African Journal of Biotechnology Vol. 8 (19), pp. 4983-4990, 5 October, 2009
Available online at http://www.academicjournals.org/AJB
ISSN 1684–5315 © 2009 Academic Journals

Full Length Research Paper

Effects of light and temperature on the growth rate of potentially harmful marine diatom: *Thalassiosira allenii* Takano (Bacillariophyceae)

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Accepted 18 June, 2009

Thalassiosira allenii **is a potentially harmful marine diatom distributed along the Northern Aegean and Southern Black Sea coasts of Turkey. In order to better understand the effect of environmental factors on *T. allenii*, the effects of 6 different light intensities (6.5, 38.7, 77.5, 116.2, 15 and 193.7 μmol/m^{2}s (PAR)) and 4 different temperatures (4, 11, 16 and 20°C) were investigated. *T. allenii* was isolated from İzmir Bay-Northern Aegean Sea-Turkey and incubated in a f/2 enrichment medium under constant light in a batch culture system. The growth rate of the species was measured as Chl *a* (μg/l) by monitoring the exponential growth phase. The statistical analysis of the obtained data was performed by utilizing the method of least squares. As a result of the study, the light intensities of 0.8, 3.6, 13.4 and 26.4 μmol/m^{2}s were found to be saturation light intensities for 4, 11, 16 and 20°C, respectively whereas a light intensity of 6.5 μmol/m^{2}s was determined to be the compensation light intensity at 20°C. The temperatures below 11°C were detected to limit the maximum growth rate (μ_{max}). Under saturated light conditions between the temperatures 20 - 11°C the algae maintained its μ_{max} parameter while it reduced its half-saturation constant K_L and exhibited a shift from sun to shade type. It was concluded that the light intensity is more effective compared to temperature in excessive reproduction of the algae in its natural environment.**

Key words: Growth rate, light, temperature, *Thalassiosira allenii*, marine diatom.

INTRODUCTION

Besides the significance of diatoms being the main food source of pelagic and benthic organisms, it is also well known that some species cause ecological problems in nature by over-reproducing (Officer and Ryther, 1980). It is reported that 300 species among 3400-4100 phytoplanktonic species (like diatoms and dinoflagellats) are red-tide organisms (Smayda, 1997). The genera *Chaetoceros*, *Thalassiosira* and *Coscinodiscus* possess largest distribution areas among the planktonic marine diatoms and they also include some red-tide species that constitute the major topic of the kinetic studies (Paasche, 1968, 1975; Laws and Wong, 1978; Smayda, 1980; Brand and Guillard, 1981; Li et al., 2004).

The genus *Thalassiosira* is expressed to be a phytoplanktonic species with more than 100 species revealing a world wide distribution (Hasle and Fryxell, 1995). Numerous scientists reported that the *Thalassiosira* species are of significance among the phytoplanktonic species and mostly become dominant during spring in coastal ecosystems with temperate climates (Karentz and Smayda, 1984; Haris et al., 1995; Muylaert and Sabbe, 1996).

The theoretic model of the physiological adaptation in phytoplankton allows predictions concerning the separate or cumulative effect of light, nutrient limitation and temperature on its growth and composition (Shuter, 1979). Investigations on the growth kinetics providing the growth parameters of the algae that cause problems by repro-

