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Review

Thermal response analysis and compilation of cardinal temperatures for 424 strains of microalgae, cyanobacteria, diatoms and other species

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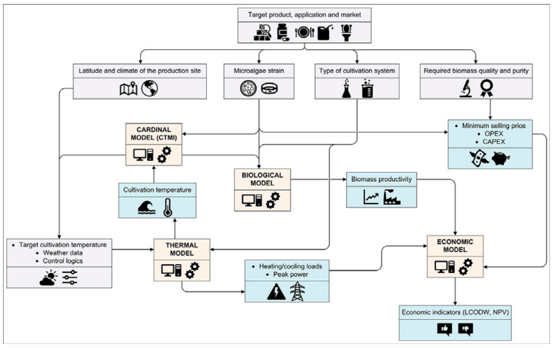
HIGHLIGHTS

- Review of temperature effects on microalgae, cyanobacteria, and other phototrophs
- Minimum, maximum, and optimal temperature comparison for 424 strains and 148 genera
- Harmonized electronic database for optimal strain identification and data selection
- Applications to thermal and biological modelling of industrially-relevant strains
- Preliminary assessment of energy consumption for different locations and strains

GRAPHICAL ABSTRACT



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ABSTRACT

Microalgae and other phototrophic microorganisms can be cultivated to produce food and valuable bioproducts, also allowing to remove nutrients from wastewater and CO_2 from biogas or polluted gas streams. Among other environmental and physico-chemical parameters, microalgal productivity is strongly influenced by the cultivation temperature. In this review, cardinal temperatures identifying the thermal response, i.e., the optimal growth condition (T_{OPT}), and the lower and upper limits for microalgae cultivation (T_{MIN} and T_{MAX}), have been included in a structured and harmonized database. Literature data for 424 strains belonging to 148 genera of green algae, cyanobacteria, diatoms, and other phototrophs were tabulated and analysed, with a focus on the most relevant genera that are currently cultivated at the industrial scale in Europe. The dataset creation aimed at facilitating the comparison of different strain performances for different operational temperatures and assisting in the process of thermal and biological modelling, to reduce energy consumption and biomass production costs. A case study was presented, to illustrate the effect of temperature control on the energetic expenditure for cultivating different *Chorella* sp. strains under a greenhouse located in different European sites.

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1. Introduction

Microalgae and other phototrophic organisms (such as cyanobacteria or other planktonic species) are typically cultivated at the industrial scale, to produce food and dietary supplements for human and animal consumption, as well as many other valuable bio-products, such as antioxidants or pigments (Khan et al., 2018). Microalgae (this term generally indicating phototrophic microorganisms) are typically richer in proteins, carbohydrates, and lipids, compared to conventional crops and livestock, which is an advantage from the nutritional point of view, and makes them attractive as a solution for the food and feed market (Koyande et al., 2019; Vigani et al., 2015). Moreover, thanks to their characteristics, microalgae have been identified as promising organisms, through which it is possible to mitigate several bottlenecks of current agricultural practices and environmental bioremediation technologies. Microalgae-based wastewater treatment is a particularly interesting application field, as these organisms can efficiently remove nutrients from wastewater (Saravanan et al., 2021; Oviedo et al., 2022). Thanks to their photosynthetic activity, exploiting the sunlight as an energy source, these microorganisms can contextually remove CO_2 from gaseous streams and provide O_2 to aerobic bacteria in algae-bacteria systems (Saravanan et al., 2021; Rossi et al., 2020a). This translates into a reduction of energy costs for oxygenation, which is the main drawback of conventional bioremediation processes (Rosso et al., 2008). In addition, the valorisation of the algal biomass grown on low-quality water resources is ensured by the recovery of added-value products, such as crop biofertilizers and biostimulants (Koutra et al., 2018; Ronga et al., 2019). A very large number of algal species has been identified during the last century (with recent estimates ranging from 100,000 to 800,000) (Koyande et al., 2019; Amaro et al., 2012), but only a few are effectively cultivated at the industrial scale (Araújo et al., 2021).

Table 1 reports a selection of industrially-relevant genera that are typically exploited for the food/feed industry (human and animal nutrition), the generation of biofuels and bio-products (bioplastics, biofertilizers, and biostimulants), or for environmental applications (CO_2 fixation and wastewater bioremediation) (Araújo et al., 2021; Spolaore et al., 2006; Camacho et al., 2019; Sharma et al., 2022). The industrial production of these organisms is a relatively well-established process, with a Technology Readiness Level (TRL) up to 6–7, based on previous reports (Rumin et al., 2020; Chauvy et al., 2019). However, the stability of microalgae cultures can be threatened by relevant variations in weather conditions, that have a strong influence on the algal growth. This is especially true in outdoor cultivation systems, which are necessarily subject to both daily and seasonal alterations of the environmental culture conditions. Among the parameters having major effects on the algal growth rate and productivity, temperature, irradiance, pH, and DO can strongly influence the growth of phototrophic cultures, and thus the success of their final applications (Costache et al., 2013; Ippoliti et al., 2016; Rossi et al., 2020b). In particular, temperature plays a major role in defining the evolution of the cultivation, especially in systems subject to external contamination (such as outdoor raceway reactors), where the onset of species that are more adapted to the actual temperature can lead to the rapid collapse of the desired algal strain (Singh and Singh, 2015). As recently reviewed, the effect of temperature on algal growth can be very different according to the algal species, phyla, and even strain (Varshney et al., 2015; Ras et al., 2013). For example, green algae of the phyla Chlorophyta (e.g., *Chlorella* and *Scenedesmus* spp.) typically grow at their maximum rate when the temperature is in the range 25–35 °C. On the contrary, cyanobacteria such as *Arthrospira* sp., or red algae like *Galdieria* sp. can grow well at higher temperatures (>35 °C) (Singh and Singh, 2015; Paerl et al., 2011). Many psychrophilic strains have been found among diatoms, such as *Nitzschia* sp., having optimal temperatures lower than 15–20 °C (Thorel et al., 2014), and several strains of polar microalgae are also known (Varshney et al., 2015). As pointed out by Varshney et al., exploiting extremophilic strains that are acclimated to particular conditions can be a major advantage to reach high productivities, e.g., in arid and desertic zones, or polar climates (Varshney et al., 2015). It is therefore clear that being able to correctly model the effects of temperature on microalgal growth is of crucial importance in the success of industrial processes. By using calibrated and validated biokinetic models accounting for temperature, it is indeed possible to predict the growth rate of such algal species within the entire range of operational temperatures, as well as to reduce the impacts and costs related to heating or cooling the culture. Cost- and energy-efficient temperature control strategies can be indeed found for each algal strain, by defining feasible trade-offs among the additional biomass productivity gained through the temperature control and the specific cost of maintaining a suitable temperature. This particularly applies to greenhouses, where thorough temperature regulation is necessary to avoid over-heating the cultures.

Within this context, several thermal response models were developed during the last decades, as summarized by previous reviews on the topic of microalgae growth modelling (Darvehei et al., 2018; Bekirogullari et al., 2020; Grimaud et al., 2017; Shoener et al., 2019). Among the available temperature models, the Cardinal Temperature Model with Inflection (CTMI) is one the most used models worldwide, being originally proposed by Rosso et al. (1993), to describe the dependence of bacterial growth on temperature. This model has been successfully applied to characterize biological cultures of bacteria (Di Biase et al., 2022; Sánchez-Zurano et al., 2022), fungi (Omuse et al., 2022), and yeasts (Salvadó et al., 2011), among others. The CTMI still applies very well to describe the thermal response in phototrophic organisms and it was extensively applied to characterize the temperature dependence of microalgal and cyanobacterial

Table 1
Selection of industrially-relevant microalgae strains, together with their applications and main products.

Classification	Genus	Strain	Products	Applications
Green algae	*Botryococcus*	*Botryococcus* sp.	Lipids	Wastewater treatment
	Chlamydomonas	*C. rheinhardii*, *C. mexicana*, *C. polypyrenoideum*	Lipids	Human nutrition, wastewater treatment
	Chlorella	*C. vulgaris*, *C. prothotecoides*, *C. zoofingiensis*, *C. pyrenoidosa*, *C. kessleri*, *C. sorokiniana*	Proteins, carbohydrates, fatty acids	Human and animal nutrition, cosmetics, biofuels, wastewater treatment, bioplastics, biostimulants/biofertilizers
	Dunaliella	*D. salina*, *D. pluvialis*, *D. tertiolecta*	Proteins, carotenoids, lipids, fatty acids	Human and animal nutrition, cosmetics, biofuels
	Haematococcus	*H. pluvialis*	Proteins, carotenoids, fatty acids	Human and animal nutrition, pharmaceuticals
	Scenedesmus	*S. obliquus*, *S. quadricauda*, *S. abundans*, *S. dimorphus*, *S. acutus*	Lipids, fatty acids	Human and animal nutrition, biofuels, wastewater treatment, bioplastics, biostimulants/biofertilizers
	Tetraselmis	*T. suecica*, *T. chuii*, *T. indica*	Carotenoids, proteins, carbohydrates, fatty acids, lipids	Animal nutrition, biofuels, wastewater treatment, biostimulants/biofertilizers
Cyanobacteria	*Anabaena*	*A. cylindrica*, *A. ambigua*	Carotenoids	Human nutrition, wastewater treatment
	Aphanizomenon	*A. flos-aquae*	Proteins, fatty acids	Human nutrition
	Arthrospira	*A. maxima*, *A. platensis*	Proteins, carbohydrates, carotenoids, fatty acids, lipids	Human and animal nutrition, cosmetics, wastewater treatment, bioplastics
	Oscillatoria	*Oscillatoria* sp.	Carbohydrates	Wastewater treatment
	Synechococcus	*Synechococcus* sp.	Lipids	Human nutrition, biofuels
	Synechocystis	*Synechocystis* sp.	Lipids	Wastewater treatment, biofuels
Diatoms	*Chaetoceros*	*Chaetoceros* sp.	Lipids	Animal nutrition
	Cyclotella	*C. menenighiana*	Carotenoids, lipids	Biofuels
	Navicula	*Navicula* sp.	Carbohydrates, fatty acids	Fatty acids, wastewater treatment
	Nitzschia	*N. laevis*	Fatty acids	Animal nutrition, biofuels
	Odontella	*O. aurita*	Fatty acids	Human and animal nutrition, pharmaceutical, cosmetics
	Phaeodactylum	*P. tricornutum*	Proteins, lipids, fatty acids	Human and animal nutrition, biofuels
	Skeletonema	*Skeletonema* sp.	Lipids, proteins	Animal nutrition
	Thalassiosira	*T. pseudonana*, *T. weissflogli*	Fatty acids	Human and animal nutrition, biofuels
Other	*Euglena*	*E. gracilis*	Carbohydrates, fatty acids	Human nutrition, wastewater treatment, cosmetics, pharmaceuticals, biofuels
	Galdieria	*G. sulphuraria*	Proteins, lipids	Human nutrition, cosmetics, pharmaceuticals, wastewater treatment
	Isochrysis	*I. galbana*	Proteins, fatty acids	Human and animal nutrition, biofuels
	Nannochloropsis	*N. oculata*, *N. gaditana*	Carotenoids, lipids, fatty acids	Animal nutrition, cosmetics, biofuels, wastewater treatment, bioplastics
	Pavlova	*Pavlova* sp.	Fatty acids	Animal nutrition, cosmetics, biofuels, wastewater treatment, bioplastics
	Porphyridium	*P. cruentum*, *P. purpureum*	Proteins, carbohydrates, fatty acids	Human and animal nutrition, cosmetics, pharmaceuticals
	Tribonema	*T. aequale*	Lipids	Wastewater treatment

cultures (Shoener et al., 2019; Bernard and Rémond, 2012). Recently, the CTMI was adopted to describe the effect of temperature on the growth and respiration of both algal and bacterial populations in complex mathematical models for algae-based wastewater treatment processes (Casagli et al., 2021; Sánchez-Zurano et al., 2021a; Solimeno et al., 2019).

The kinetic parameters of the CTMI (i.e., the minimum, optimal, and maximum temperature) can vary based on several conditions; primarily, the algal species (Bernard and Rémond, 2012; Nalley et al., 2018). These parameters can also vary based on adaptation mechanisms, as pointed out in previous works (Grimaud et al., 2017; Bonnefond et al., 2017). It is therefore of major importance to correctly evaluate these parameters, aimed at designing plants that are operated with the optimal strains for the local temperature profiles. Similarly, identifying the CTMI parameters for each organism is crucial for conducting scenario analyses on different strains (Nalley et al., 2018; Slegers et al., 2013). However, a harmonic classification of cardinal temperature parameters for phototrophic microorganisms is currently unavailable in the literature, as the information is mostly fragmented into different works. This translates into the difficulty, for the biotechnology industry, to fully benefit from the exploitation of such a mathematical tool.

In this work, a comprehensive compilation of literature values for cardinal temperature parameters is reported, along with the related testing conditions. The construction of this extensive dataset benefits from previous reviews and data collection efforts (Demory et al., 2019; Morales et al., 2021), as well as from the most recent advances in the scientific literature. The compilation consists of a total of 148 phototrophic genera and 424 strains, thus constituting the largest available database in the literature, to compare the growth response for different groups of phototrophic microorganisms (green algae, cyanobacteria, diatoms, and other species). For practical reasons, a focus is made on those species that are cultivated at the industrial scale for different applications including environmental biotechnologies, CO_2 biofixation, and the recovery of algal-based bioenergy and bio-products.

2. Methodology

2.1. The cardinal temperature model with inflection (CTMI)

The CTMI describes the dependence of the actual microalgal growth rate (μ [d^{-1}]) on the cultivation temperature (T, [°C]), and is represented by the following expression (Rosso et al., 1993; Bernard and Rémond, 2012):

$$\mu = \begin{cases} \mu_{MAX} \cdot \dfrac{(T - T_{MAX}) \cdot (T - T_{MIN})^2}{(T_{OPT} - T_{MIN}) \cdot ((T_{OPT} - T_{MIN}) \cdot (T - T_{OPT}) - (T - T_{OPT}) \cdot (T_{OPT} + T_{MIN} - 2 \cdot T))}, \text{for } T_{MIN} < T < T_{MAX} \\ 0, \text{for } T \leq T_{MIN} \text{ and } T \geq T_{MAX} \end{cases}$$

where: T_{MAX} [°C] is the maximum tolerable temperature above which the biological activity stops, T_{MIN} [°C] is the minimum tolerable temperature below which the biological activity stops, T_{OPT} [°C] is the optimal temperature at which the biological activity is maximum, μ_{MAX} [d^{-1}] is the maximum growth rate that is measured in correspondence of temperature optimum. Despite its simplicity, the CTMI can be effectively used to model the thermal response, and dedicated guidelines for optimal design of experiments are also available to correctly identify cardinal temperature values (Bernaerts et al., 2005; Van Derlinden et al., 2013). To illustrate the typical CTMI curve trend and the effect of cardinal parameters, the normalized thermal response for *Chlorella vulgaris* (Nalley et al., 2018) is shown in Fig. 1. In addition, in this model, all the kinetic parameters have a precise biological meaning that univocally defines the thermal response of a certain species. This is done through the optimum value at which the growth is maximum (T_{OPT} and μ_{MAX}), and the operational limits within which the cultivation is possible (T_{MIN} and T_{MAX}). The physical meaning of the three cardinal temperatures easily allows for classifying extremophilic algae with respect to temperature. An additional parameter can be defined, named the thermal niche, i.e., the difference between T_{MAX} and T_{MIN}, which is proportional to the tolerance of a certain strain to temperature variations. Therefore, strains with a higher thermal niche, i.e. thermal generalists, will be favoured under high thermal excursion conditions, compared to organisms having a lower thermal niche, i.e., thermal specialists (Nalley et al., 2018; Demory et al., 2019). To guarantee that the model maintains its physical meaning and that the function is positive in the interval of temperatures from T_{MIN} to T_{MAX}, the CTMI should be constrained, to satisfy the following condition (Bernard and Rémond, 2012):

$$T_{OPT} > \frac{T_{MAX} + T_{MIN}}{2}$$

This condition implies an interesting property of the CTMI curve, i.e., its asymmetry, describing the fact that most of the phototrophic microorganisms can survive in a larger range of temperatures below T_{OPT} compared to temperatures above T_{OPT}. In other words, algae following the CTMI curve are less susceptible to suboptimal low temperatures than to high temperatures. It is also interesting to notice that, for a more symmetric CTMI curve, a lower variation in the production volume can be expected throughout the year.

