ISSN 0001-4370, Oceanology, 2019, Vol. 59, No. 3, pp. 316–326. © Pleiades Publishing, Inc., 2019.
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MARINE BIOLOGY

Characteristics of Growth and Fluorescence of Certain Types of Algae during Acclimation to Different Temperatures under Culture Conditions

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Received March 22, 2017; revised May 8, 2018; accepted July 2, 2018

Abstract—The paper examines the temperature dependence of the specific growth rate and ratio of variable to maximum fluorescence (F_V/F_M) in a number of marine planktonic algae from collections of cultures. It determines the optimum growth temperatures (T_{opt}), upper and lower limits of the tolerance zone, and in some cases, changes in the dynamics of these parameters outside the tolerance zone. Temperature characteristics of the species corresponded to the growth conditions of these species in a natural environment. Prolonged stress exposure to a low positive temperature (4–6°C) was reversible; recovery of the growth rate and F_V/F_M was observed immediately after the temperature increased. In diatoms, temperatures 2–3°C above the T_{opt} for diatoms induced gradual degradation of the culture, which, depending on the duration of exposure, could lead to the death of algae. Springtime dinoflagellates exhibited higher temperature resistance and remained viable at temperatures 5–8°C above T_{opt} with lower specific growth rates. The increasing portion of temperature dependence of the specific growth rate approximated a linear dependence; the regression coefficient is 0.08–0.13 for diatoms and 0.03–0.11 for dinoflagellates. The normalized values for this parameter (the relative value of change in the specific growth rate, %) was 5.3 ± 0.4 for diatoms and 6.4 ± 0.5 for dinoflagellates for 1°C of temperature change. Dinoflagellates exhibited larger values for the Q_{10} parameter. F_V/F_M for most species had high values in the entire range of temperatures at which the algae maintained a steady-state growth. A drop in this parameter outside the limits of the tolerance zone was associated with the temperature-induced inhibition of growth processes.

DOI: 10.1134/S0001437019030019

INTRODUCTION

Temperature is one of the primary factors affecting the formation of plant biocenoses, their biogeography, and biological productivity. In marine ecosystems, production potential in phytoplankton communities is commonly assumed largely depend on the hydrological conditions, which determine the level of mineral nutrition in algae of the euphotic zone [18, 31, 42]. At the same time, seasonal temperature variation is the factor that determines bloom development and the primary production rate in the boreal water species [10, 35]. Under these conditions, temperature plays a critical role; this makes research studies into the individual temperature characteristics of various plankton species highly relevant. The characteristics, including the specific growth rate, extent of the tolerance zone, and functional survivability at its limits are brought to foreground in the competitive environment of marine phytocenoses.

Among the topics discussed in the literature is the functional dependence of specific growth rate on temperature, i.e., its correspondence to the laws of enzyme kinetics (Q_{10}) or other types of relationships, which may be significant in modeling ecological and production processes [16, 29].

The relationship between temperature and the ratio of variable to maximum fluorescence F_V/F_M (a parameter that characterizes electron transport in photosystem II and is an indicator of functional performance of algae) has been insufficiently covered in the literature [5, 23].

The goal of the present work is to examine the temperature dependence of growth in marine planktonic algae (Bacillariophyceae and Dynophyceae) that vegetate under different temperature conditions, to determine the upper and lower limits of their tolerance zone and the relation between the growth parameters and F_V/F_M, and to study the dynamics of temperature-induced inhibition and recovery of functional activity at the limits of the tolerance zone in some algal species.

MATERIALS AND METHODS

The following cultures from the collection of the Department of Physiological Ecology of Algae were

used in the research: Bacillariophyceae (*Chaetoceros curvisetus*, *Cylindrotheca closterium*, *Skeletonema costatum*, *Thalassiosira parva*, *Thalassiosira weissflogii*, *Ditilym brightwelli*), Dynophyceae (*Gymnodinium wulffii, Prorocentrum pusilla, Glenodinium foliaceum*, *Heterocapsa triquetra*, *Gyrodinium fissum*, *Prorocentrum micans*, *Prorocenrum cordatum*), and Chlorophyceae (*Chlorella vulgaris suboblonga*). In the collection environment, species growth was maintained under natural light illumination and temperatures of 18–20°C on *f*/2 medium for a year or more.

Culture conditions for algae. The necessary light and temperature regimes for culturing were obtained by incubating the algae inside two cooling chambers, each equipped with a fast-response low-inertia heating element, LED light source, and ventilation. The provided temperature controller relay was switched off and replaced by a digital controller to effectuate a cooling and heating regime to an accuracy of ±0.1°C. Lighting for algae was 85 μE m^{-2} s^{-1} in continuous mode in all experiments. The *f*/2 culture medium was employed. The cultures were grown in 350 mL Erlenmeyer flasks, 20 mL aliquots were taken for the analysis, and fresh nutrient medium was added to maintain the cultures in a particular range of densities in exponential growth phase.