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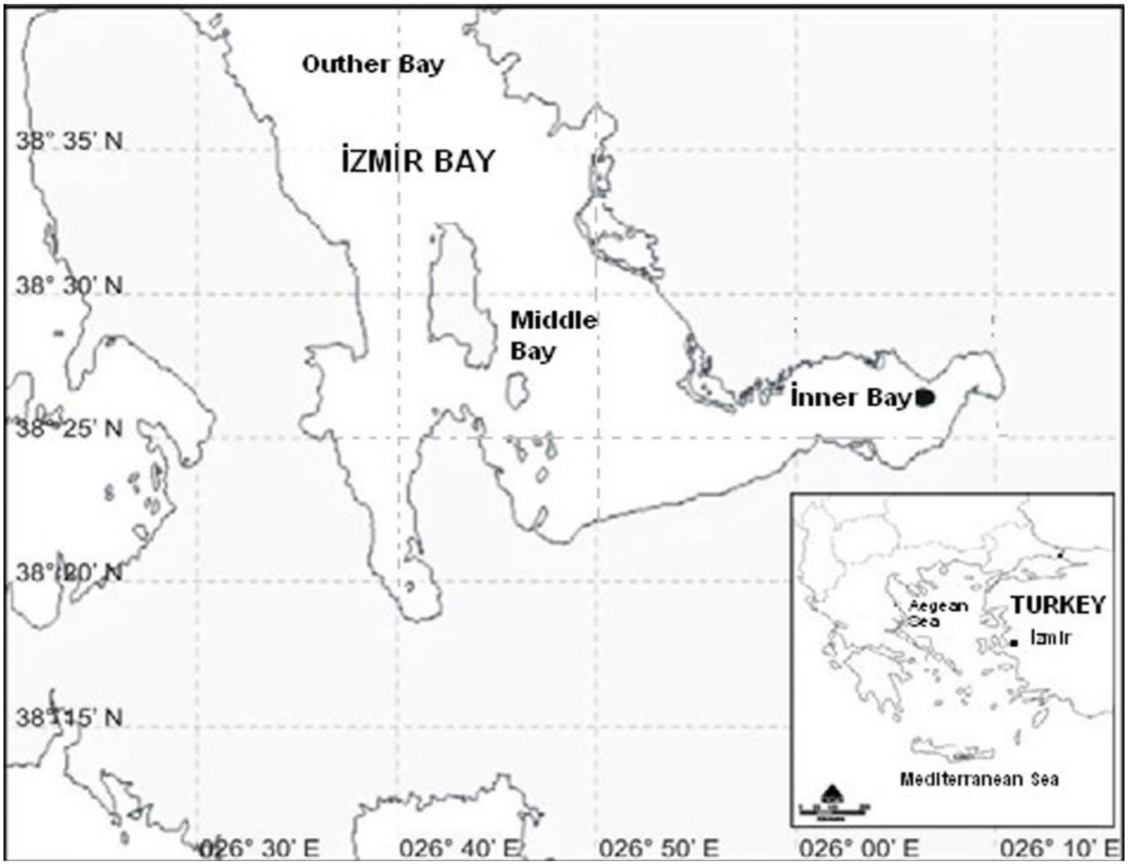

Figure 1. İzmir Bay, Aegen sea , Turkey.

ducing along the Turkish coasts (Koray et al., 1996; Koray, 2004) as in many coastal areas posses importance in terms of excessive reproduction control and allow us to predict their distribution with the help of mathematical modeling. Therefore, the studies related to the growth rates, the kinetic parameters of nutrient-limited growth (K_s; half saturation constant, μ_{max}; maximum specific growth rate etc.) and physical parameters of the harmful algae would be a worthy ecological investment for the future.

Microalgal blooms of harmful or toxic algae have been reported for many decades from the coasts of the Middle East countries (Hallegraeff, 1995; Chiu et al., 1994). The algal blooms of toxic and harmful microalgae species in Eastern Mediterranean, Agean and Black Seas have been emphasized since the late 20th century (Nümann, 1955) and the influence of pollution due to the industrial and domestic waste waters on the natural sea water (Aydın and Büyükışık, 2004) and consequently on the phytoplankton composition is becoming increasingly evident. The kinetic studies concerning the phytoplankton growth rates along the Turkish coasts and especially in Aegean Sea commenced in 1990s (Aydın and Büyükışık, 1994; Büyükışık et al., 1994; Büyükışık, 1995; İzgören and Büyükışık, 1999) and still continues. It was reported that 36 potentially toxic and harmful species (including *T. allenii*) observed along the Turkish coasts in 1980-2002 (Koray, 2002, 2004).

The subject of our study, marine diatom *T. allenii* was found to distribute along the Northern Aegean and Southern Black Sea coasts of Turkey (Koray, 2004) and *T. allenii* was reported that a potentially harmful marine phytoplankton species in Turkish coast and cause to hyperoxia and anoxia (Koray, 2002, 2004). In the scope of this study, it was aimed to determine the effects of the main physicochemical parameters, namely the light and temperature, on growth rates in order to manage the ecological problems that may arise as a consequence of the over-reproduction of *T. allenii*.