2.2. Literature review methodology

As mentioned, some authors already reviewed the temperature dependence in microalgae, providing an accurate description of the thermal response, as well as the main models adopted to describe it (Singh and Singh, 2015; Ras et al., 2013; Grimaud et al., 2017). These reviews compared the thermal response for different algal groups and strains but did not provide actual cardinal temperature values for these species. On the other hand, a few authors recently reported a comparison of CTMI parameters obtained for different algal and cyanobacterial species (Demory et al., 2019; Morales et al., 2021; Thomas et al., 2016), though the focus of these studies was not to compile such values to obtain a harmonized dataset. In the work by Nalley et al. (2018), such values are reported for 26 algal species and it is suggested that the database could be further incremented. The data contained in the present review try to join all the

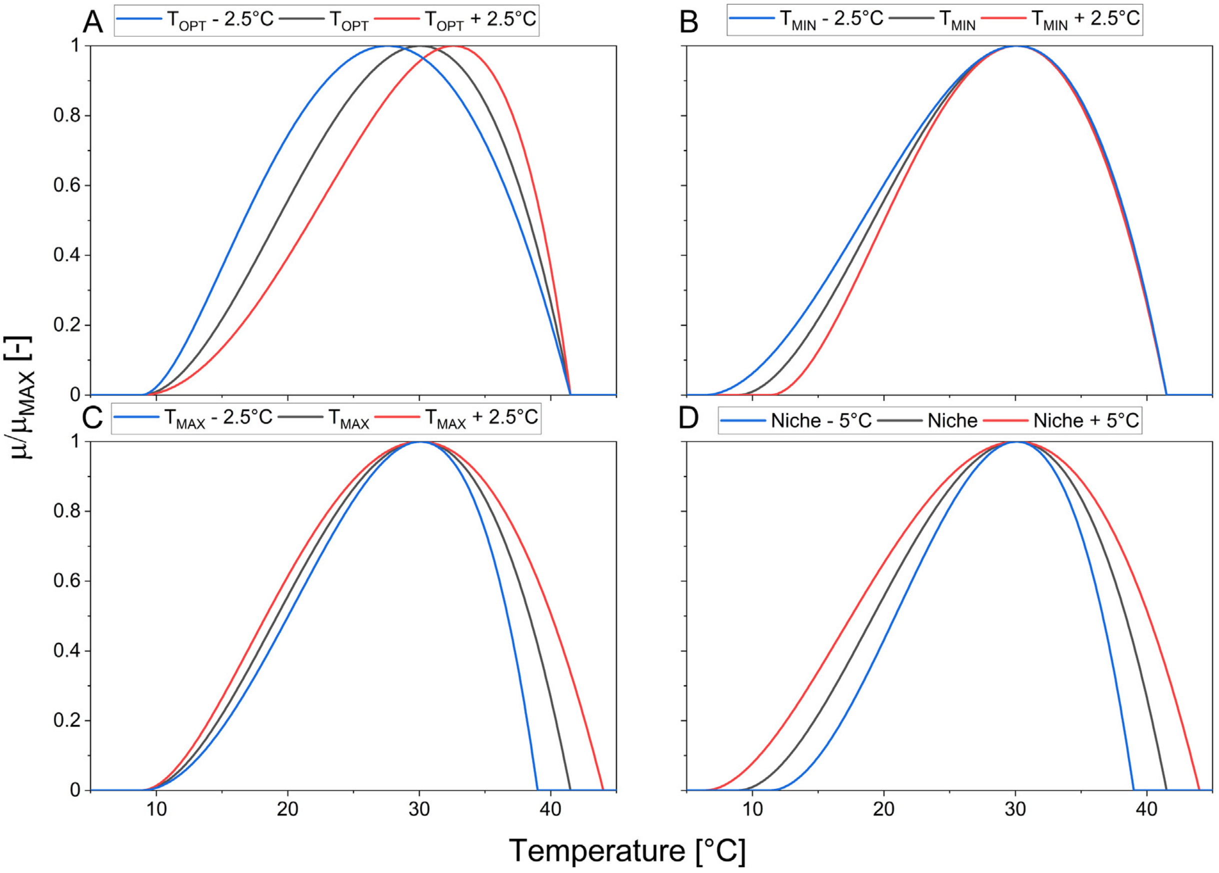

Fig. 1. Normalized cardinal temperature model with inflection (CTMI) describing the thermal response of *Chlorella vulgaris* (data from Nalley et al. (2018)) and effect of ± 2.5 °C variations in CTMI parameters, i.e., minimum temperature, T_{MIN} (A), optimal temperature, T_{OPT} (B), and maximum temperature, T_{MAX} (C), and the thermal niche (D).

efforts done by previous researchers. The literature review methodology was thus organized as follows. First, data from previous reviews and available studies compiling the cardinal temperatures for different species were harmonized and combined into a single datasheet. Then, the dataset was expanded with data from more recent experimental studies.

The initial search terms for the performed review were: "(Microalga* Or Alga* OR *Chlorella* OR *Scenedesmus* OR *Acutodesmus* OR *Tetradesmus* OR *Nannochloropsis* OR *Tetraselmis* OR *Chlamydomonas* OR *Euglena* OR *Stigeoclonium* OR *Ankistrodesmus* OR *Micractinium* OR *Spirogyra* OR *Closterium*) OR (Cyanobacteri* OR *Spirulina* OR *Arthrospira* OR *Synechococcus* OR *Synechocystis* OR *Synedra* OR *Oscillatoria* OR *Phormidium* OR *Anabaena*) OR (Diatom* OR *Cyclotella* OR *Skeletonema* OR *Cylindrotheca* OR *Phaeodactylum* OR *Thalassiosira* OR *Navicula* OR *Nitzschia*) OR (Phytoplankton) AND ((cardinal AND (optimum OR minimum OR maximum)) AND temperature AND model)". The search was then expanded by including relevant related articles. The search was conducted on the *Scopus* and *Google Scholar* databases, covering years from 2000 to 2022. During the literature search, the abstracts of the works containing the mentioned keywords were manually reviewed, to define whether a study could be included in the database.

2.3. Dataset description

Apart from the cardinal temperatures, other elements were included in the database. Among them, information about primary data, and related references, were included. For each record in the dataset, the following information is reported: i) details about the algal species involved (group, phylum, genus, and strain of the organism), ii) the cardinal temperatures defining the thermal response (T_{MIN}, T_{OPT}, T_{MAX}) and the number of works reporting such pieces of information, iii) the characteristics of the experimentation (whether the test was a growth experiment or a short-term activity assessment), iv) the growth characteristics (specific growth rate or oxygen production rate, where available, according to the previous point), iv) detail about the experimental conditions under which the data were obtained (including the range of temperatures tested, incident irradiance, and pH maintained during the experiments), and: v) the complete information record about the origin of available data (references to primary data reported in previous review papers). More details regarding the dataset explanation are given in Supporting information (SI.1).

2.4. Statistical methods

Tukey's range test was used to perform simultaneous pairwise comparisons among the means of cardinal parameters for different groups and/or genera, and to identify statistically-significant differences at the confidence level of 95 % ($\alpha = 0.05$). The software OriginPro 2020b (64-bit) was used for statistical analyses and for graphing.

2.5. Thermal modelling of the greenhouse – pond system: case study explanation

As a practical application of the results provided in this study, a specific case study was considered, in which the energy consumption required to maintain an optimal growth temperature was calculated. In this case study, the CTMI model was coupled to a modified greenhouse – pond system (GPS) model that was originally developed by Li et al. (2009), allowing to assess yearly cumulated heating and cooling loads that are associated with temperature control in a microalgae cultivation system placed under a single-cover greenhouse. Within this framework, a temperature-controlled system was simulated using the software MATLAB R2021b (The Mathworks, Inc.). To target an ideal cultivation condition in terms of growth temperature, a simple conditional proportional controller was implemented, through which the temperature of the cultivation system was kept around strain-specific optima (i.e., maintained at the value of T_{OPT} for each strain, with a temperature-dependent normalized growth rate set to one). The resulting inputs to the water-energy balance were calculated as detailed in Supporting information (SI.2). Tested scenarios included the cultivation of three microalgae strains under the climatic conditions of three European sites, characterized by different latitudes and climatic conditions. To target a medium- to high-value market product, the selected microalgae strains belong to the industrially-relevant genus *Chlorella*, from which it is possible to produce biostimulants of biofertilizers, among other bio-products. In particular, the strains selected to evaluate energy requirements for the case study were: i) *Chlorella vulgaris*, ii) *Chlorella sorokiniana*, and iii) *Chlorella miniata*. Average values of the three cardinal temperatures were calculated from the data compilation (provided as an electronic database in Supporting information SI.3) and used to simulate a temperature-controlled environment based on the CTMI curves. Among the strains selected for comparison, *C. vulgaris* has an intermediate thermal response ($T_{MIN} = 4.4$ °C, $T_{OPT} = 28.9$ °C, and $T_{MAX} = 42.1$ °C), compared to *Chlorella sorokiniana* that is more thermophilic (with $T_{MIN} = 12.5$ °C, $T_{OPT} = 36.7$ °C, $T_{MAX} = 44.4$ °C) and to *Chlorella miniata* that is more psychrophilic (being characterized by $T_{MIN} = 0.0$ °C, $T_{OPT} = 22.4$ °C, and $T_{MAX} = 42.9$ °C). To obtain reliable weather data, Typical Meteorological Years (TMY) for the period 2005–2020 (PVGIS – SARAH2 metadata) were retrieved from the Photovoltaic Geographical Information System (PVGIS) platform (Huld et al., 2012). TMYs were considered for the following sites: i) Almeria, Spain (warm Mediterranean climate, classified as *Csa*, according to the Köppen-Geiger classification by Peel et al. (Peel et al., 2007)), ii) Milan, Italy (classified as humid subtropical climate, or *Cfa*), and iii) Wageningen, the Netherlands (representative of a temperate oceanic climate, or *Cfb*).

3. Results

The results shown in this section are aggregated based on different criteria. First, results for industrially-relevant microalgae strains belonging to the most relevant groups of phototrophic microorganisms for industrial production were aggregated and discussed (see Section 3.1). Then, the full compilation of cardinal parameters is reported, by dividing the available information into four major groups of phototrophs: green algae, cyanobacteria, diatoms, and other phototrophic species (Section 3.2). The aggregated results are then discussed in Section 4. The complete list of results from the literature review is available as electronic Supporting information (SI.3).

3.1. Cardinal temperatures for industrially-relevant species

Cardinal temperatures for industrially-relevant genera are reported in Table 2. More information regarding each specific strain can be found in the electronic database (SI.3).

3.2. Compilation of cardinal temperatures

In this section, the cardinal temperatures for all the algal groups reviewed are reported. As mentioned, results are classified according to the

Table 2

Cardinal temperature parameters for industrially-relevant microalgae genera. For strains in which more than one set of cardinal temperature is provided, the values are expressed as mean ± standard deviation (minimum-maximum).