Algae obtained from the collection were held at 18–22°C for initial acclimation. Then, one part of the examined culture was gradually exposed to a temperature decrease, and another part, to a temperature increase in increments of 2–4°C. In each temperature regime, the cell concentration was controlled daily by measuring the optical density of the culture and the respective quantitative propagation of the culture to maintain density within the range that would allow exponential growth of algae and density sufficient for measurement. Acclimation was deemed completed when steady growth was achieved, i.e., from two to six days, depending on temperature. At the limits of the tolerance zone, if a stabilized growth rate was not achieved, the specific growth rate was determined on the first or second day after a change in the conditions and temperature-induced inhibition of the algae was recorded.

The specific growth rate of algae (day^{-1}) was determined by the formula

$$\mu = \ln \frac{D2 - D1}{\Delta t},$$

where D_1 and D_2 are the optical densities at the start and end of exposure and Δt is the time between measurements (days).

The experiment was conducted in triplicate for all examined algal species and values of the temperature dependence of the specific growth rate; each culture vessel was sampled for three to six optical density measurements of cell suspensions. The mean specific growth rate and standard error of the mean were calculated based on the resulting measurement data.

The optical density of the cell suspension was determined using an SF 26 spectrophotometer at a wavelength of 750 nm in 10 cm cylindrical cuvette fastened inside the cuvette section by a specially made holder.

The possibility of using the optical density as an indicator of the specific growth rate of various species was studied earlier; a linear dependence was obtained between this value and the amount of organic carbon determined by combustion using a CHN Analyzer in algal suspensions [7]. The standard deviation (S) of optical density measurement was established by statistical processing of a series of measurement procedures ($n = 12$) at 0.047 opt. u. At minimum experimental densities of the measured suspensions of 0.3 opt. u., the coefficient of variation did not exceed 16%.

The pH value of the culture medium was monitored and remained within the range of 8.2–8.5.

The ratio of variable to maximum fluorescence (F_V/F_M) was determined with a *MEGA* 25 fluorimeter [4, 5, 11]:

$$F_V/F_M = \frac{F_M - F_0}{F_M},$$

where F_0 is the fluorescence value with open reaction centers and F_M is the maximum fluorescence after a sequence of light flashes saturating the photosynthetic reaction centers. Prior to measurement, the samples were exposed to darkness for 15 min at the acclimation temperature.

The Q_{10} temperature coefficient was determined by the formula

$$Q_{10} = \left(\frac{\mu_2}{\mu_1}\right)^{10/(t_2 - t_1)},$$

where μ_1 and μ_2 are the specific growth rates at temperatures t_1 and t_2, respectively.

Experimental points approximated the polynomial functions. Such a representation characterized the general form of the temperature dependences and made it possible to determine T_{opt}, which is the temperature of the maximum specific growth rate, defined as the midpoint of the polynomial approximation of the dependence and ΔT_{opt}, which is the width of the dome maximum specific growth rates with parameter T_{opt} fluctuating within the limits of 20%. To determine the ΔT_{opt} value, we employed a polynomial function equation and introduced the T_{opt} value reduced by 20%.

RESULTS

Figure 1 shows the temperature dependences of the specific growth rates for the examined algal species. Table 1 gives the numerical values for a number of the parameters of these dependences.