MATERIALS AND METHODS

T. allenii was isolated from the surface sea water of the Inner part of Izmir Bay (Figure 1.) by using the dilution method under conditions presenting with a 11 ± 0.5°C temperature, 33% salinity, 24L:0D daylength, 38.7 µmol/m^{2}s light intensity, 40 watts day light fluorescent and f/2 enrichment medium (Guillard, 1975). The culture medium prepared was incubated under constant 45-193.7 µmol/m^{2}s

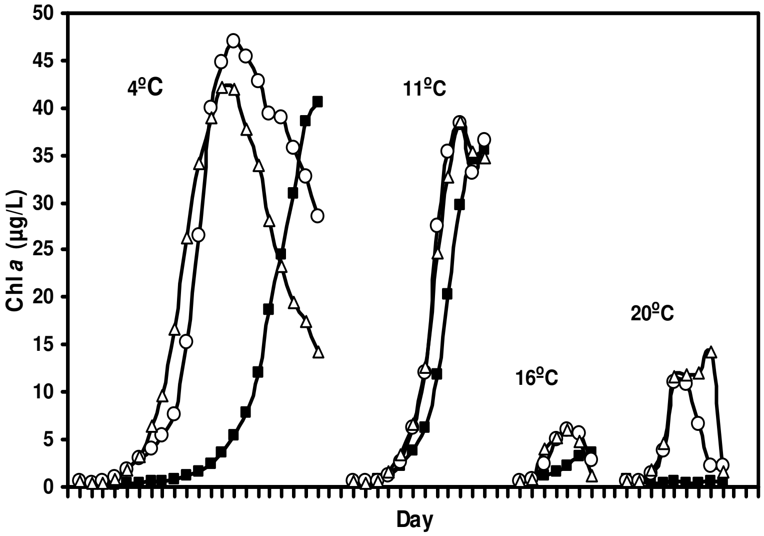

Figure 2. Growth curves of *T. allenii* in different temperature and light intensity (■:6,46 µmol/m^{2}s; ○: 38,74 µmol/m^{2}s; △ :77,47 µmol/m^{2}s).

light intensities at 4, 11, 16, 20°C temperatures and the exponential phase was monitored. The measurements were estimated as the amount of Chl *a* by using the Turner Designs 10-AU Field Flouemeter (Brand and Guillard, 1981). The chlorophyll based specific growth rates were calculated following Guillard (1973):

$$\mu = 1/(t_2 - t_1) * \log_2(N_2/N_1) \qquad (1)$$

Where µ: specific growth rate (day^{-1}), N_1: the Chl *a* measure at the beginning of the exponential growth phase, µg/lt; N_2: Chl *a* measure at the end of the exponential growth phase, µg/lt, t_1: the time period during which N_1 was determined, t_2: the time period during which N_2 was determined. The maximum specific growth rates and the half-saturation constants were statistically calculated with the help of the Michaelis-Menten equation by using the least squares method:

$$\mu = \mu_{max} * (I_0' / (K_L + I_0'))$$

Where µ is the specific growth rate obtained from equation 1, μ_{max} is the maximum specific growth rate, I_0' is the light intensity, K_L is the half-saturation constant.

