, & Querejeta, 2016). For example, slow rates of Rubisco activity, limited electron transport through the Cytochrome b6–f complex in the thylakoid membrane, and slow metabolism of 3-phosphoglycerate have been referred in some plants and algae (Farquhar & Sharkey, 1982; Hasan & Cramer, 2012; Marcus et al., 2011; Paul, 2001; Stitt, 1986; Stitt & Schulze, 1994). Moreover, over-saturating light intensity may lead to photobleaching and growth inhibition (Rubio Camacho, García Camacho, Fernández Sevilla, Chisti, & Molina Grima, 2003). Understanding and overcoming the rate limiting reactions is critical to improving the offshore biomass yields, including the case when algae are grown under light saturation in the offshore environment.

Two major approaches have been proposed to overcome the energy conversion limiting reactions kinetics: re-engineering of the photosynthetic machinery (Lin, Occhialini, Andralojc, Parry, & Hanson, 2014; Orr, Pereira, da Fonseca, Zsögön, & Araújo, 2017) and specially designed photobioreactors that expose cells to pulsed light (Simionato, Basso, Giacometti, & Morosinotto, 2013). The re-engineering of photosynthesis system to improve its efficiency is an extremely complex task (Maurino & Weber, 2013) and the suitability of the engineered plants and especially algae grown offshore is an open question because of their potential environmental threats (Chandrasekaran, Arun Nagendran, Pandiaraja, Krishnankutty, & Kamalakannan, 2008; Conklin & Smith, 2005). Previous studies in tomato have shown that equal photosynthetic rates can be achieved by continuous and pulsed light (Tennessen, Bula, & Sharkey, 1995). Flashing light cultivation has been used in microalgae photobioreactors aiming at reducing photobleaching and increasing conversion efficiency yields (Abu-Ghosh, Fixler, Dubinsky, & Iluz, 2016; Degen, Uebele, Retze, Schmid-Staiger, & Trösch, 2001; Kim et al., 2014; Lee & Palsson, 1994; Matthijs et al., 1996; Sforza, Simionato, Giacometti, Bertucco, & Morosinotto, 2012; Vejrazka, Janssen, Streefland, & Wijffels, 2011; Yoshimoto, Sato, & Kondo, 2005).

In a previous theoretical work, we showed the potential benefits of mixing to increase the biomass yield per unit area in a model macroalgae, *Ulva* sp. (Chemodanov, Jinjikhashvily, et al., 2017; Golberg & Liberzon, 2015). However, the design of such a device where macroalgae are grown offshore in large volumes and each thallus is exposed only to the portion of the solar incident light surface requires further knowledge on *Ulva* sp. growth under the pulsed light. Although biomass growth of plant and microalgae under pulsed light has been reported before (Gris, Morosinotto, Giacometti, Bertucco, & Sforza, 2014; Nedbal, Tichý, Xiong, & Grobbelaar, 1996; Tennessen et al., 1995), most recently reviewed in (Schulze, Guerra, Pereira, Schüler, & Varela, 2017), to the best of our knowledge there are no reports on macroalgae, and specifically of *Ulva* species, grown under pulsed light. These data will be of importance not only for a fundamental understanding of algal metabolism under the pulsed light but it will also enable a rational design of macroalgal cultivation in photobioreactors both onshore and offshore cultivation.

Hence, we aimed the current study to determine growth rates and exergy conversion efficacy of *Ulva* sp., our model macroalgae when cultivated under the pulsed light. The hypothesis is that macroalgae exergy conversion efficiency of light into biomass can be increased under the pulsed light. To test this hypothesis, we designed a laboratory scale photobioreactor to grow *Ulva* sp. under various light regimes. We used the photobioreactor to determine the macroalgae growth rates and exergy conversion efficiency under constant and pulsed light conditions with constant intensity, which simulated constant solar illumination outdoors. It allowed for studying the energy budget of *Ulva* sp. thalli in terms of marginal chemical energy gain for each quantum of absorbed energy of light. We describe an experimental system and provide modeling tools that enable determination of part of the illumination parameters that predicate macroalgae growth rates, productivity, and could enable higher yields per unit of installation area in future offshore cultivation.

2 | MATERIALS AND METHODS

2.1 | *Ulva* Sp. as a model organism for biomass production

Ulva sp., green marine macroalgae of worldwide distribution found in the intertidal and shallow waters within the Israeli Mediterranean Sea shores was used as a model species. For the current study, specimens were taken from stocks maintained at Israel Oceanographic & Limnological Research, Haifa, Israel (IOLR). Each experiment used a fresh supply of algae biomass and were performed from December 12, 2016 to March 1, 2017. The algae stocks contain a mix of *Ulva fasciata*

and *Ulva rigida*, both species bearing very similar morphologies as described recently by the ref (Krupnik et al., 2018). For each experiment, a new batch of artificial seawater was prepared using deionized water mixed with dried sea salt (Red Sea Salt, Cheddar, UK). Macronutrients were supplied by adding ammonium chloride (NH_4Cl, Sigma, Rehovot, Israel) and sodium phosphate (NaH_2PO_4, Sigma) to maintain 462 mol m^{-3} of nitrogen and 0.031 mol m^{-3} of phosphorus in the seawater medium. Air flow rates into the cultivation vessels assured for an equal nutrients flux to the thalli. Seawater pH and salinity levels were monitored with a waterproof double junction pH tester 30 (Oakton, Cole-Parmer, IL) and a refractometer (Pentair, Apopka, FL), respectively. The experiments started with pH values of 8.0 ± 0.5 and salinities of 3.5–3.6 %.