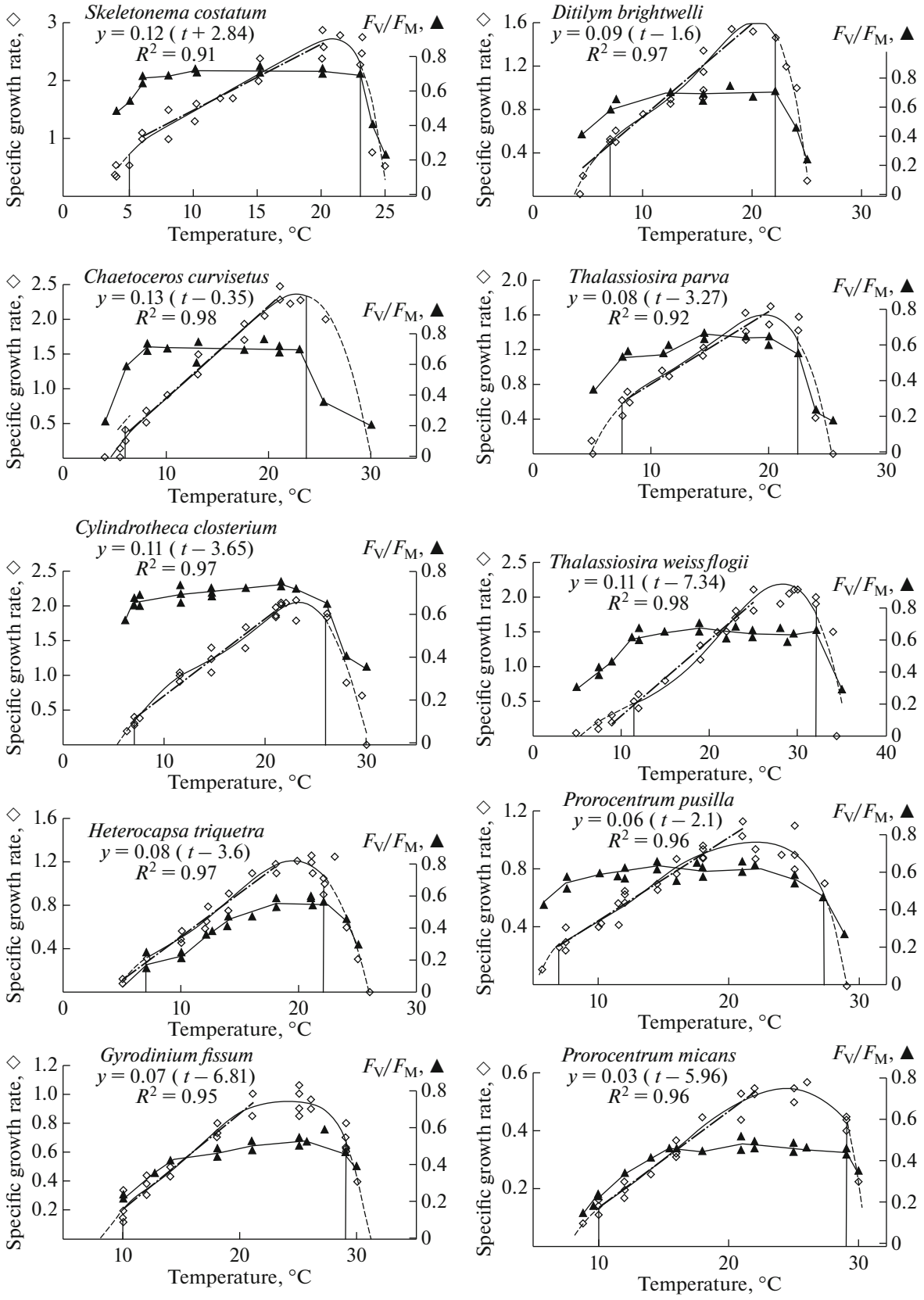

Fig. 1. Temperature dependences of specific growth rate and ratio of variable to maximum fluorescence in studied microalgae species.

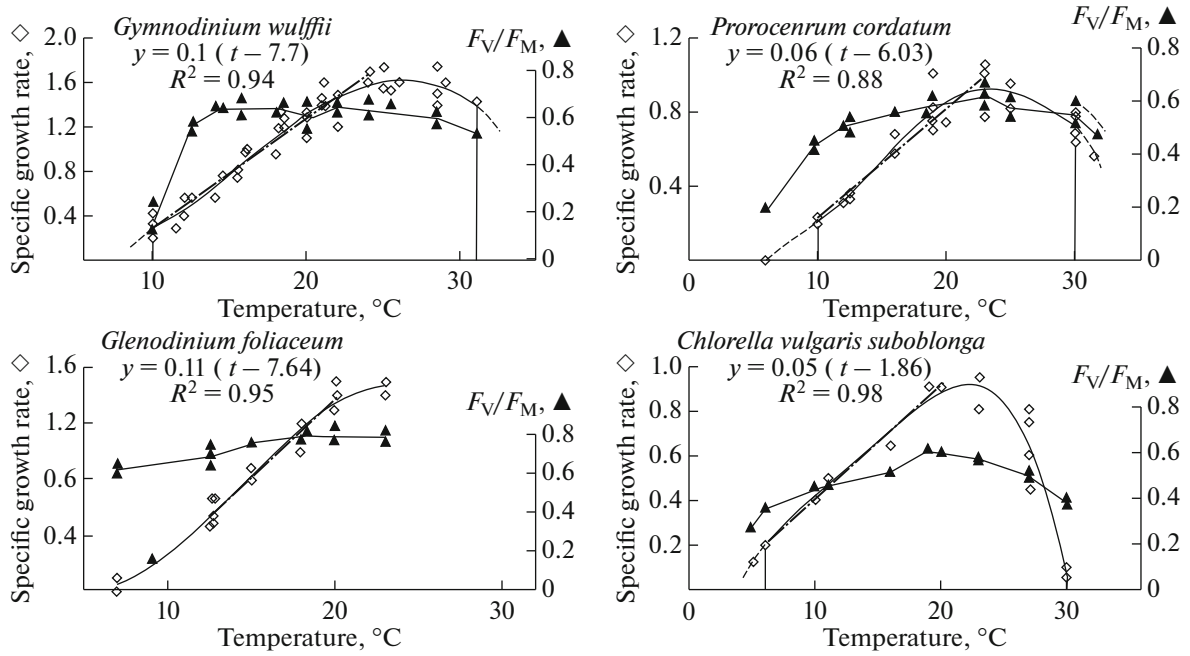

Fig. 1. (Contd.)

Limits of the Optimum Temperature and Growth Temperature Range in Algae

Diatom species *Ch. curvisetus*, *S. costatum*, *T. parva*, and *D. brightwelli*, representing Black Sea phytoplankton in winter–spring and fall, were observed to share similar optimum temperatures and specific growth rates (T_{opt} 20–22°C) and extent of the optimum temperature range (ΔT_{opt} 4–5°C) around temperatures of 18–23°C. Phytoplankton *C. closterium* isolated in the collection from the Mediterranean Sea had T_{opt} at 24°C and ΔT_{opt} at 5°C (21–26°C). The diatom *T. weissflogii* isolated from South Atlantic phytoplankton attained maximum growth at a temperature of 27°C and ΔT_{opt} of 7°C (25–32°C).

Dinophytas (dinoflagellates), which develop in the Black Sea in summer and early fall, featured higher optimum growth temperatures (24–26°C) and a significantly wider plateau of maximum growth (–7 to 9°C within a range of 18–28°C). The more psychrophilic *H. triquetra*, growing in spring and fall, was comparable to diatoms in these indicators.