RESULTS

The growth curves of *T. allenii* obtained at 4, 8, 11, 16, and 20°C under 6.5, 38.7, 77.47, 116.2, 155 and 193.7 µmol/m^{2}s light intensities were presented at Figures 2 and 3. An extended lag phase was clear at 4°C under a light intensity of 6.5 µmol/m^{2}s and the lag phase was shortened while the light intensity increased. The max Chl *a* concentration achieved decreased with the rising temperature and no growth was observed at 20°C under a light intensity of 6.5 µmol/m^{2}s. Under these conditions, this rate that caused cessation of growth for *T. allenii* indicates the compensation light intensity. The relationships between the exponential growth rates calculated from the growth curves and the light intensities were expressed via the Michaelis-Menten equation for each temperature. The data fitted well with the monod equation (Figure 4). The initial incline of the curve decreased with the temperature rise. The μ_{max} parameters were nearly the same except 4°C. The K_L half-saturation constant for 4°C was extrapolated from K_L/T exponential relationship obtained (Figure 5) by using the other data. The μ_{max} value significantly lower than the values at different temperatures was detected as a mean rate of 0.717 day^{-1}. As can be seen in Figure 5, whereas *T. allenii* did not change its max growth rate under saturated light at a temperature range of 20-11°C, it responded the condition by lowering its half-saturation constant K_L. The maximum growth rate of the alga was limited below 11°C and the K_L half-saturation constant was slightly changed. Under the conditions above 11°C at a 6.5 µmol/m^{2}s light intensity, the light was found to cause a limitation.

It was observed that an increase in light intensity at lower temperatures caused the lag phase to end nearly on the same day however shortening the exponential phases. Nonetheless, as seen in Figure 2, following the temperature rise, a prominent decrease was evident for the maximum Chl *a* amounts which the species could achieve at the exponential phase. It was observed that 20°C was the compensation light intensity of the species for 6.5 µmol/m^{2}s light intensity and the temperature increase limited the growth rate under relatively lower light intensities.

During the temperature fall from 20 to 11°C *T. allenii* was detected to adapt the shade type by decreasing its half-saturation constant, K_L. However, it reduces its maxi-

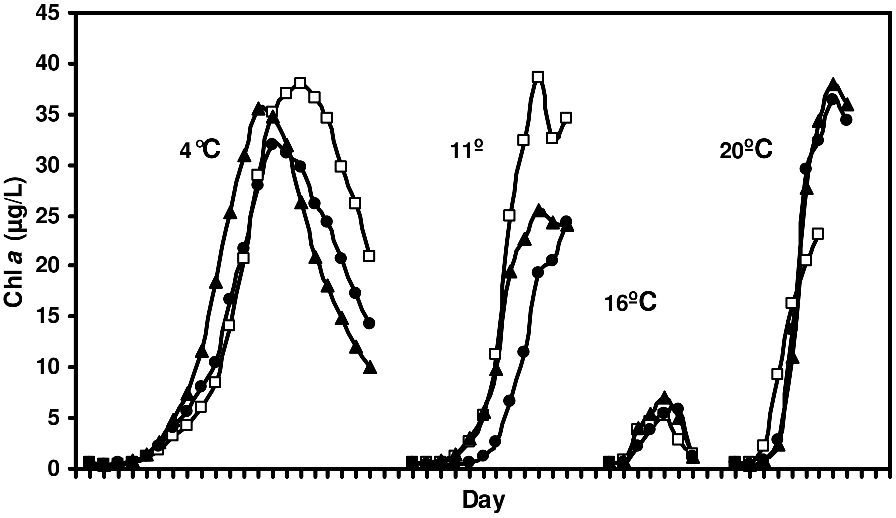

Figure 3. Growth curves of *T. allenii* in different temperature and light intensity (□:116,21 µmol/m^{2}s; ●:154,95 µmol/m^{2}s; ▲:193,68 µmol/m^{2}s).