Group	Phylum	Genus	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Cyanobacteria	Cyanobacteria	*Anabaena*	3.2 ± 4 (−2.9–8.8)	28.2 ± 4.2 (19.9–33.7)	37.2 ± 2.9 (33–42.9)	34 ± 4.8 (24.1–41)	10
		Aphanizomenon	−5.6 ± 16.2 (−35.7–8.6)	28.1 ± 3.1 (23.6–33.5)	37.3 ± 4.5 (30.6–45.2)	42.9 ± 13.3 (30.1–66.3)	9
		Arthrospira	11.3 ± 8.2 (−5–18.9)	34.8 ± 2.4 (31.4–39.9)	45.1 ± 4 (40–50.6)	33.7 ± 10 (21.7–50)	9
		Oscillatoria	−1.7 ± 9.6 (−18.1–10.1)	27.9 ± 2.1 (23.5–30.7)	36 ± 1.5 (33–38.1)	37.7 ± 9.2 (26.8–54.5)	8
		Synechococcus	8.4 ± 17.2 (−17–36.7)	28.4 ± 10.9 (19.7–50.5)	37.2 ± 11.6 (26–59.9)	28.7 ± 11.4 (11–46.5)	6
		Synechocystis	8.3 ± 5.2 (3.1–15.5)	25.9 ± 9.5 (12.5–33.2)	35.3 ± 10.9 (20–45)	27 ± 7.4 (16.8–34.7)	3
Diatoms	Ochrophyta	*Chaetoceros*	−4.4 ± 14.9 (−38.4–11.1)	24.1 ± 8.6 (3.5–31.9)	32.7 ± 8.7 (14.9–40)	37.2 ± 12.8 (21.8–60)	11
		Cyclotella	−1.9 ± 9.3 (−14.8–10)	25.9 ± 1.9 (24.1–30)	31.4 ± 2.2 (28.3–35)	33.3 ± 8.2 (20–43.1)	6
		Navicula	10.7 ± 9.2 (1.4–20)	26.3 ± 8.6 (17.6–35)	33.1 ± 1.8 (31.3–35)	22.4 ± 7.4 (15–29.8)	2
		Nitzschia	−6.7 ± 17.3 (−37.7–10)	21.2 ± 10.7 (1.1–31.4)	34.8 ± 17.3 (5–54)	41.5 ± 15 (25–67.2)	5
		Odontella	5.4 ± 6.9 (−1.5–12.4)	19.4 ± 7.4 (12–26.8)	27.4 ± 7.4 (20–34.8)	21.9 ± 0.4 (21.5–22.3)	2
		Phaeodactylum	−14.4 ± 16.6 (−47.9–3.4)	22.3 ± 1.3 (20–25.3)	29 ± 3.2 (25.2–36.3)	43.4 ± 15.5 (26.8–77.9)	9
		Skeletonema	−13 ± 26.3 (−63.4–11.8)	25.7 ± 3.4 (17.8–32.4)	35 ± 3.2 (27.9–40)	48 ± 24.8 (24.3–94.6)	39
		Thalassiosira	−7.9 ± 15.6 (−56.3–3.9)	20.9 ± 4.5 (9.7–26.6)	29.5 ± 4.4 (15.6–33.7)	37.5 ± 15.2 (20.5–76.3)	19
Green algae	Chlorophyta	*Botryococcus*	5	30	35	30	1
		Chlamydomonas	−9.4 ± 19.3 (−51.5–5.2)	21 ± 8 (11.2–31.7)	32.8 ± 16.4 (19.6–65.9)	42.3 ± 22.3 (19.9–74.9)	6
		Chlorella	3.3 ± 8.8 (−26.4–20)	30 ± 4.8 (20.7–38.7)	41.2 ± 6.1 (28–50.9)	37.9 ± 9.5 (15–54.4)	26
		Dunaliella	4.6 ± 6.5 (−7.8–12.4)	30.4 ± 4.6 (20.5–34.6)	37.8 ± 4 (28.9–43)	33.1 ± 7.5 (25–50.8)	9
		Haematococcus	−7.7 ± 23.2 (−40.1–13.7)	23.9 ± 1.5 (21.9–25.7)	33.2 ± 0.7 (32.3–34.2)	40.9 ± 22.8 (19.2–72.4)	3
		Scenedesmus	2.9 ± 9.6 (−30.6–10.3)	29.4 ± 3 (23–35)	42.1 ± 6.3 (32.7–50)	39.2 ± 11.9 (24.2–78.8)	15
		Tetraselmis	−1.8 ± 9.3 (−14.7–7.1)	26.7 ± 2.9 (24.2–30.9)	34.9 ± 0.6 (34–35.6)	36.7 ± 9.3 (28.4–49.9)	3
Other	Haptophyta	*Isochrysis*	9.8 ± 6 (−2.8–16)	28.5 ± 3.6 (21.1–35.7)	36.2 ± 5.4 (26.8–46.1)	26.3 ± 6.6 (18–36.4)	10
		Pavlova	15	27	30	15	1
	Euglenophyta	*Euglena*	20	29	40	20	1
	Ochrophyta	*Nannochloropsis*	5.9 ± 4.7 (−0.2–13)	27.1 ± 1.9 (25–32)	35.8 ± 2.5 (32.5–41)	29.8 ± 4.1 (23–36.4)	9
		Tribonema	−0.8	20.2	30.1	31	1
	Rhodophyta	*Galdieria*	10 ± 0 (10−10)	39 ± 4 (35–43)	51.5 ± 4.5 (47–56)	41.5 ± 4.5 (37–46)	2
		Porphyridium	5.4 ± 0.3 (5–5.8)	22 ± 2.9 (19.1–25)	32.5 ± 2.5 (30–35)	27.1 ± 2.8 (24.2–30)	2

specific group, i.e., green algae (Table 3), cyanobacteria (Table 4), diatoms (Table 5), and other genera (Table 6).

4. Discussion

4.1. Cardinal temperatures for industrially-relevant microalgae

Among the industrially-relevant microalgae species presented in Tables 1 and 2, only a few show good productivities at the European latitudes and are effectively exploited for commercial purposes (Araújo et al., 2021). These species (mainly, *Arthrospira*, *Chlorella*, *Haematococcus*, *Nannochloropsis*, and *Dunaliella*) are typically produced to use the whole mass or exploited for the extraction of valuable compounds (such as astaxanthin, carotenoids, β-carotene, and polyunsaturated fatty acids, among others) (Chini Zittelli et al., 2021). As shown in Fig. 2, the normalized CTMI curves for these species exemplify different thermal responses. *Haematococcus* can typically grow at lower temperatures (T_{OPT} = 20–30 °C), making it more suitable for cold climates and locations with cold summers. Other industrial species showing a similar resistance to cold climates are *Porphyridium* and diatoms such as *Thalassiosira*, *Phaeodactylum*, *Odontella*, and *Chaetoceros* (Table 2). On the other hand, some industrially-relevant species having $T_{OPT} > 35$ °C will require an appropriate heating system to protect the culture from low temperatures reached in cold climates. For example, *Arthrospira* is well known to require a hot environment (Lürling et al., 2013), as for other species typically grown under thermophilic conditions (e.g., the cyanobacterium *Synechococcus* or the red alga *Galdieria*). An intermediate thermal response can be identified in *Nannochloropsis* and many other green algae (*Chlorella*, *Scenedesmus*, *Botryococcus*, *Dunaliella*) and cyanobacteria (*Anabaena*, *Aphanizomenon*, *Oscillatoria*) species, that typically have an optimum condition around 30 °C. Within the mentioned algal and cyanobacterial species, the variations in the thermal niche can be appreciated. Wide thermal niches (> 38 °C) can be found in the following species belonging to different groups: *Aphanizomenon*, *Anabaena* (cyanobacteria), *Phaeodactylum* (diatoms), *Chlorella*, *Scenedesmus*, *Chlamydomonas*, *Haematococcus* (green algae) and *Galdieria* (red algae). These species can be therefore considered more suitable for outdoor cultivation, even though the final productivity will also depend on other conditions, such as substrate availability or other factors (i.e., light, pH, and dissolved oxygen).

4.2. Comparison of cardinal temperatures among different groups and genera

As shown in Table 7 and Fig. 3, considering aggregated values, and excluding extremophilic strains (i.e., strains having $T_{MIN} \leq -20$ °C or $T_{MAX} \geq 55$ °C), the cardinal temperatures tend to be significantly different among groups. Cyanobacteria have a higher thermal tolerance and hardly tolerate colder conditions, while green algae show a similar tolerance to high temperatures but are characterized by a much larger thermal niche (by having lower minimum temperatures). On the other hand, diatoms and other algal groups typically show lower cardinal temperatures and thermal niches. Looking at the statistical significance of the aggregated results, cardinal temperature parameters do not significantly differ between green algae and cyanobacteria (Fig. 4), which is consistent with available experimental data and literature surveys, showing that cardinal temperatures are typically lower for Bacillariophyceae and Cryptophyceae, compared to Chlorophyceae and Cyanobacteria (Nalley et al., 2018; Lürling et al., 2013; Suzuki and Takahashi, 1995). In the same way, none of the cardinal temperatures were statistically different for the group identifying other phototrophic organisms, compared to green algae and cyanobacteria. As shown in Fig. 4A-C, the minimum temperature was similar for all the groups, with no statistical difference. On the contrary, a relevant difference was found for all the other cardinal temperature parameters, among diatoms and other genera. Optimal temperatures of diatoms were statistically significant for both green algae ($p \leq 0.05$) and cyanobacteria ($p \leq 0.01$), while diatom maximum temperatures were only different compared to cyanobacteria ($p \leq 0.05$). Regarding the thermal niche, green algae are characterized by the higher values with almost 33 °C of niche width, on average, compared to a niche lower than 30 °C for all the other groups (Table 7). This reflects the ubiquity of green algae, and their ability to grow in several climatic conditions. It is also a partial explanation of the fact that most of the algal species found as contaminants in pure cultures, or used for wastewater treatment, belong to green algae (Larsdotter, 2006; Mehrabadi et al., 2017; Park et al., 2011). Both minimum and maximum temperatures were correlated with the optimal temperature (Fig. 5),

Table 3
Cardinal temperature parameters for green algae. For strains in which more than one set of cardinal temperature is provided, the values are expressed as mean ± standard deviation (minimum-maximum).

Genus	Species	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Acutodesmus	*Acutodesmus acuminatus*	11.3	28.6	53.8	42.4	1
	Acutodesmus obliquus	5.5 ± 5.9 (−2.8–15.3)	28.7 ± 2.7 (25.1–32.2)	42.8 ± 10.8 (34.6–66.3)	37.2 ± 10.6 (22.8–55.7)	6
Ankistrodesmus	*Ankistrodesmus falcatus*	0.7	27.3	33.6	32.9	1
	Ankistrodesmus sp.	18	26	31	13	1
Botryococcus	*Botryococcus braunii*	10.1 ± 4.2 (5–15.4)	24.9 ± 3.5 (22 − 30)	41.6 ± 7.6 (35–52.2)	31.4 ± 3.8 (27.6–36.8)	3
Bracteacoccus	*Bracteacoccus grandis*	2.7	15.3	21	18.2	1
Chlamydomonas	*Chlamydomonas acidophila*	13	19.5	38.4	25.3	1
	Chlamydomonas alpina	−0.2	13.7	19.7	19.9	1
	Chlamydomonas reinhardtii	−0.2 ± 6.2 (−8.9–5.2)	28.9 ± 1.9 (27.4–31.7)	45.8 ± 14.3 (33.9–65.9)	46 ± 20.4 (30.9–74.9)	3
	Chlamydomonas segnis	−51.5	14.5	20.2	71.8	1
	Chlamydomonas sp.	2.2	8.1	101.3	99	1
	Chlamydomonas subcaudata	−4.4	11.2	19.6	24	1
Chlorella	*Chlorella ellipsoidea*	9.3 ± 10.6 (−1.2–20)	29.8 ± 0.1 (29.7–30)	41.1 ± 6.1 (35–47.3)	31.8 ± 16.8 (15–48.6)	2
	Chlorella emersonii	3	30	38	35	1
	Chlorella miniata	0	22.3	42.8	42.8	1
	Chlorella minutissima	10	25	45	35	1
	Chlorella protothecoides	10.2	30.2	39	28.8	1
	Chlorella pyrenoidosa	5.3 ± 0.2 (5.2–5.7)	33 ± 8 (21.7–38.7)	40.8 ± 7 (30.8–45.8)	35.4 ± 7.3 (25–40.6)	3
	Chlorella sorokiniana	12.5 ± 0.4 (12 − 13)	36.6 ± 0.3 (36.3–37)	44.4 ± 0.5 (43.8–45)	31.8 ± 0.1 (31.7–32)	2
	Chlorella sp.	4.2 ± 12.9 (−26.4–13.7)	26.2 ± 3.3 (20.7–31.4)	42.4 ± 9.7 (28–62.6)	38.2 ± 10.6 (25.3–54.4)	7
	Chlorella vulgaris	2.2 ± 6.3 (−12.2–13)	28.9 ± 4.5 (17.8–37.2)	42.8 ± 6 (29.3–50.9)	40.5 ± 8.3 (28–54.2)	13
	Chlorella raciborskii	−2.1	32.7	39	41.1	1
Chlorococcum	*Chlorococcum* sp.	0	25	30	30	1
Crucigenia	*Crucigenia tetrapedia*	−0.5	27.8	34.6	35.1	1
Dunaliella	*Dunaliella bioculata*	12.4	34.6	39.5	27	1
	Dunaliella primolecta	9.7 ± 0.2 (9.4–10)	31.6 ± 1.6 (30–33.2)	36.4 ± 1.4 (35–37.8)	26.7 ± 1.7 (25–28.4)	2
	Dunaliella salina	−1.2 ± 6.5 (−7.8–5.2)	29 ± 4.9 (24–34)	39.1 ± 3.8 (35.2–43)	40.4 ± 10.3 (30–50.8)	2
	Dunaliella sp.	−0.4	31.1	40	40.4	1
	Dunaliella tertiolecta	4.3 ± 5.3 (−2.5–10.5)	28.9 ± 5.9 (20.5–33.7)	36.6 ± 5.6 (28.9–42.1)	32.3 ± 1.1 (31.4–33.9)	3
	Dunaliella viridis	5.2	26.3	54.7	49.5	1
Golenkinia	*Golenkinia radiata*	4.9	30.4	54	49	1
Haematococcus	*Haematococcus pluvialis*	8.8 ± 3.6 (3–13.7)	21.1 ± 3.2 (17.5–25.7)	49 ± 20.2 (32.9–87.3)	40.1 ± 21.3 (19.2–80.2)	5
	Haematococcus sp.	−40.1	21.9	32.3	72.4	1
Heteromastix	*Heteromastix pyriformis*	−2.9	19.4	28.1	31	1
Koliella	*Koliella antarctica*	2.6	12.6	20	17.3	1
Micractinium	*Micractinium pusillum*	12.9	32.1	48.5	35.6	1
Micromonas	*Micromonas pusilla*	−9 ± 21.5 (−45.9–6.3)	22.7 ± 1.9 (19.3–24.4)	30.1 ± 0.6 (29.2–30.7)	39.1 ± 20.9 (24.3–75.1)	4
	Micromonas sp.	3.4 ± 4.5 (−2–9.6)	20.6 ± 8.1 (6.6–26.7)	27.9 ± 7.5 (14.9–32.6)	24.5 ± 5.3 (17–31.9)	4
	Micromonas commoda	3.2 ± 7.8 (−7.9–9.5)	26.1 ± 2.2 (24–29.2)	32.3 ± 3.9 (27.5–37)	29.1 ± 5 (22.9–35.4)	3
	Micromonas bravo	−0.6 ± 4.5 (−6.4–4.5)	22.8 ± 2.9 (19.1–26.3)	28.3 ± 3.6 (23.5–32.5)	28.9 ± 7.1 (18.9–35.3)	3
	Micromonas polaris	−4 ± 1.2 (−5.3 to −2.8)	7.3 ± 0.2 (7–7.6)	16.1 ± 0.7 (15.3–16.9)	20.2 ± 2 (18.1–22.2)	2
Mixed	*Chlorella* - *Scenedesmus* consortium	−5 ± 4.9 (−10 to −0.1)	23.8 ± 3.8 (20–27.6)	42.2 ± 0.2 (42–42.5)	47.3 ± 4.7 (42.6–52)	2
Monoraphidium	*Monoraphidium* sp.	7.8 ± 5.1 (2.6–13)	31.9 ± 8 (23.9–40)	52.9 ± 17 (35.8–70)	45.1 ± 11.8 (33.2–57)	2
	Monoraphidium contortum	−7.5 ± 2.9 (−10.4 to −4.6)	23.3 ± 5.1 (18.2–28.5)	31.8 ± 1.6 (30.1–33.5)	39.3 ± 1.2 (38.1–40.5)	2
	Monoraphidium griffithii	−4.4	28.4	35.9	40.4	1
	Monoraphidium minutum	−12.8	28.2	34.2	47.1	1
Mucidosphaerium	*Mucidosphaerium pulchellum*	11 ± 0.9 (10.1–12)	29.4 ± 0.2 (29.1–29.7)	36.8 ± 0.2 (36.6–37.1)	25.8 ± 0.6 (25.1–26.4)	2
Nannochloris	*Nannochloris atomus*	5.4 ± 0.4 (5–5.8)	21.5 ± 0.8 (20.7–22.3)	32.1 ± 0.3 (31.7–32.5)	26.7 ± 0.7 (25.9–27.5)	2
	Nannochloris sp.	−3.7 ± 12.5 (−16.3–8.7)	30.8 ± 2 (28.7–32.8)	40.5 ± 0.4 (40–41)	44.2 ± 12 (32.2–56.3)	2
Neochloris	*Neochloris oleoabundans*	8.6 ± 3.6 (5–12.3)	23.3 ± 8.3 (15–31.6)	35.9 ± 0.9 (35–36.9)	27.3 ± 2.6 (24.6–30)	2
Oocystella	*Oocystella mongolica*	1.5	12	42.7	41.2	1
Oocystis	*Oocystis borgei*	−17.7	28.9	40.1	57.9	1
	Oocystis sp.	8.5 ± 4.2 (5–14.5)	26 ± 0.9 (25–27.2)	56.9 ± 32.4 (33–102.7)	48.3 ± 28.2 (26.7–88.2)	3
Ourococcus	*Ourococcus* sp.	1.6 ± 0 (1.6–1.6)	26.9 ± 0 (26.9–27)	38 ± 0 (38–38)	36.3 ± 0 (36.3–36.4)	2
Pandorina	*Pandorina morum*	4.5	15.6	34.9	30.4	1
Pediastrum	*Pediastrum boryanum*	3.4	19.4	30	26.5	1
	Pediastrum simplex	14.7	28.7	33.7	18.9	1
Picochlorum	*Pycochlorum* sp.	15	30	41	26	1
Pleodorina	*Pleodorina californica*	10.7	23.6	34.7	23.9	1
Pseudodidymocystis	*Pseudodidymocystis planctonica*	−63.1	22.7	30	93.2	1
Pyramimonas	*Pyramimonas disomata*	8	17.2	28	20	1
Raphidocelis	*Raphidocelis subcapitata*	10.9 ± 5.2 (5.6–16.1)	24.7 ± 0.8 (23.8–25.6)	50.5 ± 4.5 (45.9–55)	39.5 ± 0.7 (38.8–40.3)	2
Scenedesmus	*Scedesmus ecornis*	3.9	30.1	38	34.1	1
	Scenedesmus almeriensis	−0.7 ± 15 (−30.6–8.6)	29.9 ± 2.6 (26–34.2)	47.8 ± 1 (46–49)	48.6 ± 15.3 (39–78.8)	5
	Scenedesmus intermedius	5	30	50	45	1
	Scenedesmus obliquus	3.9 ± 3.1 (0.7–7)	27.5 ± 1.9 (25.5–29.5)	37.3 ± 0.4 (36.8–37.8)	33.4 ± 3.6 (29.7–37.1)	2
	Scenedesmus quadricaudatus	12.7 ± 5.9 (3.8–21.6)	28.4 ± 3.4 (22.5–32.2)	41.4 ± 4.4 (35.3–47.6)	28.7 ± 6.3 (19.4–38.1)	5
	Scenedesmus sp.	4.8 ± 4.7 (−3.1–10.3)	28.6 ± 4.1 (23–35)	38.6 ± 6 (32.7–46.1)	33.7 ± 5.8 (24.2–41)	5
Selenastrum	*Selenastrum* sp.	6.1 ± 6.1 (0–12.3)	31.4 ± 3.5 (27.9–35)	36.2 ± 3.7 (32.5–40)	30.1 ± 9.8 (20.2–40)	2
Stichococcus	*Stichococcus* sp.	5.5	21.4	33.1	27.6	1
Tetraselmis	*Tetraselmis* sp.	6 ± 2.9 (2–8.8)	23.2 ± 1.9 (20.6–25)	49.2 ± 20.4 (34–78.2)	43.2 ± 18.5 (28.4–69.4)	3
	Tetraselmis suecica	−2.3 ± 12.3 (−14.7–10)	25.4 ± 5.4 (20–30.9)	32.6 ± 2.6 (30–35.2)	34.9 ± 14.9 (20–49.9)	2
Volvox	*Volvox aureus*	7 ± 2.3 (4.7–9.4)	22 ± 0.4 (21.6–22.4)	34.1 ± 2.2 (31.9–36.3)	27 ± 4.6 (22.4–31.6)	2
	Volvox globator	5.8	21.8	29.9	24.1	1
GREEN ALGAE	*Overall*	2.8 ± 11.8 (−63.1–21.6)	25.9 ± 6.2 (6.6–40)	39.5 ± 12.6 (14.9–102.7)	36.6 ± 15.1 (13–99)	153