In the course of the experiment, we determined the temperature extremes T_{min} and T_{max} at which the algae maintained steady-state and reproducible growth. However, as the factor continued to increase or decrease, the functional activity gradually declined and the specific growth rate ceased. In Fig. 1, these temperatures are plotted as vertical lines, the distance between which was defined as a span of growth tolerance temperatures (ΔT).

The upper temperature limits were found to be in the range of 22–24°C for psychrophilic diatom species, at 26°C for *C. closterium*, and 32°C for *T. weissflogii*. The upper limits of survivability for diatoms exceeded the T_{opt} value (midpoint of approximated growth curve) by about 3°C. Larger deviations resulted in gradual degradation of algae, growth inhibition, and death of the culture. At low temperatures, extreme values were at 5–7°C, below which the specific growth rate in the majority of diatoms was recorded to decline, depending on the length of exposure.

The maximum growth temperatures were above 29–30°C in the summer dinoflagellate species and 23 and 26°C in more psychrophilic *H. triquetra* and *P. pusilla*, respectively, exceeding the values of their optimum temperatures T_{opt} by 5–6°C. At these temperatures, the algae maintained a steady-state growth, even if at a decreased specific growth rate. The dinoflagellates featured a wider (when compared with diatoms) range of temperatures of the maximum specific growth rates (ΔT_{opt} ~ 8°C). Minimum temperatures of steady-state growth were recorded at 7–10°C.

Figure 2 illustrates the temporal dynamics of changes in the specific growth rate and ratio of variable to maximum fluorescence F_V/F_M in algae during exposure at temperatures beyond the tolerance zone and the subsequent return of the temperature factor to a favorable level. At high temperatures (Figs. 2a and 2b), the specific growth rate at the specified temperatures was observed to fall in both species, although the decline was reversible for *C. closterium*, while the exposure of *Ch. curvisetus* at 26°C over four days led to culture death. Recovery of functional parameters in *C. closterium* had a prolonged character (the lag phase lasted three days), which suggests a decrease in the number of viable cells under these conditions.

Table 1. Main parameters of temperature dependence of specific growth rate

Species	T_{opt} °C, ΔT_{opt} °C	ΔT °C	T_{max} °C	$a \pm$ SE μ/day °C	a_{norm} %/day °C	Q_{10}	$\mu_{max\ av} \pm SE$, day^{-1}	$F_V/F_{M\ av} \pm SE$ within range T, °C
Bacillariophyceae								
S. costatum	21 4	18	23	0.12 ± 0.004	4.9 ± 0.2	2.0	2.7 ± 0.2	0.69 ± 0.02 6–23
D. brightwelli	20 4	15	22	0.09 ± 0.005	5.7 ± 0.3	2.4	1.6 ± 0.1	0.70 ± 0.02 7–22
Ch. curvisetus	22 5	18	25	0.13 ± 0.006	5.6 ± 0.2	2.6	2.3 ± 0.2	0.70 ± 0.03 6–23
T. parva	20 5	16	23	0.08 ± 0.007	5.1 ± 0.4	2.4	1.6 ± 0.3	0.61 ± 0.03 7–22
C. closterium	24 5	19	26	0.11 ± 0.005	5.5 ± 0.3	2.6	1.9 ± 0.2	0.72 ± 0.03 7–26
T. weissflogii	27 7	20	32	0.12 ± 0.06	5.6 ± 0.3	2.9	2 ± 0.3	0.64 ± 0.02 12–32
Average ± S				0.108 ± 0.019	5.3 ± 0.4	2.4 ± 0.2	2.1 ± 0.5	0.68 ± 0.04
CV				18%	7%	8%	24%	6%
Dynophyceae								
H. triquetra	20 5	15	23	0.08 ± 0.004	6.8	2.7	1.2 ± 0.2	0.55 ± 0.01 18–22
P. pusilla	23 7	19	27	0.06 ± 0.003	6.1	2.3	1.0 ± 0.2	0.58 ± 0.02 9–27
G. fissum	25 8	19	29	0.07 ± 0.004	7.0	3.4	0.9 ± 0.1	0.48 ± 0.02 18–29
P. micans	25 7	19	29	0.03 ± 0.002	6.3	2.9	0.5 ± 0.1	0.44 ± 0.02 14–29
G. wulffii	26 8	21	31	0.10 ± 0.005	6.2	3.1	1.6 ± 0.2	0.62 ± 0.03 12–29
P. cordatum	24 9	20	30	0.06 ± 0.002	5.8	2.9	0.9 ± 0.3	0.58 ± 0.04 12–30
G. foliaceum	>23 n.d.	>19	>23	0.11 ± 0.004	7.3	3.3	1.5 ± 0.2	0.71 ± 0.04 7–23
Avearge ± S				0.073 ± 0.027	6.5 ± 0.5	3.0 ± 0.4	1.1 ± 0.4	0.54 ± 0.07
CV				37%	8%	12%	35%	13%
Chlorophyceae								
Ch. vulgari sub.	23 6	24	30	0.05 ± 0.004	5.6	2.2	0.9 ± 0.2	0.60 ± 0.01 18–22

T_{opt}, temperature of maximum specific growth rate determined as midpoint of polynomial approximation of dependence; ΔT_{opt}, width of dome of maximum specific growth rate with parameter fluctuating within 20%; T_{max}, experimentally established growth maximum temperature above which gradual degradation of algae was observed; ΔT, span of tolerance zone; a, regression coefficient; $a_{norm}(a \times 100/\mu_{max})$, normalized regression coefficient in percent; Q_{10}, van 't Hoff coefficient; $\mu_{max\ av}$, mean maximum specific growth rate within range ΔT_{opt}, day^{-1}; $F_V/F_{M\ av}$, mean values of ratio of variable to maximum fluorescence in given temperature range; *SE*, standard error of mean; *S*, standard deviation; *CV*, coefficient of variation.