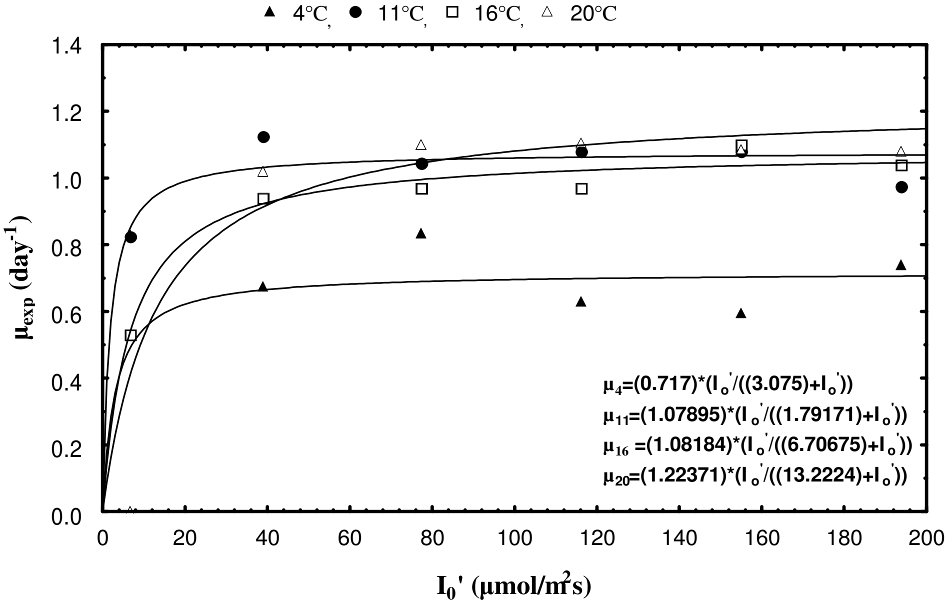

Figure 4. Growth rates of *T. allenii* as a function of the light intensity at different temperatures: $p < 0, 05$, $R = 0,823$ (●11℃); $R=0,982$ (□16℃); $R=0,970$ (△ 20℃), and K_L value for 4ºC was extrapolated from exponential curve in Figure.5

mum growth rate during the temperature fall from 11 to 4℃, whereas it raises the biomass concentration that the water is capable to hold.

DISCUSSION

Diatoms possess a major role in biochemical cycle and tend to cause predominance of the export production (Sarthou et al., 2005; Buesseler, 1998). Generally in temperate ecosystems diatoms are dominant where nutrient and light intensities are high and reproduce relatively fast under these conditions compared to the other groups (Harrison et al., 1993). Diatoms are capable of adapting themselves to different light intensities (photoadaptation). During this period of photoadaptation several morpho-

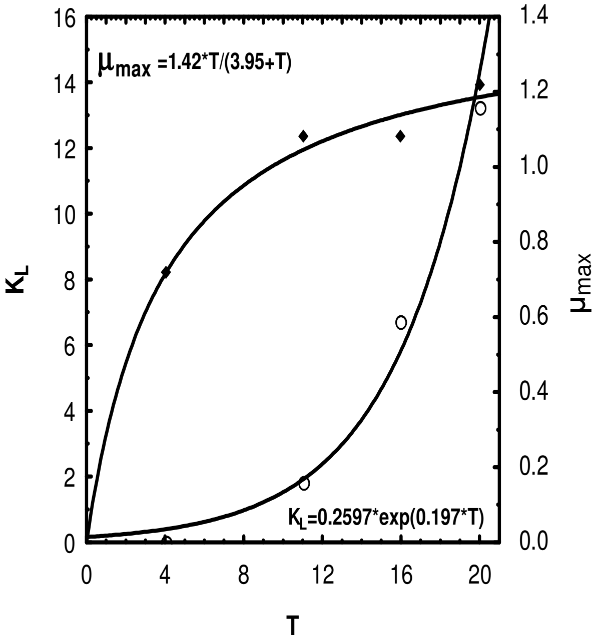

Figure 5. Variation of maximum specific growth rate with increasing temperature.

logic and biochemical changes occur in the amount of photosynthetic and photoprotective pigments, photosynthetic parameters, morphology of the chloroplasts, the enzymatic activities including photosynthesis and respiretion (Terry et al., 1983), cell volume (Finkel, 2001; Finkel and Irmin, 2000), respiration rate and the chemical composition (Yin et al., 1998) within the phytoplanktonic cell.