2.2 | Photobioreactor for macroalgae cultivation under pulsed light

The experimental closed system, Figures 1a and 1b, included a 75 L reservoir tank (Plasson, Maagan Michael, Israel) equipped with a centrifugal pump (ESPA, PISCIS1, Banyoles, Spain) to allow for the circulation of the artificial seawater through six reactors (1 L, 6.5 cm diameter, Figure 1c) in which *Ulva* sp. thalli (~0.6 g FW) were cultivated. The temperature in the tank was controlled with a 300 W heating body and a thermostat (JEBO 2010, Jebo, China) at 20–25 °C. The temperature was measured twice a day in the tank near the inlet of the pump using a thermometer ([−10°]−150°, 1° resolution, Livingstone, NSW, Australia). The water flew from the tank through the pump through 32 mm PVC flexible tube (Pal-Yam, Tnuvot, Israel) to a distribution pipe (PVC, length 1 m, width 5 mm, Plasson), Figure 1b. From the distribution pipe, six thin pipes (Legris 8 × 5.5 polyurethane polyether) are connected to a series of valves including bypass system and a rotameter (50–800 ml/min, error 1.25% FS, Emporio, Israel), Figure 1b. This set of devices enables to fix the flow rate for each test tube 850 ml min^{-1}. From each reactor, the water flew out through the outlet pipe returning the water to the tank. A 130 µ filter was integrated on the bypass line in order to collect organic waste from the water, Figure 1b.

Thalli in each reactor were illuminated with an LED system (60 W PAR grow light LED, Flora Photonica, Israel) enabling to control the illumination parameters for each reactor, Figure 1c. The LED light includes six colors in the wavelengths: 380, 430, 460, 630, 660, and 740 nm. Each LED was connected to a signal generator (1–3,000 Hz, 1–99% Duty Cycle), Figure 1d, and a power supply (MCH-303A, 3 0V/3A, Lion electronics, Haifa, Israel) controlling illumination intensity (up to 4,000 µmol-photons m^{-2} s^{-1}). The wavelengths were measured with MK350 spectrometer (360–750 nm, UPRtek, Ocean Optics, UK). All intensity measurements were taken at the center of the cultivation reactor using Li-Car 192 PAR radiation sensor (400–700 nm, error 5%, Li-Car, Lincoln, NE). The reactors were isolated using simple carton boards to prevent mutual influences. A photograph of the system is shown in Figure 1e.

Every setup of flashing light is characterized by illumination intensity (I), frequency (f), and duty cycle (DC). The experimental design aimed to test the impact of various illumination parameters on the *Ulva*