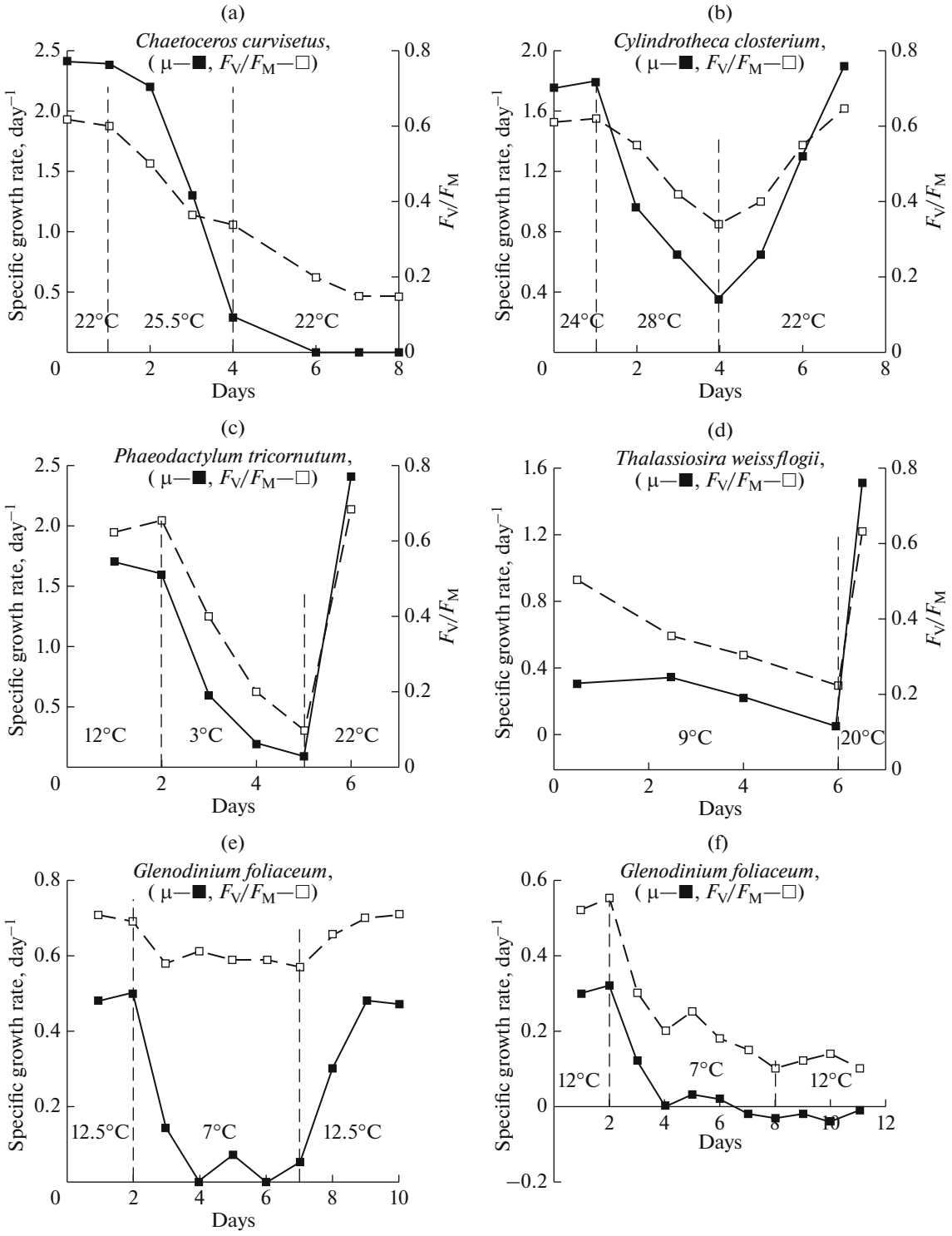

Fig. 2. Dynamics of specific growth rate and ratio of variable to maximum fluorescence with temperature variations. Dashed vertical lines denote moments of change in cultivation temperature with indicated values.