Table 4
Cardinal temperature parameters for cyanobacteria. For strains in which more than one set of cardinal temperature is provided, the values are expressed as mean ± standard deviation (minimum-maximum).

Genus	Species	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Anabaena	*Anabaena bergii*	14.9	25	37.8	22.9	1
	Anabaena cylindrica	10.7 ± 5.4 (5.2–18.2)	29.5 ± 3.1 (25–31.7)	48.3 ± 15.2 (33–69)	37.5 ± 10.9 (24.1–50.8)	3
	Anabaena flos-aquae	6.3 ± 1.3 (5–7.7)	25.2 ± 8.4 (16.8–33.7)	35.1 ± 5.9 (29.2–41)	28.7 ± 4.5 (24.1–33.2)	2
	Anabaena macrospora	1.7	25.3	34.2	32.4	1
	Anabaena sp.	0.4 ± 3.4 (−2.9–6.8)	26.3 ± 4.4 (19.9–31.5)	36.9 ± 1.4 (34.4–38.6)	36.4 ± 4 (29.8–41)	5
	Anabaena ucrainica	6.1	28.6	36.4	30.2	1
Aphanizomenon	*Aphanizomenon aphanizomenoides*	−23.2	30	37.7	60.9	1
	Aphanizomenon flos-aquae	−2.8 ± 16.7 (−35.7–8.6)	26.3 ± 1.9 (23.6–28)	36.8 ± 4.8 (30.6–45.2)	39.6 ± 13.5 (30.1–66.3)	5
	Aphanizomenon gracile	−8.2 ± 16.2 (−24.4–7.9)	29.5 ± 4 (25.4–33.5)	37.9 ± 5.6 (32.3–43.5)	46.2 ± 10.5 (35.6–56.8)	2
	Aphanizomenon ovalisporum	3.2	32.1	38.1	34.8	1
Arthrospira	*Arthrospira fusiformis*	18.9	32.9	41.6	22.6	1
	Arthrospira leopoliensis	14.3	39.9	46.6	32.2	1
	Arthrospira maxima	17	33	45	28	1
	Arthrospira platensis	10.3 ± 8.7 (−5–18.7)	34.2 ± 1.8 (31.4–37)	44.6 ± 4.6 (40–50.6)	34.2 ± 9.7 (21.7–45)	5
	Arthrospira sp.	0	36	50	50	1
Chroococcus	*Chroococcus minutus*	0.6	28.8	39.4	38.8	1
Crocosphaera	*Crocosphaera watsonii*	23.2 ± 1.4 (21.7–24.9)	28.7 ± 0.1 (28.5–29.1)	33 ± 1.9 (31–35)	9.8 ± 3.3 (6.1–13.2)	6
Cylindrospermopsis	*Cylindrospermopsis raciborskii*	13.5 ± 3.9 (7.4–20)	30.1 ± 1.2 (27.4–33)	40.4 ± 2.6 (36.4–47.5)	26.8 ± 3.6 (19.7–31.8)	16
Mastigocladus	*Mastigocladus laminosus*	25.2	46.3	57.1	31.9	1
Merismopedia	*Merismopedia* sp.	13	28.4	32.3	19.3	1
Microcoleus	*Microcoleus vaginatus*	−11.3	28.4	33	44.3	1
Microcystis	*Microcystis aeruginosa*	11 ± 4.5 (0–17.5)	30.1 ± 3.9 (19.3–34.4)	42.2 ± 5.8 (36.1–59.5)	31.2 ± 6.5 (21.6–47.3)	12
	Microcystis viridis	10.1	24.6	34.8	24.7	1
	Microcystis wesenbergii	2.7	28.6	31.4	28.6	1
Nostoc	*Nostoc muscorum*	10.4	31.9	37.7	27.3	1
Oscillatoria	*Oscillatoria agardhii*	0.1 ± 9.3 (−17.2–10.1)	28.3 ± 2.6 (23.5–30.7)	36.6 ± 1.1 (35–38.1)	36.4 ± 9.6 (26.8–54.5)	5
	Oscillatoria redekei	0.7	26.7	34.8	34.1	1
	Oscillatoria sp.	−7.8 ± 10.2 (−18.1–2.3)	27.6 ± 0.2 (27.4–27.8)	34.9 ± 1.9 (33–36.8)	42.7 ± 8.3 (34.4–51.1)	2
Phormidium	*Phormidium simplicissimum*	18.9	27.8	38.8	19.8	1
Prochlorococcus	*Prochlorococcus marinus*	4.2 ± 12.6 (−25.5–13.7)	24.8 ± 1.4 (23.2–27.1)	29.5 ± 1.7 (27.9–33.2)	25.2 ± 12.3 (15.9–54.6)	7
Synechococcus	*Synechococcus lividus*	36.7	50.5	59.9	23.2	1
	Synechococcus sp.	4.1 ± 12.1 (−17–15)	25.3 ± 5.5 (19.7–32.9)	44.1 ± 26 (26–101)	39.9 ± 25 (11–90.1)	6
Synechocystis	*Synechocystis limnetica*	3.1	12.5	20	16.8	1
	Synechocystis sp.	11 ± 4.5 (6.4–15.5)	32.6 ± 0.6 (32–33.2)	43 ± 1.9 (41.1–45)	32 ± 2.6 (29.4–34.7)	2
Trichodesmium	*Trichodesmium erythraeum*	16.9 ± 1.3 (15.9–19.2)	27.8 ± 0.4 (27.3–28.5)	35 ± 0.1 (34.9–35.3)	18 ± 1.1 (16–19)	4
	Trichodesmium radians	23	26.2	35.5	12.4	1
Trichormus	*Trichormus variabilis*	6.6 ± 7.5 (−0.9–14.2)	33.6 ± 0.3 (33.3–34)	41.8 ± 2 (39.7–43.8)	35.1 ± 9.6 (25.4–44.7)	2
Tychonema	*Tychonema bourrellyi*	1.3 ± 0.9 (0.4–2.2)	21.7 ± 0 (21.6–21.8)	29.8 ± 0.1 (29.6–30)	28.5 ± 1 (27.4–29.6)	2
CYANOBACTERIA	*Overall*	8.3 ± 11.4 (−35.7–36.7)	29 ± 5 (12.5–50.5)	38.8 ± 9.3 (20 − 101)	30.4 ± 12.6 (6.1–90.1)	107

as previously observed in pooled datasets for microalgae (Grimaud et al., 2017; Demory et al., 2019). In particular, the correlation between the maximum and optimum temperature explains well the variability in the reviewed data, compared to the correlation between the minimum and optimal temperature. Thanks to these correlations, it is possible to easily identify the temperature range for a certain group of phototrophs, without the need of estimating all the cardinal temperatures, though a certain variability must be accounted for, at the phylum level (see below). On the other hand, it is well known that the correlation among parameters for a certain model makes parameter identification more difficult (Rosso et al., 1993), so it is of primary importance to focus future research efforts on identifying the reasons behind this behaviour.

Besides the relatively low variability found among algal groups, a larger variability is found, looking at the data pooled by species. Indeed, the intergroup variability evaluated at the species level shows that some species are typically characterized by a much larger variation in cardinal temperatures, compared to others of the same group. To exemplify these characteristics, the boxplots reported in Figs. 6, 7, 8, and 9 show the interspecies variability for industrially-relevant cyanobacteria, diatoms, green algae, and other species, respectively. For cyanobacteria (Fig. 6), the only species with significantly different cardinal temperatures is *Arthrospira* sp., with significantly higher T_{MIN} compared to *Oscillatoria* sp. ($p \leq 0.05$), and T_{MAX} and T_{OPT}, compared to *Anabaena* sp. ($p \leq 0.05$). For green algae (Fig. 7), the minimum temperature is not statistically different among all the industrial species considered. On the contrary, both the optimal and maximum temperatures show a certain variability, and the values for *Chlamydomonas* sp. are typically lower than other species. Indeed, the average T_{OPT} for *Chlamydomonas* sp. is statistically different compared to *Dunaliella* and *Scenedesmus* sp. ($p \leq 0.01$) and to *Chlorella* sp. ($p \leq 0.001$). Regarding T_{MAX}, a similar difference ($p \leq 0.01$) was found among the same species. For diatoms, the interspecies variability in T_{MIN} is not significantly different, while T_{OPT} and T_{MAX} are characterized by a certain degree of variability (Fig. 8). *Thalassiosira* sp. typically shows lower optimal temperatures compared to *Cyclotella* and *Chaetoceros* spp. ($p \leq 0.05$) and especially to *Skeletonema* sp. ($p \leq 0.001$). Looking at their maximum tolerable temperatures, major differences can be found among *Thalassiosira* sp. and other species, i.e., *Nitzschia* sp. ($p \leq 0.01$), *Chaetoceros*, and *Skeletonema* spp. ($p \leq 0.05$). Concerning other algal species differing from cyanobacteria, green algae, and diatoms (Fig. 9), a much higher variability can be found among averaged cardinal temperatures. As for T_{MIN}, *Euglena* sp. shows a higher mean compared to *Tribonema* sp. ($p \leq 0.01$) and to *Nannochloropsis* and *Porphyridium* spp. ($p \leq 0.05$). On the other hand, *Tribonema* sp. is characterized by a lower minimum temperature compared to both *Isochrysis* and *Pavlova* spp. ($p \leq 0.05$). Regarding T_{OPT}, the values found for *Nannochloropsis* and *Galdieria* sp. are typically higher than other species, especially compared to *Tribonema* sp. ($p \leq 0.05$). Finally, *Galdieria* sp. is the species with a higher tolerance to high temperatures, with mean T_{MAX} values being statistically higher than *Pavlova* and *Porphyridium* spp. ($p \leq 0.05$) and *Tribonema* sp. ($p \leq 0.01$).

4.3. Applications to reduce energy and biomass production costs

The dependence of microalgal growth on temperature is of primary importance when evaluating the techno-economic feasibility of culturing a specific strain at a specific plant latitude. This evaluation requires a proper biological growth model, to simulate different scenarios and to output

Table 5
Cardinal temperature parameters for diatoms. For strains in which more than one set of cardinal temperature is provided, the values are expressed as mean ± standard deviation (minimum-maximum).