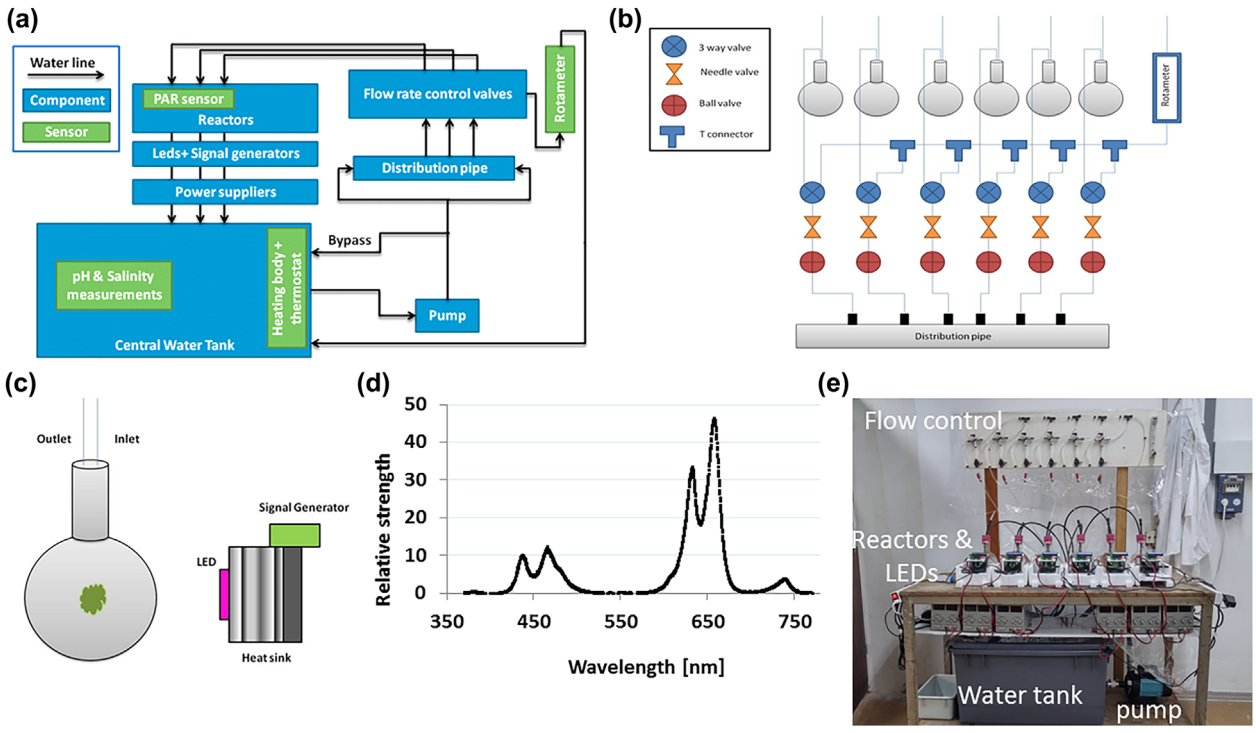

FIGURE 1 (a) The schematic design of the laboratory scale macroalgae photobioreactor for macroalgae cultivation under the pulsed light. (b) Schematic design of a flow regulation system. (c) Schematic presentation of a single reactor. (d) Measured spectrum of used LEDs. (e) Digital image of the developed laboratory macroalgae photobioreactor

sp growth rate and light energy to chemical energy conversion efficiency. In the first set of experiments, we impact of frequency and duty cycle. The first set of chosen frequencies and duty cycles for pulsed light cultivation was based on previous research on different plants growth under pulsed light (Abu-Ghosh, Fixler, Dubinsky, & Iluz, 2015; Phillips & Myers, 1954; Terry, 1986). The second set of chosen pulsed light parameters focused on the impact of DC on the growth rates for a constant frequency of 1 Hz. The important element of our experiment design keeping the intensity constant in all pulsed light experiments. This was done to simulate algal cultivation conditions outdoors where illumination intensity is constant relative to mixing frequencies.

2.3 | Biomass growth rates measurement

The daily growth rates, *DGR* (% d^{-1}), were determined as described in Equation (1) following (Penniman, Mathieson, & Penniman, 1986; Schmidt, Nunes, Maraschin, & Bouzon, 2010):

$$DGR = 100\%\cdot\frac{FW_{out} - FW_{in}}{FW_{in}\cdot N_{days}} \quad (1)$$

Where FW_{in} (g) is the fresh weight of the thalli at the beginning of the experiment, FW_{out} (g) is the fresh weight of thalli at the end of the experiment, N_{days} is the number of cultivation days under specific illumination conditions. The areal productivity, P (gDW m^{-2} d^{-1}) was calculated as in Equation (2):

$$P = \frac{FW_{out} - FW_{in}}{A\cdot N_{days}}\cdot\frac{DW}{FW} \quad (2)$$

where A (m^2) is the illuminated area. In all our studies, N was equal to 3 days.

Fresh weight (FW) of the thalli was determined after disregarding excessive seawater using a lettuce dryer spinner for the 30 s and paper towel, altogether taking less than 2 min before biomass measurements using analytical scales (BBA-600, MRC, Israel).

As we tested biomass growth at different light regimes, we also defined the normalized Daily Growth Rate (%) where the values of DGR at various light regimes were normalized to DGR at constant light (DGR_c):

$$NDGR[\%] = DGR/DGR_c \quad (3)$$

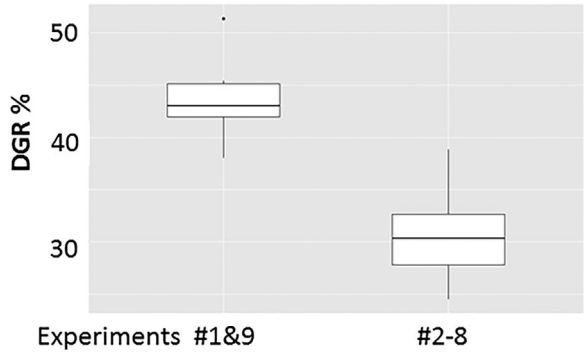

FIGURE 2 Boxplot of daily growth rates (DGR%) at control (constant light) experiments. $N = 30$

2.4 | Biomass exergy accumulation efficiency estimation

The irreversibility effects of light energy conversion to chemical energy of the biomass can be analyzed using the concepts from the second law of thermodynamics (Gaggioli & El-Sayed, 1989; Tsatsaronis, 1987). Studies on the irreversibility of the process that occur in the anthropic energy conversion systems, which are the case of macroalgae production for food, chemicals and fuels, led to the concept of "energy available to do a work," (Arons, 1927), defined as "exergy" by Rant (Rant, 1953). The goal of the optimization of energy conversion system, including macroalgae cultivation, is to maximize the exergy produced by the system per invested exergy (Szargut, Morris, & Steward, 1988). The exergy efficiency (Dewulf, Van Langenhove, & Van De Velde, 2005; Golberg, 2015; Luis, 2013; Sciubba, 2003) of light conversion to biomass was calculated using Equation (4):

$$\eta = E_g/E_i \quad (4)$$

where η is the exergy conversion efficiency, E_g ($J\cdot m^{-2}$) is the energy accumulated in the biomass during N_{days} per illuminated area of the reactor and E_i ($J\cdot m^{-2}$) is the light energy invested during N_{days}. The accumulated energy in the biomass during N_{days} was calculated using Equation (5):