Figures 2c and 2d show the dynamics of changes in the specific growth rates of two diatom species under low temperatures. The low-temperature inhibition is has a reversible nature. For example, a delay in growth (*T. weissflogii*) or complete cessation of growth (*Ph. tricornutum*) was observed at the adopted temperatures. A subsequent temperature increase led to rapid recovery of the specific growth rate, corresponding to new conditions. There was no lag phase in this case. High viability and rapid recovery were observed

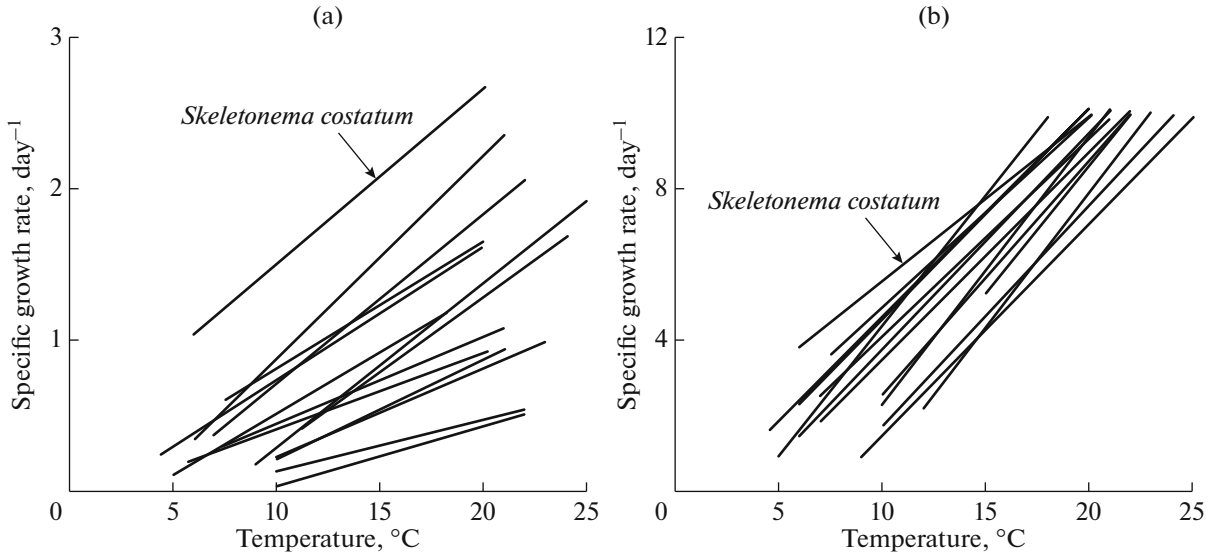

Fig. 3. Regression line of rising portion of temperature dependence of specific growth rate in studied algae species, absolute (a) and relative (b) values.

for the majority of the studied diatoms during acclimation to temperatures below the T_{min} values (4–7°C).

Dinoflagellate species exhibited two types of reactions under acclimation temperatures 2–3°C below the T_{min} values (Figs. 2e and 2f). In one case, the algae continuously sustained their viability at a zero- or very low growth rate (*G. foliaceum*, *P. pusilla*, and *H. triquetra*). For the remaining four species, low-temperature exposure resulted in immobilization and gradual irrecoverable elimination of cells in the cultures.

These data allowed us to assess the extent of temperature tolerance in the algae. The tolerance zone ranged from 15–18°C for the psychrophilic to 19–21°C for thermophilic species and did not appear to depend on their taxonomic identity. Thus, with respect to this parameter, as well as the ΔT_{opt} value, the spring dinoflagellate *H. triquetra* corresponds to psychrophilic diatoms, while the thermophilic Diatomea *T. weissflogii* is comparable with the summer dinoflagellates. In this regard, the paper [37] should be pointed out, where the wider span of growth temperatures has been similarly reported for thermophilic species.

The maximum heat resistance was observed in green *Ch. vulgaris suboblonga*. This species maintained its viability and ability to recover after the three-day period of strong temperature-induced inhibition at 30°C.

Functional Characteristic of the Specific Growth Rate Dependence on Temperature

For the rising portion of temperature dependence of the specific growth rate, we employed a linear approximation in a form $\mu = a(t - t_0)$, which yielded high determination coefficients. The linear function makes it possible to formalize the obtained dependences using two parameters: the regression slope coefficient, which characterizes the degree of correlation between temperature and the specific growth rate (a), and the extrapolated value of zero-growth temperature. An exponential approximation was similarly used to determine the Q_{10} coefficient, but within a narrower temperature range in the mid-rising portion of the dependence. The regression coefficient varied between 0.08 and 0.13 day^{-1} °C (*CV* 18%) for different diatoms and between 0.03 and 0.11 day^{-1} °C (*CV* 37%) in microdinoflagellates. The interspecific variability of regression coefficient decreased to 7–8% after normalization of the dependences with regard to the maximum specific growth rates. Figures 3a and 3b separately show the regression lines of species based on two methods of data representation. The values of the normalized regression slope coefficient fluctuated within narrow limits and averaged 5.3 ± 0.4 and 6.4 ± 0.5% of the change in the specific growth rate by 1°C for diatoms and dinoflagellates, respectively.

Ratio of Variable to Maximum Fluorescence F_V/F_M

In diatoms, the ratio of variable to maximum fluorescence F_V/F_M (which determines the maximum efficiency of electron transport) remained high within the tolerance zone; the mean values in some species varied between 0.64 and 0.72 with a coefficient of variation close to 6% (Table 1). Temperatures below 5–7°C (12°C for *T. weissflogii*) led to a decrease in F_V/F_M, which commonly coincided with the point of the onset of low-temperature growth inhibition T_{min}. At high temperatures, a decline in this parameter was similarly associated with temperature-induced inactivation of algae (Fig. 1).