Genus	Species	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Amphiprora	*Amphiprora hyalina*	20	27.5	35	15	1
	Amphiprora sp.	9.6	28.2	33.9	24.3	1
Amphora	*Amphora* sp.	15	30	40	25	1
Asterionella	*Asterionella formosa*	−6.8 ± 6.5 (−15–3.4)	21.2 ± 2.6 (17.9–25.9)	29.7 ± 1.9 (26.3–32.5)	36.6 ± 4.8 (29–42)	5
	Asterionella glacialis	−31.4 ± 16.3 (−44.1 to −8.3)	23.1 ± 4 (18.1–27.9)	31.3 ± 3 (28.3–35.5)	62.8 ± 13.4 (43.8–72.4)	3
Chaetoceros	*Chaetoceros affinis*	8.1	23.7	30	21.8	1
	Chaetoceros calcitrans	14.9	22.8	33.3	18.4	1
	Chaetoceros deflandrei	−38.4	10.7	16.3	54.7	1
	Chaetoceros didymus	10.9	21.2	35.3	24.3	1
	Chaetoceros gracilis	7.6 ± 2.3 (5.3–10)	26.2 ± 3.7 (22.4–30)	35.2 ± 4.7 (30.4–40)	27.5 ± 2.4 (25–30)	2
	Chaetoceros lorenzianus	−4.4 ± 11.2 (−14.7–11.1)	28.2 ± 2.3 (24.9–30.2)	36.1 ± 0.2 (35.9–36.5)	40.6 ± 10.9 (25.3–50.8)	3
	Chaetoceros muelleri	5	27	40	35	1
	Chaetoceros pseudocurvisetus	15	24.4	34.9	19.9	1
	Chaetoceros sp.	−1.6 ± 14.9 (−19.9–19)	23.9 ± 11.8 (3.5–31.9)	36.3 ± 13 (14.9–50.4)	38 ± 13.1 (25.7–60)	4
Conticribra	*Conticribra weissflogii*	6.6 ± 1.4 (5.2–8.1)	17.4 ± 2.2 (15.1–19.6)	48.1 ± 22 (26–70.2)	41.4 ± 20.6 (20.8–62)	2
Corethron	*Corethron pennatum*	−29.3	3.1	6.9	36.2	1
Coscinodiscus	*Coscinodiscus* sp.	8.6	15.1	72.5	63.9	1
	Coscinodiscus wailesii	−35	23.8	31.8	66.9	1
Cyclotella	*Cyclotella* sp.	−2.6	25.6	32.9	35.5	1
	Cyclotella cryptica	10	30	35	25	1
	Cyclotella meneghiniana	−4.7 ± 9.3 (−14.8–10)	25 ± 0.8 (24.1–26.4)	30.1 ± 1.4 (28.3–32.3)	34.9 ± 8.9 (20–43.1)	4
Cylindrotheca	*Cylindrotheca closterium*	10 ± 4.2 (6.3–15.9)	23.6 ± 1.3 (22.2–25.5)	36.9 ± 1.6 (34.7–38.5)	26.9 ± 4.2 (21.6–32.1)	3
Dactyliosolen	*Dactyliosolen fragilissimus*	6.8	17.2	113.6	106.7	1
Detonula	*Detonula confervacea*	−4.6 ± 5.4 (−10.1–0.7)	7.7 ± 0.5 (7.1–8.3)	16.5 ± 1.5 (15–18)	21.2 ± 3.9 (17.2–25.1)	2
Diatoma	*Diatoma tenue*	13.6	18.8	52.6	38.9	1
Ditylum	*Ditylum brightwellii*	−17.1 ± 18.9 (−36–1.8)	22.9 ± 2.2 (20.6–25.2)	33.8 ± 1.7 (32–35.6)	50.9 ± 17.1 (33.7–68.1)	2
Eucampia	*Eucampia zodiacus*	−28.1	22.9	28.7	56.8	1
Fragilaria	*Fragilaria bidens*	6.2	20.9	34.3	28.1	1
	Fragilaria capucina	0.9	19.6	28.7	27.7	1
	Fragilaria crotonensis	−2.6 ± 9.8 (−16.4–5.6)	24.6 ± 1 (23.1–25.7)	34.1 ± 2.1 (32–37.1)	36.8 ± 8.6 (27.6–48.5)	3
Fragilariopsis	*Fragilariopsis cylindrus*	−50.4	4.5	10.3	60.7	1
	Fragilariopsis kerguelensis	−38.7	3.6	7.9	46.7	1
Helicotheca	*Helicotheca tamesis*	9.2	24.3	32.7	23.4	1
Leptocylindrus	*Leptocylindrus danicus*	13.1	27.6	33.9	20.7	1
Melosira	*Melosira italica*	−0.2	17.8	27.1	27.4	1
Navicula	*Navicula acceptata*	20	35	35	15	1
	Navicula pelliculosa	1.4	17.6	31.3	29.8	1
Nitzschia	*Nitzschia dissipata*	20	25	30	10	1
	Nitzschia frigida	−37.7	1.1	5	42.7	1
	Nitzschia frustulum	5	28.5	50	45	1
	Nitzschia holsatica	−13.1	31.4	54	67.2	1
	Nitzschia paleacea	2.1	20.3	29.9	27.8	1
	Ntizschia communis	10	25	35	25	1
Odontella	*Odontella aurita*	−1.5	12	20	21.5	1
	Odontella mobiliensis	12.4	26.8	34.8	22.3	1
Phaeodactylum	*Phaeodactylum tricornutum*	−11.3 ± 16.4 (−47.9–4.7)	21 ± 3.1 (13.4–25.3)	29.2 ± 2.9 (25.2–36.3)	40.5 ± 15.4 (25.2–77.9)	11
Proboscia	*Proboscia inermis*	−3.5	3.7	7.8	11.3	1
Pseudo-nitzschia	*Pseudo-nitzschia americana*	8.5	27.4	41.5	32.9	1
	Pseudo-nitzschia granii	3.7	13.7	23.5	19.7	1
	Pseudo-nitzschia multiseries	−27.7	22.5	30.6	58.3	1
	Pseudo-nitzschia turgiduloides	−1.3	4.2	9	10.4	1
Rhizosolenia	*Rhizosolenia setigera*	5.9 ± 4.8 (1–10.8)	17.1 ± 6.8 (10.2–24)	27.3 ± 7.1 (20.1–34.5)	21.3 ± 2.3 (19–23.6)	2
Skeletonema	*Skeletonema ardens*	4.5 ± 3 (0.3–9.8)	31.1 ± 2.2 (26.6–32.4)	39 ± 2 (35–40)	34.5 ± 4.9 (25.2–39.6)	5
	Skeletonema costatum	−3.9 ± 21.2 (−63.4–8.3)	23.3 ± 2.4 (17.8–26.9)	33.7 ± 2.6 (27.9–36.7)	37.7 ± 20.4 (25–94.6)	9
	Skeletonema japonicum	−50.6 ± 7.5 (−62.8 to −39.8)	22.1 ± 0.6 (21.1–23)	30 ± 0 (30 − 30)	80.6 ± 7.5 (69.8–92.9)	5
	Skeletonema marinoi	−49.1	23.7	31.1	80.2	1
	Skeletonema marinoi–dohrnii	−47.7 ± 5.3 (−57.6 to −42.7)	25.1 ± 0.5 (24.3–25.9)	35 ± 0 (35–35.1)	82.8 ± 5.2 (77.8–92.6)	5
	Skeletonema menzelii	−1.9 ± 12.2 (−22.5–7.3)	27.8 ± 3.4 (23.5–32.2)	39.8 ± 0.2 (39.5–40)	41.7 ± 12.4 (32.2–62.6)	4
	Skeletonema pseudocostatum	−29.6	27.1	35	64.7	1
	Skeletonema tropicum	9.1 ± 1.7 (5.5–11.8)	26.7 ± 1.6 (24.3–29.5)	35.1 ± 0.7 (34–36.2)	25.9 ± 1.1 (24.3–28.5)	9
Skelotema	*Skelotema costatum*	8	24.5	26	18	1
Stellarima	*Stellarima microtrias*	−45.5	3.5	8	53.6	1
Stephanodiscus	*Stephanodiscus astraea*	0.5	14.2	25	24.5	1
	Stephanodiscus hantzschii	0 ± 5 (−5–5)	21.9 ± 1.8 (20–23.8)	35.3 ± 0.3 (34.9–35.7)	35.3 ± 5.4 (29.8–40.7)	2
Stephanopyxis	*Stephanopyxis palmeriana*	9.9	18.5	75.9	66	1
Synedra	*Synedra* sp.	−46.8	4.5	8	54.9	1
Thalassionema	*Thalassionema nitzschioides*	−23.1 ± 31.2 (−54.3–8.1)	23 ± 3.9 (19–27)	30.7 ± 3.3 (27.3–34)	53.8 ± 27.8 (25.9–81.6)	2
Thalassiosira	*Thalassiosira guillardii*	1.7	16.6	29.8	28.1	1
	Thalassiosira nordenskioeldii	−30.6 ± 25.7 (−56.3 to −4.8)	11.1 ± 1.4 (9.7–12.6)	17.8 ± 2.1 (15.6–20)	48.4 ± 27.9 (20.5–76.3)	2
	Thalassiosira pseudonana	−10.2 ± 14.2 (−36.1–3.5)	25 ± 1.6 (21.6–26.6)	32.1 ± 1.4 (30.1–33.7)	42.3 ± 14.9 (27–69.2)	8
	Thalassiosira rotula	−1.8 ± 4.7 (−11.1–3.9)	19.8 ± 1.2 (18.6–22)	30.5 ± 1.2 (29.9–33.6)	32.4 ± 4.6 (26–41.2)	7
	Thalassiosira weissflogii	2.9	19.1	26	23.1	1
Unidentified	*Men. 5*	10.3	27.3	37.3	26.9	1
DIATOMS	*Overall*	−7.1 ± 20.7 (−63.4–20)	22.1 ± 6.7 (1.1–35)	32.6 ± 11.9 (5–113.6)	39.8 ± 20.1 (10–106.7)	153

Table 6

Cardinal temperature parameters for other algal genera. For strains in which more than one set of cardinal temperature is provided, the values are expressed as mean ± standard deviation (minimum-maximum).

Genus	Species	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Akashiwo	*Akashiwo sanguinea*	6 ± 4.1 (−0.1–11.7)	23.6 ± 0.8 (22.2–24.7)	33.5 ± 1.8 (30–35)	27.4 ± 5.1 (20.5–34.9)	5
Alexandrium	*Alexandrium catenella*	−6.8	14.2	16.3	23.2	1
	Alexandrium fundyense	2.4 ± 0.4 (1.9–2.8)	16.3 ± 0.6 (15.7–16.9)	24 ± 0.1 (23.9–24.1)	21.5 ± 0.5 (21–22.1)	2
	Alexandrium minutum	10.5	20.6	70.4	59.9	1
	Alexandrium monilatum	15.5	28.2	33.8	18.2	1
	Alexandrium ostenfeldii	9	20.3	26.2	17.1	1
	Alexandrium tamarense	−0.7 ± 4.7 (−5.5–4)	17.9 ± 0.2 (17.7–18.1)	25.5 ± 0.4 (25–25.9)	26.2 ± 4.2 (21.9–30.5)	2
Apedinella	*Apedinella radians*	7.9	19.3	66.6	58.6	1
Calcidiscus	*Calcidiscus leptoporus*	6.6 ± 0.1 (6.5–6.7)	16.9 ± 1.5 (15.4–18.5)	24.9 ± 0 (24.9–24.9)	18.3 ± 0 (18.2–18.3)	2
Calciodinellum	*Calciodinellum albatrosianum*	5.3	32.9	61.5	56.2	1
Ceratium	*Ceratium furca*	8.1 ± 1.9 (5.7–10.3)	23.2 ± 1.7 (20.7–24.6)	30.3 ± 2.3 (26.9–32.1)	22.1 ± 1 (21.2–23.7)	3
	Ceratium furcoides	7.6 ± 0.7 (6.9–8.3)	22.5 ± 0.2 (22.3–22.8)	29.9 ± 0 (29.9–30)	22.3 ± 0.7 (21.6–23.1)	2
	Ceratium fusus	6.2 ± 2.3 (4.2–9.5)	22.7 ± 4.6 (16.1–26.5)	30.7 ± 1 (29.4–31.9)	24.4 ± 1.6 (22.4–26.5)	3
	Ceratium tripos	−37.4	16.3	31.1	68.6	1
	Ceratium lineatum	1.3	21.5	28.9	27.6	1
Chattonella	*Chattonella marina*	13.6 ± 3.4 (10–17.1)	27.4 ± 2.7 (23.6–30)	34.3 ± 1.9 (30.9–35.7)	20.6 ± 2.5 (18.6–24.9)	4
	Chattonella ovata	14.3 ± 0.7 (13.6–15.1)	30 ± 0 (30–30)	35.7 ± 0 (35.7–35.7)	21.3 ± 0.7 (20.6–22.1)	2
Chryosochromulina	*Chrysochromulina acantha*	11.2	24.3	29.9	18.7	1
	Chrysochromulina ericina	5.4	19.1	24.9	19.5	1
	Chrysochromulina hirta	6.1	19.3	24.9	18.8	1
	Chrysochromulina polylepis	1.7 ± 2.1 (−1.2–3.7)	17.1 ± 1.4 (15.6–19)	24 ± 1.8 (22.5–26.6)	22.3 ± 2.4 (18.8–24)	3
	Chrysochromulina simplex	10	23	29.9	19.9	1
Closterium	*Closterium acerosum*	4.7	16.3	30.6	25.8	1
	Closterium acutum	5.5	29.6	43	37.4	1
	Closterium ehrenbergii	−6.3 ± 18.2 (−49.8–5.1)	16.2 ± 4.6 (11.1–28.5)	43.5 ± 26.9 (29.8–135.1)	49.9 ± 28.1 (27.1–130.4)	14
	Closterium limneticum	7	34.3	47	40	1
	Closterium parvulum	−31.8	22.9	30	61.8	1
Coccolithus	*Coccolithus pelagicus*	3.1	16.4	27.4	24.3	1
Cochlodinium	*Cochlodinium polykrikoides*	7.8 ± 3.9 (1–10.7)	27.9 ± 0.3 (27.6–28.3)	35 ± 0.9 (33.7–36.4)	27.2 ± 3.1 (25.1–32.6)	4
Cosmarium	*Cosmarium abbreviatum*	−9.7	25.5	31.5	41.2	1
	Cosmarium beatum	3.1	25.5	36.6	33.5	1
	Cosmarium biretum	6.1	34.5	71.4	65.2	1
	Cosmarium botrytis	3	20.5	35.5	32.5	1
	Cosmarium crenatum	−0.2	17.6	35.7	36	1
	Cosmarium kjellmanii	0.8	26.5	33.7	32.9	1
	Cosmarium meneghinii	1.5	19.8	36	34.4	1
	Cosmarium punctulatum	0.6 ± 0.1 (0.5–0.8)	19.9 ± 0.3 (19.6–20.2)	35.9 ± 0.1 (35.7–36)	35.2 ± 0.2 (34.9–35.4)	2
	Cosmarium regnesii	2	21	36.5	34.5	1
	Cosmarium sp.	−4.9	24.2	35.1	40.1	1
Cryptomonas	*Cryptomonas curvata*	−19.4	18.8	23.2	42.7	1
	Cryptomonas erosa	12.5	20.6	30.9	18.4	1
	Cryptomonas marssonii	−1.4 ± 0.9 (−2.4 to −0.5)	21 ± 4.8 (16.2–25.9)	30.2 ± 0 (30.2–30.3)	31.7 ± 0.9 (30.7–32.7)	2
	Cryptomonas ovata	9.8	18.5	28.4	18.6	1
	Cryptomonas pyrenoidifera	−8.8	23.1	26.7	35.5	1
	Cryptomonas sp.	−4.1 ± 22.3 (−26.4–18.2)	23.6 ± 3.1 (20.4–26.8)	31 ± 1.8 (29.2–32.9)	35.2 ± 20.5 (14.7–55.7)	2
Desmidium	*Desmidium swartzii*	3.6	23.3	36.6	33	1
Diacronema	*Diacronema lutheri*	4 ± 9 (−5–13)	22 ± 0.9 (21 − 23)	30.9 ± 2 (28.9–33)	26.9 ± 11 (15.9–38)	2
Dinobryon	*Dinobryon divergens*	−3.3 ± 2.4 (−5.8 to −0.8)	16.8 ± 0.1 (16.7–17)	29.1 ± 0.7 (28.4–29.8)	32.4 ± 1.7 (30.6–34.2)	2
Emiliania	*Emiliania huxleyi*	−8.9 ± 28.2 (−85.1–10)	21.6 ± 1.6 (17.7–24.2)	28 ± 2.1 (24–31.3)	36.9 ± 27.7 (18.7–112.2)	12
Euglena	*Euglena gracilis*	20	29	40	20	1
Eutreptiella	*Eutreptiella gymnastica*	−10.9	18.6	26.7	37.6	1
Fibrocapsa	*Fibrocapsa japonica*	7.6 ± 1.8 (5.7–9.8)	22.1 ± 0.9 (20.4–22.8)	33.5 ± 1.5 (31.8–35.2)	25.8 ± 3.3 (21.9–29.2)	4
Galdieria	*Galdieria sulphuraria*	10 ± 0 (10–10)	39 ± 4 (35–43)	51.5 ± 4.5 (47–56)	41.5 ± 4.5 (37–46)	2
Gephyrocapsa	*Gephyrocapsa oceanica*	8.9 ± 4 (5.2–14.6)	24.9 ± 2 (22.2–27.2)	33.6 ± 2.6 (30.1–36.6)	24.6 ± 2 (22–26.9)	3
Gonatozygon	*Gonatozygon monotaenium*	7.9	26.4	35	27.1	1
Gonyostomum	*Gonyostomum semen*	5.1 ± 1.6 (3.4–6.7)	11.8 ± 1.2 (10.6–13.1)	32.4 ± 1.1 (31.3–33.6)	27.3 ± 2.7 (24.6–30.1)	2
Gymnodinium	*Gymnodinium aureolum*	10.9	20.2	35.1	24.2	1
	Gymnodinium catenatum	7.2 ± 0.1 (7.1–7.4)	24.1 ± 0 (24.1–24.1)	31 ± 1.7 (29.2–32.7)	23.7 ± 1.9 (21.8–25.6)	2
	Gymnodinium corollarium	−2.5	2.8	10.7	13.2	1
	Gymnodinium sp.	15.1 ± 0.2 (14.9–15.3)	25.4 ± 0.4 (24.9–25.9)	32.6 ± 0.3 (32.3–33)	17.5 ± 0.5 (16.9–18)	2
Gyrodinium	*Gyrodinium uncatenum*	7.7	27.5	35.7	28	1
Haptophytes	*Unidentified prymnesiophyte*	6.7	28.9	35	28.2	1
Heterocapsa	*Heterocapsa rotundata*	1.8	17.3	29.3	27.4	1
Heterosigma	*Heterosigma akashiwo*	−9.4 ± 13.4 (−22.9–4)	24.8 ± 1.8 (23–26.6)	31.3 ± 1.3 (30–32.7)	40.8 ± 14.8 (26–55.6)	2
Hymenomonas	*Hymenomonas carterae*	3	25.5	45	42	1
Isochrysis	*Isochrysis galbana*	8.4 ± 7.3 (−2.8–16)	29 ± 4.5 (21.1–35.7)	37 ± 6.9 (26.8–46.1)	28.5 ± 7.7 (18–36.4)	6
	Isochrysis sp.	8.6	22.2	37.2	28.6	1
	Tahitian isochrysis	10	27.5	35	25	1
	Tisochrysis lutea	12.7 ± 1 (11.6–14.1)	27.8 ± 0.7 (26.9–28.8)	35.2 ± 0.7 (34.5–36.2)	22.5 ± 1.7 (20.4–24.6)	3
Karenia	*Karenia brevis*	12 ± 0.9 (11.1–12.9)	22.1 ± 1.5 (20.6–23.7)	30.4 ± 0.9 (29.5–31.4)	18.4 ± 1.8 (16.5–20.2)	2
	Karenia mikimotoi	−4.8	26.1	31.5	36.4	1
Karlodinium	*Karlodinium veneficum*	−10	20.5	27.2	37.3	1
Klebsormidium	*Klebsormidium* sp.	1.4	13.6	31.5	30	1
Leonella	*Leonella granifera*	6.7 ± 7.6 (−0.9–14.4)	29.4 ± 2.8 (26.5–32.3)	35.9 ± 3.8 (32–39.7)	29.1 ± 11.5 (17.5–40.6)	2