$$E_g(N_{days}) = \frac{(FW_{out} - FW_{in})\cdot c_p\cdot DW/FW}{A} \quad (5)$$

where c_p ($kJ\cdot g^{-1}$) is the energy density of the biomass, DW/FW is the ratio of dry weight to wet weight and A (m^2) is the illuminated area of the reactor with thalli. In this work we used 11 kJ g^{-1} for *Ulva* biomass, as measured in our previous studies (Chemodanov, Jinjikhashvily, et al., 2017; Chemodanov, Robin, & Golberg, 2017), A was 0.00432 m^2. The dry weight of the biomass was measured by drying the biomass at 105 °C for 3 hr. The used DW/FW was 0.15 as measured in (Chemodanov, Robin et al., 2017). The invested energy (E_i) was calculated using Equation (6):

$$E_i(N_{days}) = I_s\cdot\varepsilon\cdot DC\cdot t\cdot N_{days} \quad (6)$$

where I_s (μmole photons m^{-2} s^{-1}) is the Photosynthesis Activate Radiation (PAR) generated by the LEDs, ε (W /μmole photons m^{-2} s^{-1}) is the transformation factor specific to the solar spectrum (0.219 used in this study), DC is the duty cycle of the illumination (ratio of light to dark periods within one illumination cycle), and t (s) is the total illumination time per day.

TABLE 1 *Ulva* sp. growth rates and productivities under a constant illumination of 1,000 μmol photons m^{-2} s^{-1}

Experiment	Cultivation dates	Average P [g m^{-2} d^{-1}]	Median P [g m^{-2} d^{-1}]	SD [g m^{-2} d^{-1}]	Average DGR [%]	Median DGR [%]	SD [%]	η [%]
#1–3 (*N* = 18)	13-29/12/16	7.23	7.47	1.22	35.17	35.84	6.63	1.12
#1–9 (*N* = 30)	13/12-23/2/17	7.06	6.71	1.39	34.11	32.22	7.04	1.09
#2–8 (*N* = 22)	20/12/17-9/2/17	6.41	6.37	0.85	30.67	30.31	4.08	0.99
#1&9 (= 8)	13-15/12/16, 21-23/2/17	8.83	8.74	0.98	43.58	43.03	3.97	1.37

N is the number of measurements.

2.5 | Statistical analysis

Statistical analysis was done with Excel ver. 10 data analysis package (Microsoft, SE). Statistical analysis was done using Spearman (r_s) and Pearson correlation (R^2) methods, implemented in R (ver. 3.4.2). Data normality distribution was assessed with Shapiro–Wilk test. Linear and non-linear regression models were constructed using a solver available in R (Bates & Chambers, 1992). To test if coefficients of the developed models are significant, 10^3 coefficients were generated with the random shuffling of the measured parameter. For the control group, where algae were grown under constant light, outliers, defined as values farther than ± standard deviation (SD) were removed.

For all models, developed in this study, we calculated the total relative error (TRE) using Equation (7):

$$\mathrm{TRE} = \frac{100}{m}\sqrt{\sum_{i=1}^{m}\left(\frac{S_i - PV_i}{PV_i}\right)^2} \quad (7)$$

where m is the number of measurements, S_i is the measured values, and PV_i is the predicted value. Student's *t*-test, two-tail, and Mann–Whitney–Wilcoxon tests were done for groups comparisons if not mentioned otherwise. The significance level was set at 0.05.

3 | RESULTS AND DISCUSSION

3.1 | Growth rates of *Ulva* sp. under constant light

Two different groups of growth rates were identified among the algae cultivated at the exactly the same conditions under constant light. From the total nine experiments, for experiments #2–#8 the measured DGR was 25–39%; however, for the experiments #1 (cultivated from December 13 to December 16, 2016) and # 9 (Cultivated from 21 February to 23 February 2017), all the DGR of replicates exceeded 38% (Figure 2) (The weekly average of DGR for repetitions #1&9 was 42–47% while for repetitions #2-8 it was 27–34% (Table 1). The productivities for #2-8 were 6.37 ± 0.85 g m^{-2} d^{-1} and for #1&9 the productivities were 8.74 ± 0.85 g m^{-2} d^{-1} (Table 1). The *t*-test comparison between these two groups results in Student's *t*-statistic of $2.11 \cdot 10^{-8}$, and Mann–Whitney–Wilcoxon test *p*-value of $4.95 \cdot 10^{-5}$ suggesting a significant difference between these two groups. The boxplots of the measured DGR under constant light for experiments #2–8 and #1&9 are shown in Figure 2. The DGR averages, medians, and SDs are shown in Table 1 below.

Data from Table 1 show that even though the average DGR of replicates from experiments #1 and #9 was higher than DGR of the rest of the groups (43.58% vs. than 30.67%), the SD was similar (3.97% vs.