Dinoflagellates exhibited specific differences in the character of the F_V/F_M dependence on temperature.

As the temperature decreased, the ratio of variable to maximum fluorescence was observed to decrease within the tolerance zone at temperatures below 12°–15°C in four species; the dependence for *H. triquetra* and *Ch. vulgaris suboblonga* (green) had a dome-shaped form. *G. foliaceum* and *P. pusilla* continuously displayed high values for this parameter within a wide temperature range. Cultivation temperatures exceeding T_{max} caused a rapid decrease in the F_V/F_M value (Fig. 1), as was the case with diatoms.

Figure 2 shows the dynamics of changes in the ratio of variable to maximum fluorescence in individual species of algae at temperatures 2–3°C below or above T_{min} and T_{max}. A close relationship is observed between growth parameters and the ratio of variable to maximum fluorescence at sublethal temperatures during inhibition and recovery of functional activity in the algae. High stability of F_V/F_M was observed during low-temperature inactivation of growth processes in *G. foliaceum*, whereas in all other cases, the amplitude of variation in this parameter was large and corresponded to the extent of temperature-induced growth inhibition. The mean F_V/F_M values for diatoms were higher than the those for dinoflagellates: 0.68 ± 0.04 and 0.54 ± 0.07, respectively (Table 1).

Temperature Coefficient Q_{10}

We provide the Q_{10} values determined by exponential extrapolation in the midsection of the rising portion of the growth curve. These Q_{10} values ranged from 2 to 3.5 (Table 1). The larger values were obtained for dinoflagellates compared to diatoms; they averaged 3.0 ± 0.4 and 2.4 ± 0.2, respectively.

DISCUSSION

Temperature is not generally considered the primary factor determining the amount of primary production in the World Ocean [13, 16]. Maps of productivity distribution across the World Ocean reveal that the amount of primary production is largely associated with hydrological processes of various scales that enrich surface waters in nutrients [2, 3]. At the same time, in local marine ranges of the middle latitudes, specifically, the Black Sea, seasonal temperature variations cause vertical mixing of seawaters; this regulates the species composition of phytoplankton. Thus, *S. costatum* is the dominant species (up to 99%) in the Black Sea during cold winter seasons (water temperature of 5–7.5°C, with intense convective mixing). The species diversity index increases during warmer years (8–12°C and poor mixing), though overall the production may drop. In the course of the winter–spring succession, as the water heats up and the concentration of nutrients decreases, *S. costatum* is replaced by *Ch. curvisetus* in late April–early May [6].

The studied species of the spring–summer diatom complex occur in phytoplankton nearly all year round (occasionally in summer due to breakup of temperature stratification by wind-induced mixing), but their quantitative participation strongly varies from season to season and, in addition, apart from it, strongly depends on the water temperature in different years [1]. Based on the experimental data, diatoms feature close values of main parameters of temperature dependence of the specific growth rate, namely, T_{opt}, upper and lower growth temperature, Q_{10}, and normalized values of slope of the rising portion (a_{norm}). That is why species alternation in diatom complex of the fall–winter–summer successions cannot be attributed exclusively to temperature characteristics. It is our opinion that, under otherwise equal conditions, one of the factors, ensuring the dominant development of a species is the maximum specific growth rate. Thus, the most numerous species of the winter–spring succession in the Black Sea nearshore waters *S. costatum* exhibited the maximum specific growth rate both at low and high temperatures. The second commonly dominant species of spring succession *Ch. curvisetus* falls behind *S. costatum* in specific growth rate under optimum conditions. In an open environment, *Ch. curvisetus* crowds out *S. costatum* as the water warms, convective mixing subsides, and the concentration of nutrients decreases [6]. This points to the effects of other environmental factors, such as temperature, nutrients, light conditions, as well as their interaction, on the development and alternation of species in the natural environment [34, 38].

Among the studied dinoflagellates, only *H. triquetra* is found in spring phytoplankton, which is in line with the temperature characteristics of the former. The low growth limit of this species was at about 7°C; the specific growth rate is considerably slower than in diatoms, which appears to determine the poor quantitative growth of this species. More thermophilic algae are capable of growing at temperatures up to 10°C; however, the low specific growth rate precludes them from competing with diatoms in colder periods. This species has a developmental advantage in the summertime when the water temperature and low nutrient content in the water column prevent diatoms from active development [1].

Temperatures below and above the ones marked in Fig. 1 lead to a gradual decline in the functional activity of algae. Low-temperature inhibition is assumed to be caused by imbalanced rates of membrane transport (active and passive) and intracellular membrane reactions, inactivation of individual enzymes, increased viscosity of the medium, and other physical factors [32, 33, 40]. Within certain limits, these changes may be reversible, which is supported by our findings for diatoms and some dinoflagellates. Nonetheless, for a number of dinoflagellates, we observed a negative

response on prolonged exposure to temperatures of 5–6°C and gradual destruction and elimination of cells.