Table 6 (*continued*)

Genus	Species	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Mallomonas	*Mallomonas acaroides*	9	19.8	24	14.9	1
	Mallomonas areolata	5.6	19.9	26.1	20.4	1
	Mallomonas caudata	−6.7 ± 9.6 (−13.9–6.9)	18.7 ± 1.1 (17.1–19.8)	24.7 ± 0.9 (24–25.9)	31.4 ± 10.2 (17–39.8)	3
	Mallomonas crassisquama	5.5	16	24.6	19.1	1
	Mallomonas elongata	−19.7	18.8	25	44.7	1
	Mallomonas tonsurata	9.9	20	24.8	14.9	1
Mesotaenium	*Mesotaenium kramstae*	3.8	22.2	34.6	30.8	1
Micrasterias	*Micrasterias americana*	4.7	23.1	56.2	51.5	1
Monodopsis	*Monodopsis subterranea*	7.6 ± 2.6 (5–10.2)	25.5 ± 0.5 (25–26)	33.2 ± 1.7 (31.5–35)	25.6 ± 4.3 (21.2–30)	2
Nannochloropsis	*Nannochloropsis* sp.	10.5	25.8	37.8	27.3	1
	Nannochloropsis gaditana	4.6	32	41	36.4	1
	Nannochloropsis granulata	2.3	27.9	32.5	30.2	1
	Nannochloropsis oceanica	3.2 ± 4.3 (−0.2–10.4)	26.9 ± 0.6 (26.3–28)	34.1 ± 0.8 (33.3–35.1)	30.9 ± 3.6 (24.7–33.5)	4
	Nannochloropsis oculata	6.6 ± 3.3 (3.2–10)	24.2 ± 0.7 (23.4–25)	41.8 ± 3.8 (38–45.7)	35.2 ± 7.2 (28–42.4)	2
	Nannochloropsis salina	13	26	36	23	1
Ochromonas	*Ochromonas* sp.	10.6	23.7	37	26.4	1
Olisthodiscus	*Olisthodiscus luteus*	1 ± 1.4 (−0.4–2.5)	20.8 ± 6.4 (14.4–27.2)	34.8 ± 11.1 (23.6–46)	33.7 ± 12.6 (21.1–46.4)	2
Pavlova	*Pavlova salina*	15	27	30	15	1
Peridinium	*Peridinium bipes*	3.9 ± 0.3 (3.5–4.2)	20.9 ± 0.1 (20.8–21)	52.2 ± 23.2 (29–75.4)	48.3 ± 22.8 (25.4–71.1)	2
	Peridinium sp.	6.9 ± 0.1 (6.7–7)	17.5 ± 0.4 (17.1–17.9)	30.3 ± 0.8 (29.4–31.1)	23.3 ± 0.9 (22.4–24.3)	2
Pernambugia	*Pernambugia tuberosa*	11.5	23.8	32.5	21	1
Phaeocystis	*Phaeocystis antarctica*	−1.9	3.4	7.8	9.8	1
	Phaeocystis globosa	9.5	25.4	36.5	26.9	1
	Phaeocystis pouchetii	−20 ± 0 (−20 to −20)	13.7 ± 3.6 (10–17.4)	16.7 ± 4.7 (12–21.5)	36.8 ± 4.7 (32–41.6)	2
Pleurochrysis	*Pleurochrysis carterae*	8	20.1	27.5	19.5	1
Pleurotaenium	*Pleurotaenium trabecula*	2.2	23.8	35.1	32.8	1
Porphyridium	*Porphyridium cruentum*	5.8	19.1	30	24.2	1
	Porphyridium purpureum	5	25	35	30	1
Prorocentrum	*Prorocentrum donghaiense*	7.1	28.2	36.1	29	1
	Prorocentrum gracile	7.9	16.9	24.8	16.9	1
	Prorocentrum micans	4.5	23.5	30	25.4	1
	Prorocentrum minimum	7.9	23.3	32.2	24.2	1
Prymnesium	*Prymnesium parvum*	11.4	19.3	32.7	21.3	1
Pseudochattonella	*Pseudochattonella farcimen*	0.6	13.1	20	19.4	1
Pseudopedinella	*Pseudopedinella pyriformis*	2.3	12.3	26.1	23.8	1
Pyrodinium	*Pyrodinium bahamense*	14.4	29.2	36.8	22.3	1
Rhodomonas	*Rhodomonas salina*	2.1	18.5	29.8	27.6	1
	Rhodomonas sp.	6.7 ± 1.2 (5.4–8)	16.3 ± 0.3 (16–16.7)	28.4 ± 2.4 (26–30.8)	21.7 ± 3.7 (18–25.4)	2
Roya	*Roya anglica*	4.2	20.9	29.9	25.6	1
Scripsiella	*Scrippsiella trochoidea*	−15.7	15.7	24.8	40.5	1
Staurastrum	*Staurastrum anatinum*	2.3	26.8	35.2	32.8	1
	Staurastrum avicula	5.2	26.7	34.6	29.4	1
	Staurastrum chaetoceras	7.9	26.7	34.1	26.1	1
	Staurastrum cingulum	7.7	28.4	44.1	36.3	1
	Staurastrum pingue	4.3 ± 0.8 (3.5–5.2)	27.6 ± 0.3 (27.2–27.9)	37.4 ± 2.3 (35–39.8)	33 ± 3.2 (29.8–36.2)	2
	Staurastrum planctonicum	6.6	28.2	37.3	30.6	1
Staurodesmus	*Staurodesmus cuspidatus*	3.2	25.2	32.8	29.5	1
Synura	*Synura* sp.	8	23.2	31.4	23.3	1
	Synura petersenii	−4.9 ± 7.9 (−17.8–2.7)	17.6 ± 3.9 (11.5–22.6)	44 ± 17.2 (28.4–71.3)	49 ± 17.5 (27–76.1)	4
	Synura sphagnicola	3.2	16.1	24.5	21.2	1
Tribonema	*Tribonema aequale*	0	14	30	30	1
	Tribonema sp.	−0.8	20.2	30.1	31	1
OTHER	*Overall*	2.6 ± 12.3 (−85.1–20)	22.1 ± 5.6 (2.8–43)	33.6 ± 11.5 (7.8–135.1)	31 ± 15.3 (9.8–130.4)	211

reliable cultivation performance indicators (typically expressed as the areal and/or volumetric biomass productivity, or as the ratio between the inlet and outlet biomass concentrations). This is especially true for complex systems, such as algae-bacteria consortia for wastewater treatment. Since microalgae cultivation systems are strongly dynamic (i.e., affected by cyclic daily and seasonal variabilities, and also variable influent compositions, in the case of wastewater treatment systems), kinetics-based mechanistic modelling of such biological processes is an appropriate tool for this purpose. Within the most versatile, complete, and robust biological models available in literature (Casagli et al., 2021; Sánchez-Zurano et al., 2021a; Solimeno et al., 2019), biomass growth kinetics are usually modelled considering a CTMI growth factor multiplier, that depends on the instantaneous culture temperature. For outdoor and/or uncontrolled systems, the actual temperature depends on both the environmental conditions and the cultivation system arrangement (e.g., the liquid height of the cultivation pond or the hydraulic retention time), and it can strongly vary along the year, with consequent limitations on the growth, especially during cold and hot periods of the year. As recently shown, biological growth models can be coupled with a proper and validated thermal model of the cultivation system for a more comprehensive evaluation of process performances (Slegers et al., 2013; Ruiz et al., 2016; Casagli and Bernard, 2022a). Open ponds were the first microalgae industrial cultivation systems and are still widely applied. Indeed, they are currently in use by > 80 % of the companies operating large-scale Spirulina (*Arthrospira* sp.) cultivation plants in Europe (Araújo et al., 2021), though they are also widely used worldwide for other species such as *Chlorella* sp. (Mobin and Alam, 2017; Costa et al., 2019). Nonetheless, most European countries have sub-optimal climatic conditions for large-scale outdoor microalgae production in open ponds (Slegers et al., 2013), which may require the use of greenhouses to allow for temperature regulation and for better control of biomass quality (as defined by the target market, in terms of contamination by bacteria or other algal species). Nowadays, one of the most reliable methods to predict open pond cultivation temperatures is via mechanistic modelling of heat flux exchanges (radiation, sensible and latent convection, conduction)

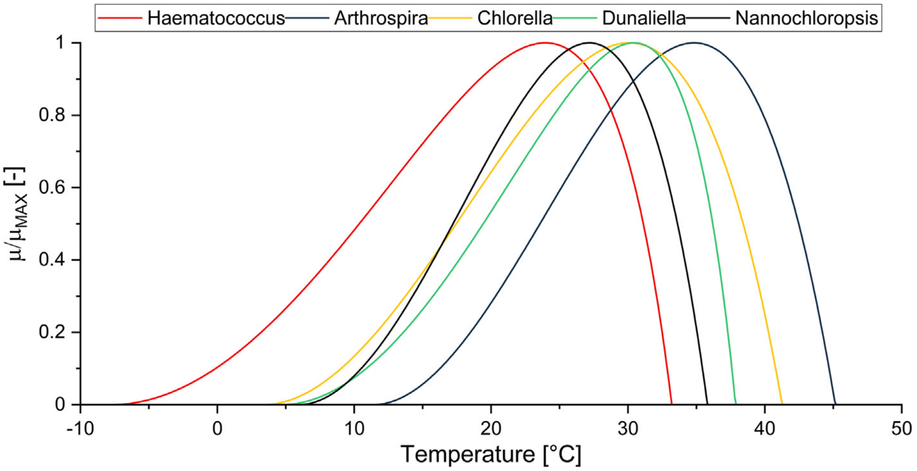

Fig. 2. Thermal response for industrially-relevant microalgae. Averaged values for each species are shown.

Table 7

Comparison of averaged cardinal temperatures and thermal niche for different groups of phototrophic organisms. For clarity, strains with extreme cardinal temperatures (i.e., $T_{MIN} < -20$ °C and $T_{MAX} > 55$ °C) are not included in the data aggregation.