TABLE 2 *Ulva* sp. growth rate and productivity under pulsed light illumination with a fixed illumination intensity of 1,000 μmole photons m^{-2} s^{-1}

Cultivation dates	Setup	Frequency, f [Hz]	DC [%]	DGR [%]	P [g m^{-2} d^{-1}]	NDGR	η [%]
3–5/1/17	A1	40	20	17.78	3.7	0.58	2.87
	A2	40	20	15	3.12	0.49	2.42
3–5/1/17	B1	4	20	14.75	3.12	0.48	2.42
	B2	4	20	21.11	4.4	0.69	3.41
10–12/1/17	C1	7	3	6.67	1.39	0.24	7.18
	C2	7	3	5	1.04	0.18	5.38
10–12/1/17	D1	50	50	20.56	4.28	0.76	1.33
	D2	50	50	25	5.2	0.92	1.61
17–19/1/17	E1	40-1* average (27)	20-50* average (30)	28.73	5.78	0.98	2.99
	E2	40-1* average (27)	20-50* average (30)	24.29	4.98	0.83	2.57
17–19/1/17	F1	1-40* average (13)	50-20* average (40)	18.03	3.82	0.61	1.48
	F2	1-40* average (13)	50-20* average (40)	16.94	3.47	0.58	1.35

*Setups E and F represent "random" flashing light when frequency and duty cycle were changed between the values through the experiment. All experimental data are shown.

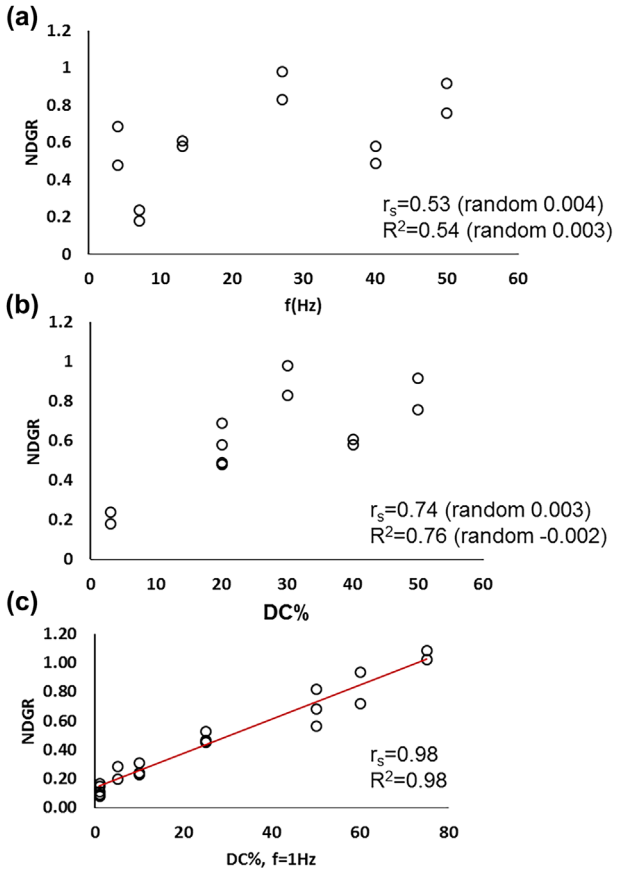

FIGURE 3 Normalized to constant light, average daily growth rate (NDGR%) as a function of (a) frequency (f), *N* = 12. (b) duty cycle (DC). *N* = 12. Exact DC and frequencies for each point appear in Table 2, (c) DC at f = 1 Hz. *N* = 20

4.08%), suggesting that the differences are not caused by variations in the system, but by physiological conditions of algae. The observed differences could be attributed to the seasonal impact on the starting biomass, provided fresh for each experiment, which was cultivated under natural illumination, and natural running seawater, as was observed in plants tissue cultures (Stone, 1963). Annual studies on *Ulva*, collected from the same locations showed seasonal patterns of growth hormones (Stirk et al., 2009). Yet, additional studies on plant tissue culture reported on seasonal impacts on plant tissue culture, grown under controlled conditions for 3 years, effects which could not be related directly to the starting biomass (Sharma, Hänsch, Mendel, & Schulze, 2005). Recent work on *Ulva* vegetative growth in the precisely controlled laboratory conditions showed that growth rates exhibited a rhythmic pattern with one major peak every 2 or 3 days, which authors

TABLE 3 Correlation of NDGR with DC% and frequency (f) under pulsed light illumination with fixed illumination intensity (I) of 1,000 µmole photons m^{-2} s^{-1}

	DC%	DC% random	f (Hz)	f (Hz)- random
Spearman (r_s)	0.74	0.003	0.53	0.004
Pearson (R^2)	0.76	-0.002	0.54	0.003

TABLE 4 Duty cycle impact on *Ulva* sp. growth rate (*N* = 2 per condition, normalized to control (*N* = 2) growth at the same week)

Frequency [Hz]	DC [%]	NDGR	P [g m^{-2} d^{-1}]	η [%]
1	1	0.08	0.46	7.18
		0.11	0.81	12.56
		0.09	0.93	14.35
1	5	0.29	1.81	5.63
		0.2	0.74	2.30
1	10	0.24	1.39	2.15
		0.31	2.2	3.41
		0.23	2.31	3.59
1	25	0.47	2.66	1.65
		0.53	3.7	2.30
		0.45	4.51	2.80
1	50	0.82	4.74	1.47
		0.57	4.05	1.26
		0.68	6.28	2.12
1	75	1.08	6.47	1.34
		1.03	6.16	1.27

rs,0.94; *R2*, 0.98.