Temperatures exceeding the upper limits of the tolerance zone, can be considered a more rigid factor causing transformation of membrane proteins and lipids (denaturation and melting) [9], as well as membrane lipid peroxidation [27]. As demonstrated in our studies, temperatures several degrees above the optimum growth temperatures led to a progressive decline in the number of viable actively dividing cells, while recovery of functional activity and specific growth rate had a prolonged duration. Dinoflagellates are more stable at high temperatures but differ from diatoms in the type of the dependence near the optimum temperature and above. Survivability and ability to recover around sublethal temperatures depended on the amount and length of exposure to stress, as well as individual species characteristics.

Increasing attention is being given to the character of the functional dependence of the specific growth rate on temperature. A number of authors point out an inconsistency between the experimental data and the Arrhenius exponential function, citing the laws of enzyme kinetics. Therefore, in the opinion of many authors, use of such parameters as Q_{10} or activation energy is unsuitable for a nonexponential dependence [8, 12, 28, 29]. It is assumed that this inconsistency stems from different enzymatic reactions become limiting at different temperatures [22]. Deviation from an exponential dependence may also occur due to factors of the physical environment [8]. Thus, based on theoretical and experimental approaches, the authors of [28] assume that exponential response holds for a small range of temperatures proximate to the growth temperature of algae in nature. Data obtained in the majority of experimental studies is a good approximation of a linear function [17, 29, 39].

The data specified in the literature with respect to the linear regression coefficients cover a wide range. Thus, while summarizing their own and other data, the authors of [29] report values from 0.02 to 0.15 day^{-1} °C for diatoms. The authors, having averaged a large amount of data and having made allowances for light conditions, report mean values on the order of 0.1 day^{-1} °C, which coincide with our findings for diatom species. The absolute values of this parameter in diatoms were also higher; however, the normalized values were larger in dinoflagellates, which appear to be more sensitive to temperature decrease. Additionally, the latter were observed to exhibit higher Q_{10} values. This parameter, similar to a normalized slope of linear regression, characterizes the relative value of change in the specific growth rate with temperature in the case of exponential approximation. This agrees with the findings of [28], which demonstrates that within the range of experimental temperatures close to conditions of species development in a natural environment, the temperature response might be exponential at Q_{10} coefficient values of about 2; however, as the temperature falls below this range, deceleration of the specific growth range becomes steeper. This may result in a larger Q_{10} and normalized regression coefficient in thermophilic diatoms for a temperature range of 10–20°C. The mean Q_{10} values in the two taxonomic groups of algae were significantly different provided the considerable variability between individual species.

The ratio of variable to maximum fluorescence is a parameter that characterizes the efficiency of light energy transport in primary photochemical reactions (maximum quantum efficiency of charge separation in photosystem II) [4]. It is a sensitive indicator of the functional performance of algae [5, 19, 23, 25]. In addition, fluorescence parameters are employed when assessing photosynthetic activity and phytoplankton production in natural environment and culture conditions [11, 15, 20, 41]. The effect of temperature on F_V/F_M can have great significance in this regard. At the same time, the literature lacks studies examining such a dependence in the wide temperature range for various phytoplankton species. In addition, the insignificant amount of data on the subject precludes systematization of the obtained results and their referral to species-specific characteristics or external and internal factors. Overall, the existing data can be conditionally divided into two types: lack of effect of the acclimation temperature on the F_V/F_M value in the tolerance zone [14, 24, 26, 36] and a dome-shaped dependence with the maximum at optimum temperatures [41]. Our data largely supports the first type of the dependence for the study species, though some dinoflagellates exhibit a decrease of F_V/F_M at temperatures from 12–15°C while still in the tolerance zone. For *H. triquetra* and *Ch. vulgaris suboblonga*, a dome-shaped relationship was observed between temperature and the ratio of variable to maximum fluorescence, which was reliably confirmed through repeated experiments. A similar response of *Ch. vulgari* was reported in [41]. Data are available in the literature that supports the observed correlation between the decrease of the F_V/F_M value and functional activity at temperatures above and below a certain level [21, 30]. It should be emphasized that changes in these values are dynamic and unfold over time, while recovery depends on the amount and length of exposure to sublethal temperatures.

CONCLUSIONS

(1) We have determined the optimum temperatures of the specific growth rates and tolerance temperature spans for a number of diatom and dinoflagellate species, as well as green *Ch. vulgari suboblonga*. Stable interspecific differences were determined by the growth conditions in a natural environment.

(2) The minimum upper sublethal temperatures exceed the temperature optimum levels by no more

than by 3°C in diatoms and 5–8°C in dinoflagellate and green species.

(3) The rising portion of the temperature dependence of the specific growth rate approximates a linear function. The values of the linear regression coefficients varied within a wide range from 0.03 to 0.12 μ/day °C for various species, whereas the normalized values of this parameter equaled 5.3 ± 0.4 (diatoms) and 6.5 ± 0.5 (dinoflagellates) percent of change in the specific growth rate per one degree of temperature change at variation coefficient of 7–8%, respectively.

(4) Exposure to temperatures in excess of the upper limits of the tolerance zone led to progressive degradation and elimination of algal cells in the culture; low-temperature inactivation was reversible in the majority of species.

(5) The value of the ratio of variable to maximum fluorescence remained high within the tolerance zone for diatoms and some dinoflagellates. Its drop correlated with a change in specific growth rate and was observed under unfavorable temperature conditions.

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Translated by E. Kuznetsova