Aggregation	T_{MIN} [°C]	T_{OPT} [°C]	T_{MAX} [°C]	Niche [°C]	n [−]
Cyanobacteria	9.1 ± 8.8 (−18.1–24.9)	28.8 ± 4.3 (12.5–39.9)	37.5 ± 5.4 (20–50.6)	28.3 ± 9.5 (6.1–54.5)	98
Diatoms	2.8 ± 8.3 (−19.9–20)	23.1 ± 6 (3.5–35)	32.8 ± 7.1 (7.8–54)	29.9 ± 9.1 (10–67.2)	114
Green algae	4.5 ± 7 (−17.7–21.6)	26.1 ± 6 (6.6–38.7)	37.4 ± 7.7 (14.9–54.7)	32.9 ± 9.2 (13–57.9)	138
Other	4.6 ± 6.9 (−19.7–20)	22.2 ± 5.4 (2.8–35.7)	31.9 ± 5.9 (7.8–47.3)	27.2 ± 7.5 (9.8–46.5)	191

between the system and the surroundings (Casagli and Bernard, 2022a; Béchet et al., 2011; Casagli and Bernard, 2022b).

When a greenhouse is adopted, mechanistic GPS models can be adapted to the specific case study, to assess the impact of, e.g., the covering system, both in terms of temperature and photosynthetically active radiation (PAR) availability, primarily depending on the greenhouse cladding material (Li et al., 2009; Casagli and Bernard, 2022b; Zhu et al., 1998; Sarkar and Tiwari, 2005). Similar physical models can be adopted to model the temperature and control systems in closed bioreactors (Mehlitz, 2009). When studying the optimization of the cultivation performance, temperature control by heating/cooling is thus an interesting option.

As discussed in Section 2.5, CTMI curves can be used to identify the ideal temperature range to be maintained by a proportional or PID controller, thus allowing for enhanced productivity, by keeping the normalized growth rate above a predefined target throughout the entire year. Since winter heating and summer cooling loads (and peak powers) are strongly related to the temperature setpoints (that, in turn, depend on both the cardinal parameters and the associated shape of the CTMI curve), the cardinal temperature model practically dictates whether a culture temperature-control strategy is cost-effective, and at which minimum target of normalized growth rate. Indeed, as depicted in Fig. 10, the outputs of thermal and biological models can be combined within an economic framework, to obtain a comprehensive techno-economic assessment. This analysis allows assessing whether the additional expenditure required to implement temperature regulation is effectively counter-balanced by the additional revenue due to improved productivity. Energy consumptions and other economic indicators such as the levelized cost of production per unit of biomass dry weight (LCO_{DW}) and the net present value (NPV) of the

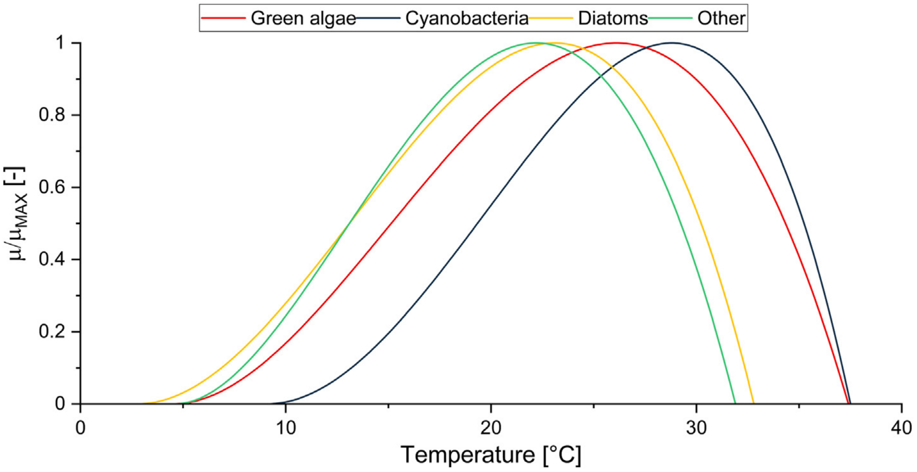

Fig. 3. Thermal response for different groups of microalgae. Averaged values for each species are shown.

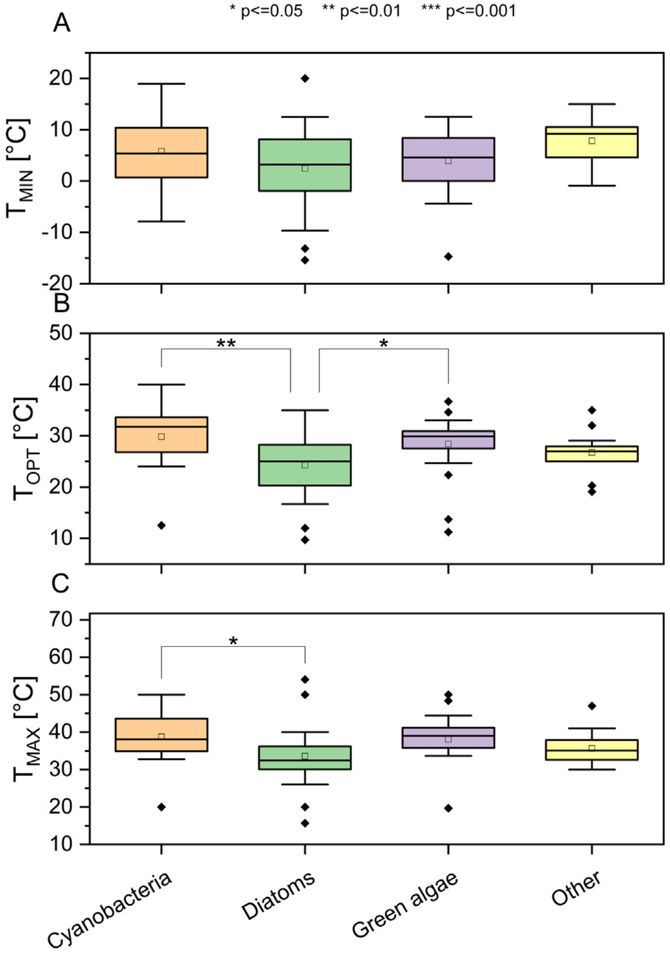

Fig. 4. Boxplots showing the distribution of cardinal temperatures among the different groups (A: T_{MIN}, B: T_{OPT}, C: T_{MAX}). Statistically significant differences are indicated with asterisks and brackets (*p-value ≤0.001, **p-value ≤0.001, ***p-value ≤0.001).

investment can be calculated for strains having different cardinal temperatures and for different temperature control strategies, allowing to assess the most profitable solution for the desired target market.

4.3.1. Case study: cultivation of Chlorella strains under a greenhouse in different locations

To compare the thermal response for different algal strains, a representative industrially-relevant species was chosen, i.e., *Chlorella* sp., for its cultivation under a greenhouse in different sites in Europe. As shown in Fig. 11, different heating and cooling loads can be expected for each *Chlorella* strain, strongly depending on the chosen location and climatology. Indeed, these conditions strongly impact the overall biomass productivity and the economic feasibility of the cultivation system (Slegers et al., 2013; Coleman et al., 2014), as well as its environmental impacts (Zaimes and Khanna, 2013). According to the results provided here (see also Supporting information, SI.2), it is possible to draw some general considerations to compare the energy requirement of different species. In the specific case study, it is assumed that the energetic expenditure has the same economic weight in all seasons, i.e., the levelized cost of energy to produce hot water ($LCOE_{HEATING}$) is similar to the levelized cost for cold water ($LCOE_{COOLING}$). Under this assumption, the actual cost is mainly determined by higher heating loads needed in colder climates (Wageningen), or by higher cooling loads necessary in hotter climates (Almeria). For both *C. vulgaris* and *C. sorokiniana*, the overall cost for maintaining the temperature at the optimal setpoint is lower when the cultivation is located in warmer climates, such as Almeria or Milan. The cultivation of the psychrophilic strain *C. miniata* is instead more profitable if the greenhouse-pond system is located in cold climates, such as in Wageningen. When looking at the specific heating and cooling loads, *C. vulgaris* is more suitable for the climatic condition of Almeria during winter (resulting in much lower heating loads required to maintain the temperature setpoint), while its cultivation would be less energy-demanding in Wageningen, especially during summer (thanks to the lower cooling loads required). Similar considerations can be drawn for the strain *C. sorokiniana*, for which the heating loads are always higher, and the cooling loads are always lower, compared to the other two strains. Since this strain is thermophilic and is characterized by a quite narrow thermal niche, a high amount of energy must be provided to the cultivation system at all European latitudes, so that the overall

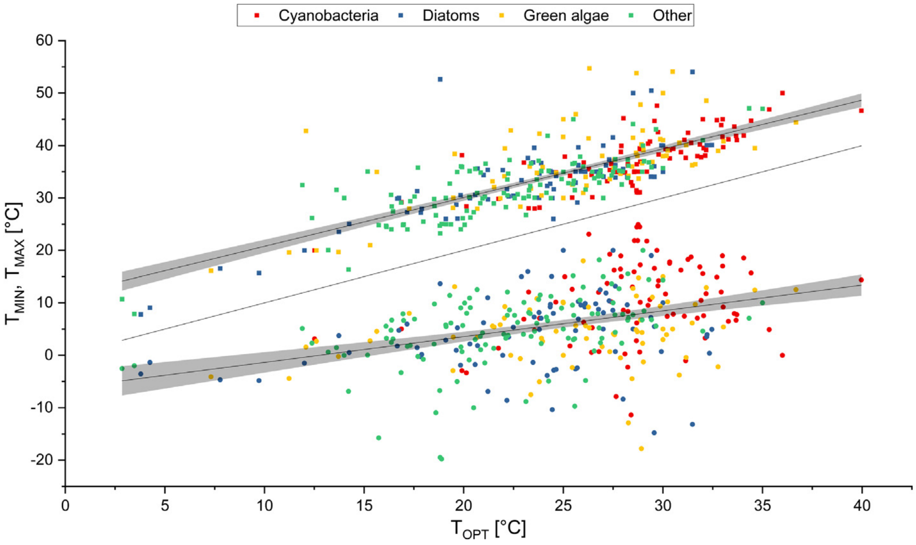

Fig. 5. Correlations between the optimal temperature and minimum and maximum temperatures for all the algal strains reviewed. Extremophilic strains (i.e., having $T_{MIN} < -20$ °C or $T_{MAX} > 55$ °C) are not shown in the graph.

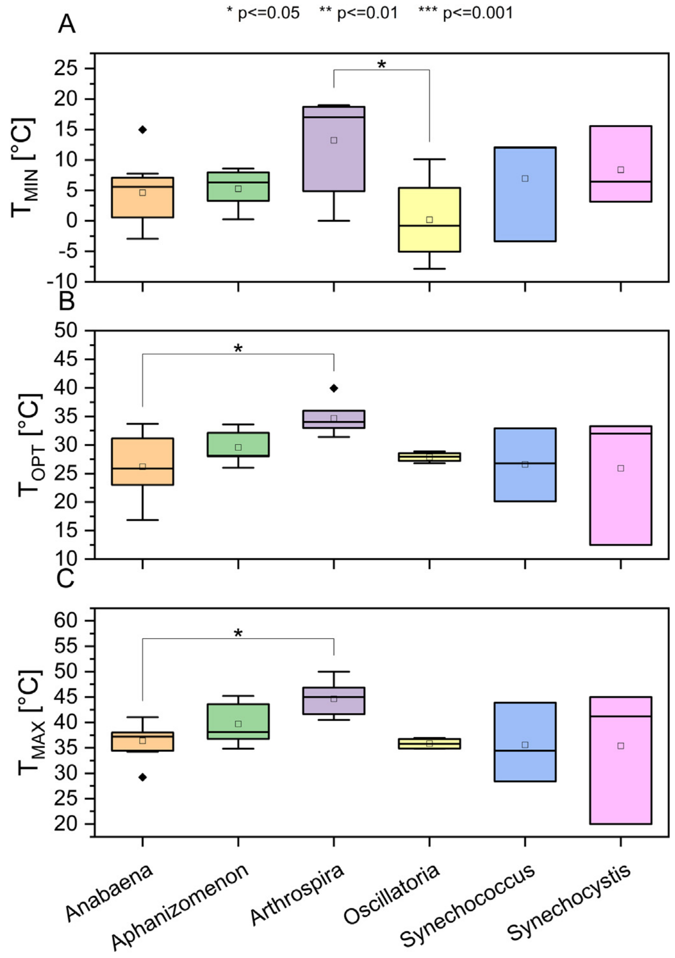

Fig. 6. Boxplots showing the distribution of cardinal temperatures among industrially-relevant species of cyanobacteria (A: T_{MIN}, B: T_{OPT}, C: T_{MAX}). Statistically significant differences are indicated with asterisks and brackets (*p-value ≤0.05, **p-value ≤0.01, ***p-value ≤0.001).

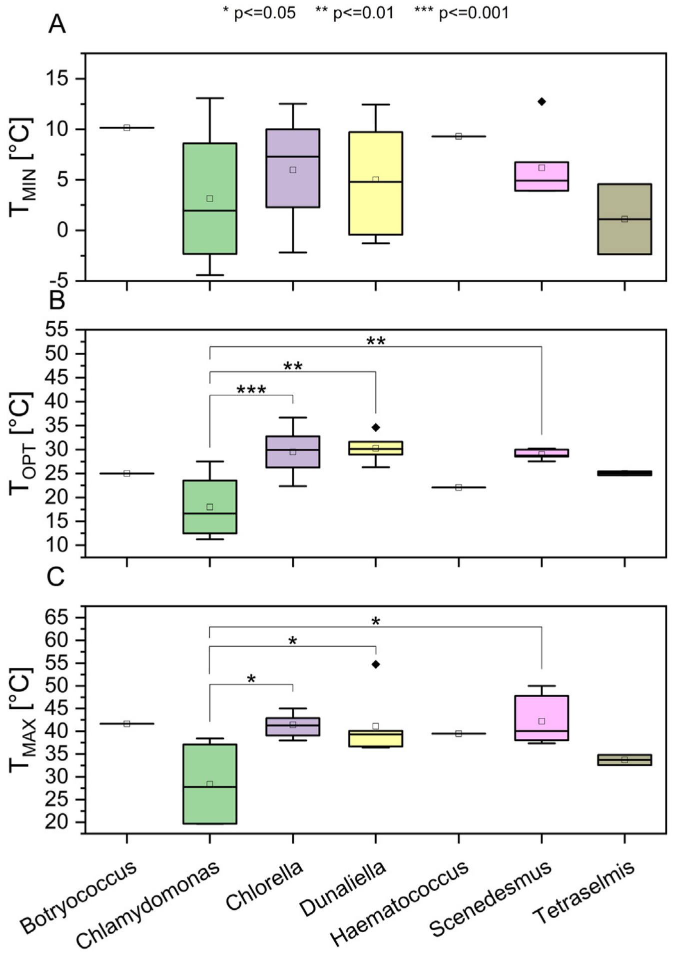

Fig. 7. Boxplots showing the distribution of cardinal temperatures among industrially-relevant species of green algae (A: T_{MIN}, B: T_{OPT}, C: T_{MAX}). Statistically significant differences are indicated with asterisks and brackets (*p-value ≤0.05, **p-value ≤0.01, ***p-value ≤0.001).

energy requirement is disproportionately higher than for the other strains. The thermal response of *C. sorokiniana* also makes this strain more suitable to be cultivated in summer times, regardless of the latitude, thanks to the lower cooling loads required. When looking at the total yearly energy consumption, as expected, growing *C. miniata* during cold seasons implies a lower energy expenditure at lower latitudes such as in Almeria. Regarding cooling loads, the hotter summer conditions of Milan and Almeria would possibly make the cultivation of *C. miniata* inconvenient, compared to Wageningen. As a general consideration, lower energy requirements are always needed for this strain, regardless of the considered location, also due to the wider niche compared to the other strains.