Average NDGR values and productivities are shown. Algae were grown under the constant frequency of 1 Hz with fixed illumination intensity (I) of 1,000 µmole photons m^{-2} s^{-1}. All data are shown.

related to large-scale Rossby and Kelvin waves that produce oscillations in the geomagnetic fields (Kalita & Titlyanov, 2013). Our results indicate that for all flashing lights experiments, parallel control, cultivated under the constant light are needed. Furthermore, normalization to these controls is essential for groups' comparison.

3.2 | *Ulva* biomass productivity under the pulsed light

Table 2 displays the NDGR (DGR of the algae grown under pulsed light normalized by DGR of algae grown under constant light during the same time as calculated using Equation (4)) and productivities for experiments with various frequencies and duty cyles. Shapiro–Wilk test on the NDGR resulted in a *p*-value of 0.84, suggesting that the data is distributed normally.

Setups E and F represent "random" flashing light when frequency and duty cycle were changed between the values mentioned in Table 2 through the experiment. The NDGR at setup D (50 Hz frequency and 50% DC) was 0.84. This suggests that under permanent light (100% DC) *Ulva* is in saturation in terms of photons conversion efficiency to biomass. Similar results, NDGR of 0.9, were observed in the setup E, where the algae were grown part of the time at the frequency of 40 Hz with DC 20% and part of the time at frequency 1 Hz with DC of 50%. The results with group C (7 Hz frequency and 3% DC) reveals an interesting phenomenon: cultivation with DC of only 3% resulted in the NDGR of 0.21. That means that only 3% of light was invested in comparison with the group grown under continuous illumination, but

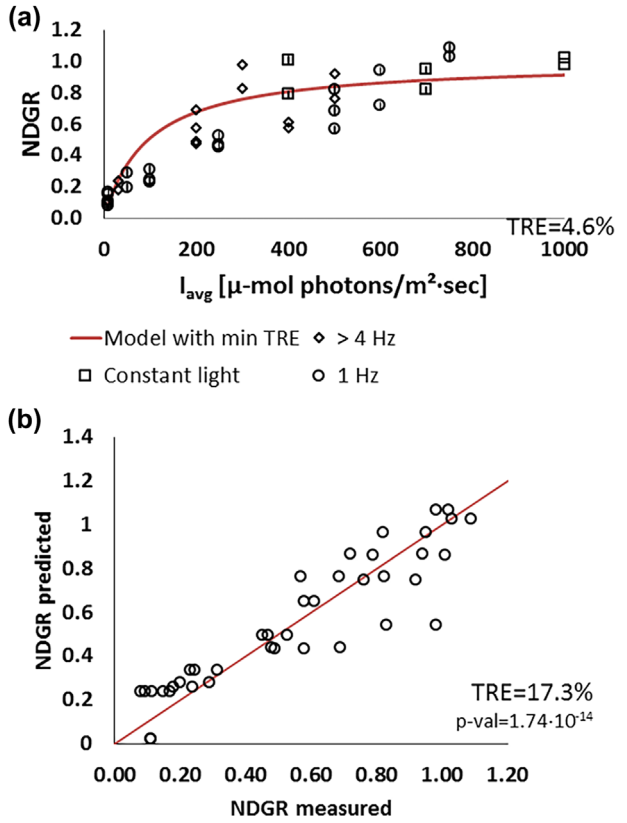

FIGURE 4 (a) Normalized to constant light, average daily growth rate (NDGR%) as a function of average light intensity (I_{avg}), fitted not linear saturation model is shown as a red line. $N = 59$. (b) A multivariate linear regression model of NDGR as a function of frequency, DC and average light intensity. $N = 59$

the yield is 21% of the biomass cultivated under constant light. In comparison with group D, the ratio of NDGR to photons invested in group C is higher by 5 ($NDGR_C/DC_C = 5NDGR_D/DC_D$).

To examine this phenomenon of conversion efficiency increase, we need to understand what the components of the illumination setup were. While taking a closer look at the relations of the frequency and DC% to the NDGR it can be seen that the frequency has a weaker correlation to the growth rate (Figure 3a, Table 3) than DC% (Figure 3b, Table 3). Spearman correlation point to stronger, not random, relation between DC% and growth rate with a r_s of 0.74 for NDGR vs DC% (random shuffling of NDGR 10^3 times resulted in r_s of 0.003) in comparison to still not random r_s of 0.53 for NDGR vs frequency (random shuffling of NDGR 10^3 times resulted in r_s of 0.004). Pearson correlation point to stronger, not random, relation between DC%, and growth rate with an R^2 of 0.76 for NDGR versus DC% (random shuffling of NDGR 10^3 times resulted in R^2 of −0.002) in comparison to still not random R^2 of 0.54 for NDGR versus frequency (random shuffling of NDGR 10^3 times resulted in R^2 of 0.003).