As mentioned, these considerations can be easily transposed to other algal species. However, it should be stressed that to identify the better strain to be cultivated at a certain site or latitude, other factors should be considered, in addition to the cultivation temperature. Indeed, the most appropriate cultivation conditions under which the system would provide the highest productivity must also include other abiotic cultivation factors. For example, the pH values and the concentration of dissolved oxygen and nutrients have a major role in shaping the evolution of the algal growth rates and associated productivity (Costache et al., 2013; Sánchez-Zurano et al., 2021b). Along with these parameters, the effective light intensity perceived in the culturing system is probably the most important factor, thus a proper coupling between dynamic thermal and biological models should take into account its impact (Casagli and Bernard, 2022a). As a consequence, if the light intensity is not controlled (e.g., by installing LED or other external light sources), the latitude will play a crucial role in defining culture productivities. In addition, the maximum specific growth rate may significantly differ within algal strains and species, as shown by the data provided in the electronic database (SI.1). For example, for the strains described in this section, the average maximum specific growth rates range from $\mu_{MAX} = 0.4\ d^{-1}$ for *C. miniata*, up to $1.7–2\ d^{-1}$ for *C. vulgaris* and *C. sorokiniana*. Moreover, these values are only properly comparable when tested under common boundary conditions (such as the light intensity and the pH values, among others), and this condition is not always met considering the values reported in this review. Therefore, the analysed case study should only be regarded as a general indication of the impact of temperature on the energetic expenditure of different strain cultivation, without the claim of being representative of all possible culture conditions.

5. Conclusions

The cardinal temperature model is a simple temperature dependence model with few parameters having a precise and intuitive physical meaning. The model represents the main link between thermal and biological modelling of microalgae cultivations and allows determining the techno-economic feasibility of producing a given strain at a given latitude or climatology, either with or without a temperature control system. A comprehensive dataset of cardinal temperature parameters was built up and reported in this study, aimed at describing the temperature response of microalgae cultivation. The CTMI is especially useful when evaluating the feasibility of commercial microalgae applications; in particular, it can assist bioprocess engineers in crucial design options, such as the choice of the

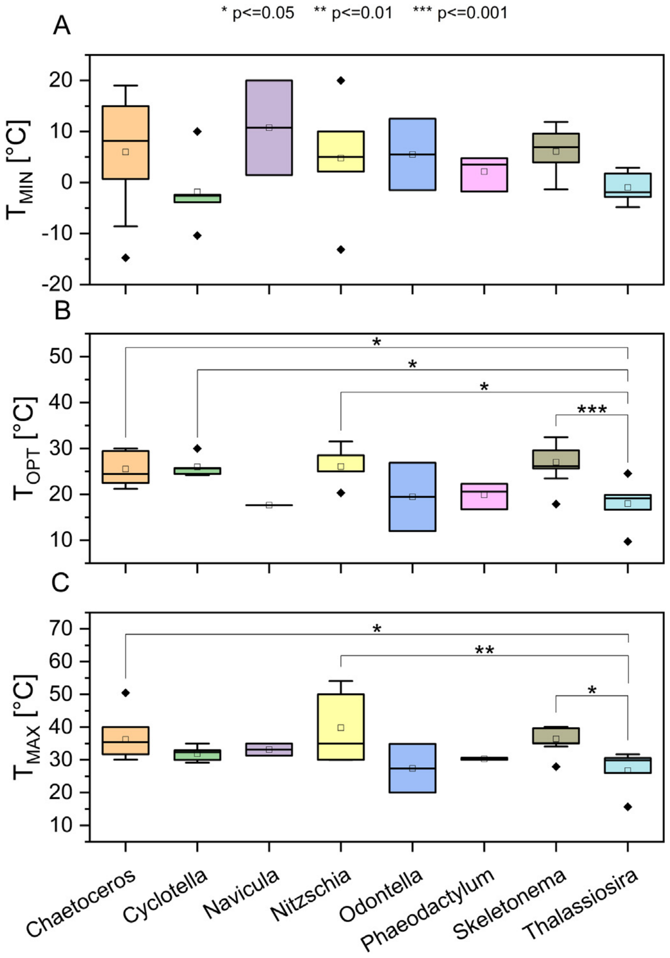

Fig. 8. Boxplots showing the distribution of cardinal temperatures among industrially-relevant species of diatoms (A: T_{MIN}, B: T_{OPT}, C: T_{MAX}). Statistically significant differences are indicated with asterisks and brackets (*p-value ≤0.05, **p-value ≤0.01, ***p-value ≤0.001).

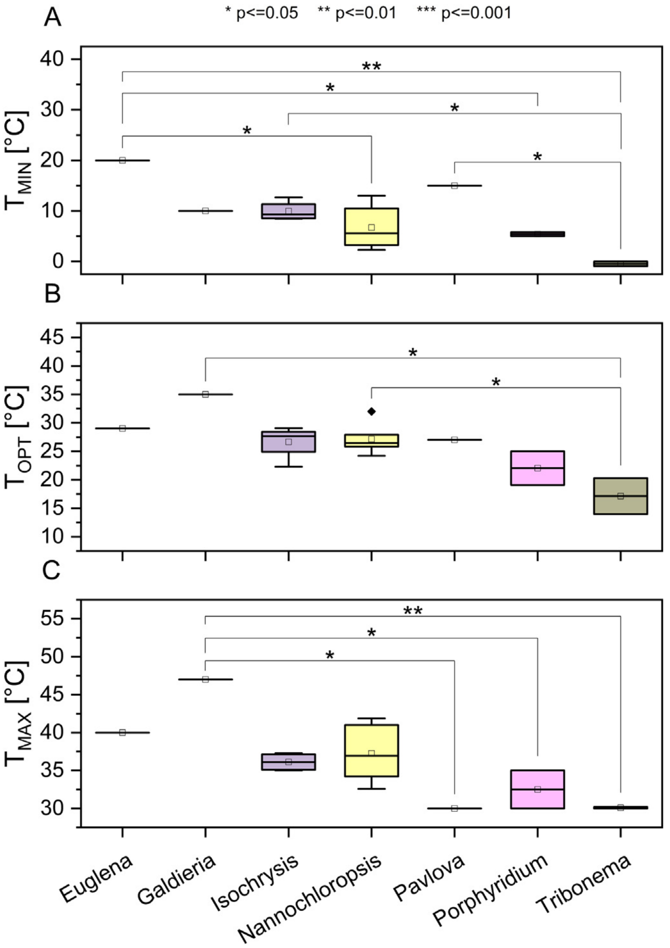

Fig. 9. Boxplots showing the distribution of cardinal temperatures among industrially-relevant species of other phototrophic microorganisms (A: T_{MIN}, B: T_{OPT}, C: T_{MAX}). Statistically significant differences are indicated with asterisks and brackets (*p-value ≤0.05, **p-value ≤0.01, ***p-value ≤0.001).

genus or strain to be cultivated, when the expected trend of plant temperatures is known. As an example, a strain characterized by a high thermal niche (e.g., *Chlorella* sp.) would be preferable for outdoor cultivation in continental climates characterized by high temperature variabilities between winter and summer. Alternatively, if the target production chain allows for a seasonal differentiation of the produced strain, an optimal culture rotation strategy can be easily established, with the help of the proposed database. To this aim, the most suitable species to be grown during winter and/or in cold climates (e.g., *Haematococcus* sp.), or those performing better during the summer and/or hotter climates (e.g., *Arthrospira* sp.), can be screened and identified. On average, green algae and cyanobacteria seem to have a similar thermal response and to be more suitable for cultivation in hot climates and with a high temperature variability. Nevertheless, at the phylum level, higher statistical variability was found for each group, so that design considerations made at the broader aggregation level can be misleading. When considering all-year-round algal monoculture cultivations under greenhouses at European latitudes, a good indication for decision makers is to select strains with the nigher niche as possible, to reduce the energy footprint of a controlled and enhanced production.

CRediT authorship contribution statement

S. Rossi: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **D. Carecci:** Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Writing – review & editing. **E. Ficara:** Conceptualization, Formal analysis, Methodology, Resources, Validation, Funding acquisition, Project administration, Supervision, Writing – review & editing.

Data availability

Data are reported as Supporting Information

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162275.

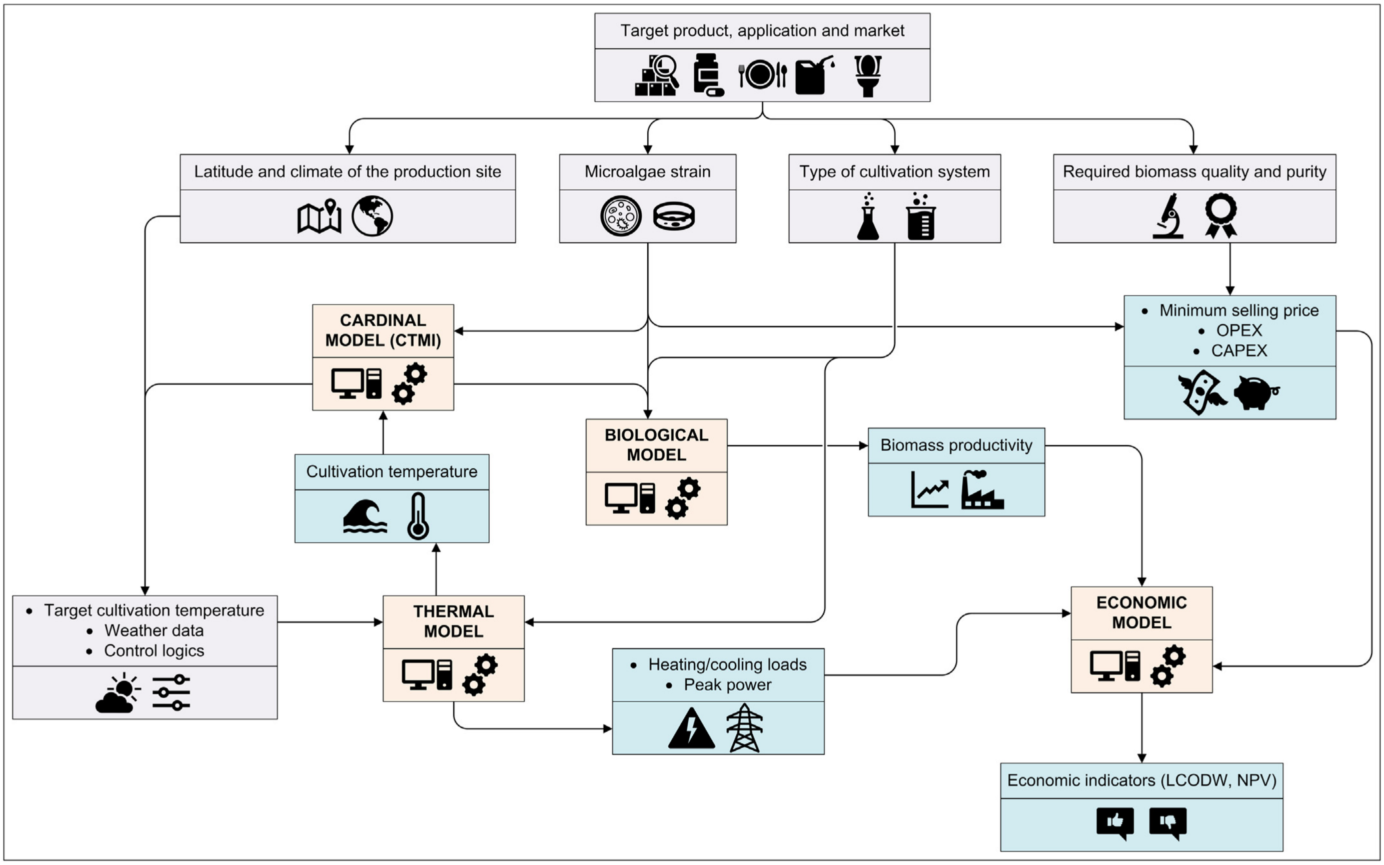

Fig. 10. Workflow of techno-economic assessment of microalgae cultivation systems, accounting for thermal and biological modelling integrated with the cardinal temperature model (CTMI). The specific modelling frameworks are depicted in orange, the main input and output variables are shown in light blue, and the design or boundary conditions are shown in grey.

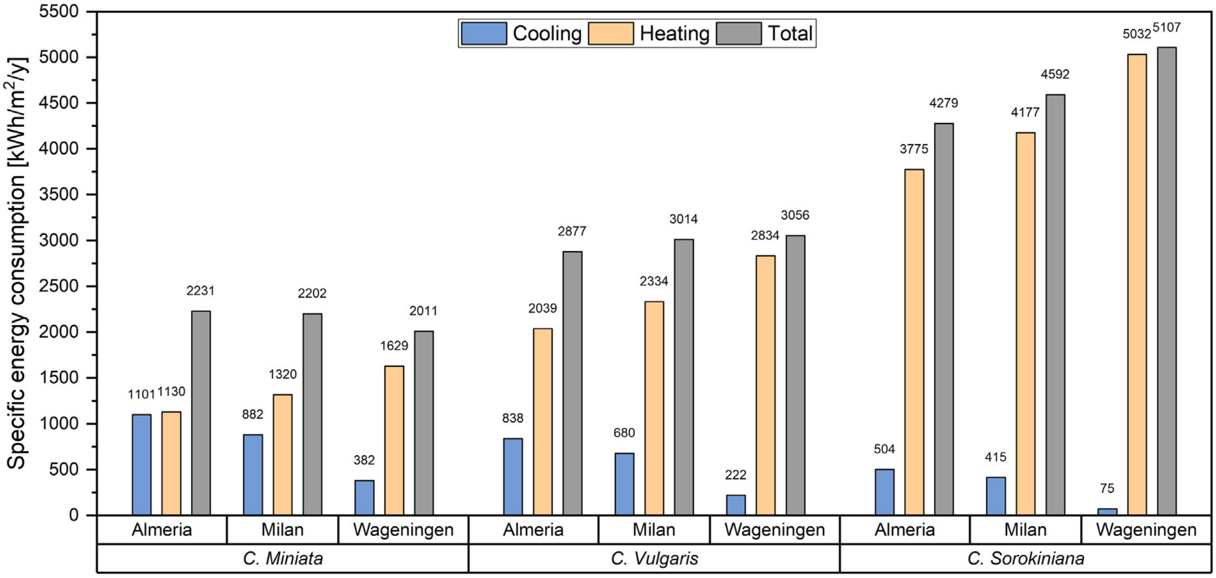

Fig. 11. Specific thermal heating and cooling loads required to maintain the optimal temperature in a microalgal raceway cultivation system placed under a greenhouse. Values are expressed as average values for different Chlorella strains (*C. vulgaris*, *C. sorokiniana*, and *C. miniata*) in different sites located in Europe: Almeria (Spain), Milan (Italy), and Wageningen (The Netherlands).

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