Table 4 shows the NDGR and productivity data for the experiments that aimed to determine the impact of DC% on the DGR at a constant frequency of 1 Hz (Figure 2c). The dependence of the NDGR on the DC (at a constant frequency of 1 Hz) appears in Figure 2c and can be described by the following function which gives the best fit (r_s and $R^2 = 0.98$):

$$NDGR = 0.0119DC + 0.1393 \quad (8)$$

Next, we compared a non-linear model that describes *Ulva* NDGR as a function of average light (I_{av}, calculated as DC · I/100) as described in Equation (9), (Figure 4a) with a multivariate linear regression model, as described in Equation (10) (Figure 4b).

$$NDGR_i = \frac{DGR_i}{DGR_c} = \frac{\frac{DGR_{max} I_{avg\_i}}{K + I_{avg\_i}}}{\frac{DGR_{max} I_{avg\_c}}{K + I_{avg\_c}}} = \frac{I_{avg\_i}}{I_{avg\_c}} \frac{K + I_{avg\_c}}{K + I_{avg\_i}} \quad (9)$$

where i is the number of the experiment (total 40 points were modeled), I_{avg_i} is the average illumination is experiment i, I_{avg_c} is the average light intensity in the control run at the same experiment and K is the specific parameter that described this

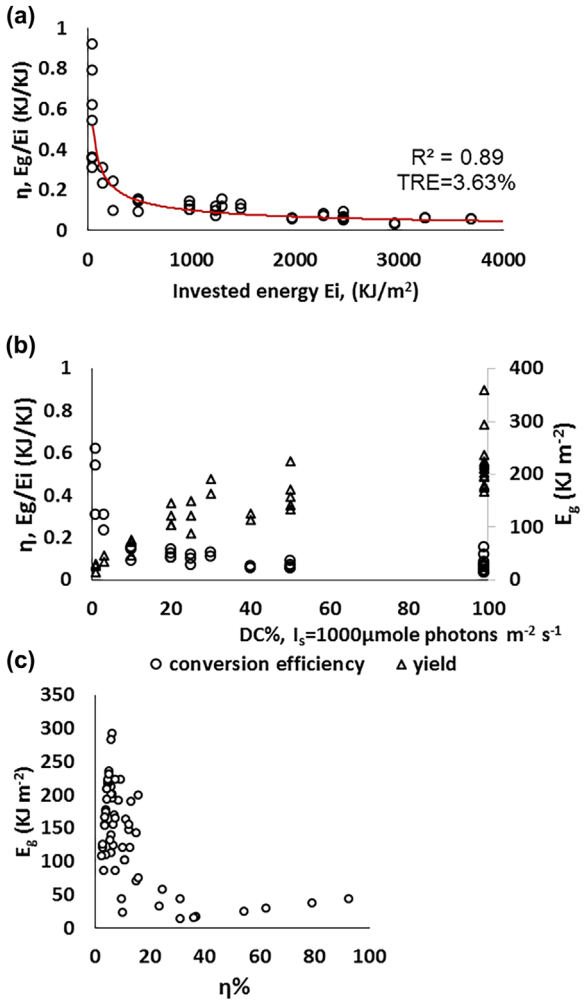

FIGURE 5 (a) Exergy efficiency of light conversion to chemical energy vs Invested energy (E_i). $N = 59$. (b) Exergy efficiency of light conversion to chemical energy and measured yield (gained energy) versus DC at a constant illumination of I_s of 1,000 µmole photons m^{-2} s^{-1}. $N = 55$. (c) Yield (gained energy) versus conversion efficiency. N = 59

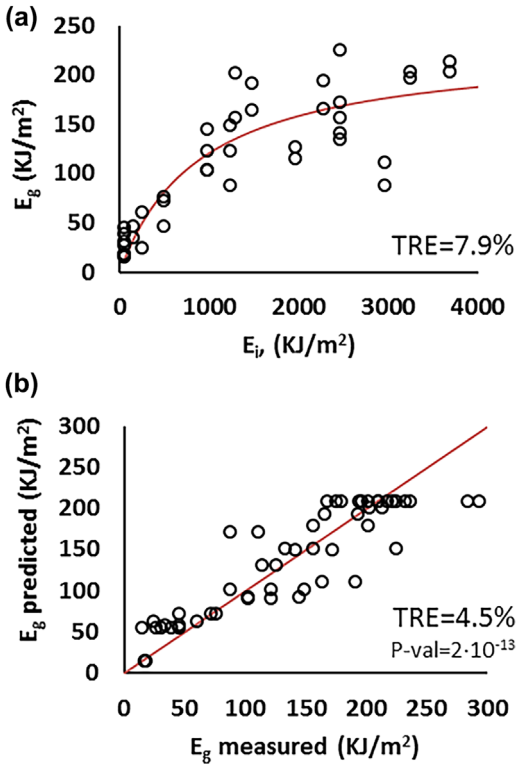

FIGURE 6 (a) Gained chemical energy (E_g) as a function of invested energy (E_i), fitted not linear saturation model is shown as a red line. (b) A multivariate linear regression model of gained energy (E_g) as a function of frequency, DC and average light intensity. $N = 59$

saturation curve calculated with Excel solver with a function to minimize TRE. The calculated K was 92.39 and the corresponding TRE was 4.6%.

$$NDGR_i = \beta_0 + \beta_1 f + \beta_2 DC + \beta_3 I_{avg\_i} + \varepsilon \quad (10)$$

where β_o is the intercept, and $\beta_1, \beta_2, \beta_3$ are the linear coefficients and ε is the model error.

The determined coefficients (using R nls (·) function) were: 0.229 (β_o), −0.00022 (β_1), 0.00724(β_2), 0.00034 (β_3), further confirming the previous observation that DC is the strongest predictor, among measured parameters, of the NDGR. The corresponding TRE was 17.3%, suggesting that non-linear Equation (9) provides a better fit for the data in this experiment. This model suggests that *Ulva* biomass growth rate is limited and achieves its maximum at the average light intensity of 200 µmol photons m^{-2} s^{-1}, similar results on maximum electron transfer rates at ~200 µmol photons m^{-2} s^{-1}, however not supplied by pulsed light, were reported for various *Ulva* species (Wang et al., 2016).

3.3 | Energy conversion efficiency

The goal of this work is to test the hypothesis that efficiency of energy conversion from solar energy to biomass (η) will be improved in *Ulva* sp. cultivated under pulsed light. Calculated results, as shown on Figure 5a, show the power dependence of the accumulated chemical energy derivative to the invested energy, as described by the Equation (11):

$$\eta = 3.52 E_i^{-0.506} \quad (11)$$

From which follows the connection between the invested light energy and the accumulated chemical energy, Equation (12):

$$E_g = 1.73 E_i^{0.494} \quad (12)$$

These results indicate, that decreasing the invested energy, increases energy conversion efficiency of light to chemical energy stored in biomass. However, we found opposite trends when plotting η and Eg versus DC (Figure 5b), for algae grown under the same frequency at constant, and flashing light conditions. As shown on Figure 5b, decreasing DC increases the efficiency, however, it decreases the total gain energy per area (Figur 5c, Table 4) for a single layer of algae. Increasing efficiency and DC to more than 20% did not increase the yield.

Next, we established the relationship between invested (E_g) and gained energies (E_g) using non-linear (Figure 6a) regression models. The saturation equation that describes the observed relations between invested and gained energies appears in Equation (13):

$$E_g = \frac{E_i E_{g\_max}}{E_i + K_E} \quad (13)$$

where E_{g_max} is the maximum energy gain (KJ/m^2) and K_i is fitted parameter. In this study, for E_{g_max} of 230 KJ m^{-2} and K_E of 907 KJ m^{-2}, the model resulted in TRE of 7.9%.

Finally, we used linear regression to model the gained chemical energy (E_g) as a function of flashing light parameters as described in Equation (14):

$$E_g = \alpha_0 + \alpha_1 f + \alpha_2 DC + \alpha_3 I_{avg\_i} + \varepsilon \quad (14)$$

where α_o is the intercept, and $\alpha_1, \alpha_2, \alpha_3$ are the linear coefficients and ε is the model error.

The determined coefficients (using R nls (·) function) were: 52.4 (α_o), −0.04 (α_1), 1.48(α_2), 0.05 (α_3), indicating that DC is the strongest predictor, among measured parameters in the tested ranges, of the E_g. The corresponding TRE was 4.5% (Figure 6b).

Our results suggest that above finite value, the invested energy is no longer effective to increase the yield, furthermore, the efficiency of the conversion is reduced. These findings suggest that growth rates and productivities of macroalgae biomass currently cultivated under normal, constant light illumination outdoors, as is currently accepted (Fernand et al., 2016), can be further improved by dividing the light by multiple layers of algae. One of the strategies to achieve this could be

increasing the density of cultivated biomass; thus, each thallus will be exposed to a small proportion of all incoming light. The approach to increase density for higher efficiency, using the flashing light effect was demonstrated for microalgae in thin photobioreactors (Qiang, Richmond, & Zarmi, 1998; Richmond, 2004). Combination of these and other emerging technologies for light harvesting and redistribution with macroalgae biomass growth, based on our models derived from laboratory experiments, could provide a new direction for more efficient utilization of offshore installations for biomass production.

4 | CONCLUSIONS

In this work, we tested the hypothesis that the marine macroalga *Ulva* sp. can be grown under pulsed light with higher energy conversion efficiency as compared to the constant light conditions, similar to open cultivation systems. We found that the efficiency of light conversion into biomass is increased with pulsed light. In the range of frequencies 1–40 Hz and DC 1–100%, tested in this study, DC has a stronger impact on the growth rate than frequency. The efficiency of light transformation to biomass increases with a decrease in DC under the frequency of 1 Hz. The maximum conversion efficiency was achieved under 1 Hz frequency and 1% DC, however, to a total yield of the biomass was the lowest. These results open a new direction for the increase of seaweed biomass yield in the offshore environment by redistributing the sunlight in the biomass.

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CONFLICTS OF INTEREST

The authors declare no financial interests.

AUTHOR'S CONTRIBUTIONS

OH designed the study, conducted experiments, analyzed data, and drafted the manuscript. ON cultivated the macroalgae for studies. AI cultivated the macroalgae for studies and drafted the manuscript. AG performed statistical analysis and developed models. AL and AG designed the study, analyzed data, supervised the work and drafted the manuscript.

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