It is clearly evident from literature that the light intensity and daylength has a doubtless effect on growth of phytoplanktonic organisms. However, it should be emphasized that the same daylength and light intensity develops distinct tendencies in separate species. Growth rate may slow down or even cease with changes in the daylength in various species (Paasche, 1968; Durbin, 1974; Holt and Smayda, 1974; Brand and Guillard, 1981; Creswel, 1993). Although some species continue to grow under constant daylight, they may exhibit a lower growth rate compared to daylengths including light-dark cycles. Therefore, as the daylength corresponds to daylight period in this study performed on *T. alenii* isolated from İzmir Bay (Turkey), it is possible that the results obtained during light-dark cycles may differ. On the other hand, in the study conducted by Brand and Guillard (1981) with 22 phytoplanktonic species, it was reported that the oceanic clones were more sensitive to constant light whereas the coastal clones grew faster under constant light. Experimentations with different light regimes under the water at the coastal area resulted in a faster growth rate under conditions of constant light (Brand and Guillard, 1981). Considering the species was isolated from a coastal region, it may be supposed that the continuous illumination we used during our experiments would not cause a problem for *T. allenii*. Although no comparable records are available in current literature concerning the behavior of *T. allenii* under light-dark regime, some reports exist stating that *T. alenii* inhabits in ballast tanks of vessels (Gollasch et al., 2009).

In Figure 5, the initial slope of μ_{max} depending on temperature is 0.175 μ°C^{-1} and this was found to be higher than the mean slope value given in Montagnes and Franklin (2001) as 0.05-0.06 μ °C^{-1}, indicating that the growth rate sharply increased with temperature rise. In contradiction to the other present studies, the fact that the species die off above 20°C, make us think that it may be adapted to the temperatures of İzmir Bay in winter. The temperature constant obtained by fitting the existing data of growth rate between 11-20°C to the Arhenius equation that reflects the exponential increase with temperature was found to be Q_{10} = 1.15. As this was significantly lower than the Q_{10} values reported in literature for the diatom genera of identical sizes (Popovich and Gayoso, 1999; Harrison et al., 1993), *T. allenii* may be deemed as an eurythermic species. Considering the whole data, the temperature-dependent change in μ_{max} (between 4 - 20°C) complied well with the Michaelis and Menten equation (μ_{max} =1.42*T/ (3.95+T). The slope implies that the temperatures below 4°C will significantly limit μ_{max}. Several authors expressed temperature-dependency as a linearly (Montagness and Franklin, 2001; Thompson et al., 1992; Weisse and Montagness, 1998) while the others by adjusting it to the Arhenius equation (Goldmand and Carpenter, 1974; Harris, 1986; Harrison et al., 1993). In this study however, it is observed that it conformed to the Michaelis Menten equation. Thus, it is realized that different diatom species follow dissimilar adaptation strategies.

The maximum growth rates of *Thalassiosira nordenskioeldii* sizing 12-45 µm obtained by patch and semi-continuous cultures were found to be 0.89 div/day at 3°C and 1.26 div/day at 10°C in Paasche (1975) revealing consistency with our results. The growth of *T. allenii* displayed a much extended lag phase at 4°C under a light intensity of 6.5 µmol/m^{2}s. The cease at 20°C under 6.5 µmol/m^{2}s indicates the compensation light intensity for the aforementioned temperature (Figures 2 and 4). The relationship between light intensity and the exponential growth rate fit well to the Monod equation. The initial slopes of the μ/I_0 curves declined with the temperature rise. The μ_{max} parameters were the same except for 4°C when it significantly decreased to 0.717 day^{-1}.

The algae are able to adapt themselves to differing light conditions as sunlight and shade (Raymont, 1980; Sournia, 1982). The raise in light intensity aimed at reaching saturation with temperature increase and the decline at the initial slope of the Monod curve indicates that the alga is able to adapt both the shade and the sunlight type. At the same time the growth efficiency of the algae also decreases

At the temperatures below 11°C, the alga changes its maximum growth rate whereas it slightly shifts its K_L half-saturation parameter. Above 11°C however, the maximum growth rate of the alga is at its saturation level due to the higher temperatures consequently causing the alga to respond to the conditions by only increasing its K_L half-saturation constant (that is to say it changes its affinity to light). Just as this, it was reported that *T. curviseriata* possessing similar sizes (~10 µm) in Bahia Balanca estuary was dominant in winter under unfavorable light conditions (Popovich and Gayoso, 1999). It is reported that the eurythermal and euryhaline species could adapt themselves to low light intensities (Popovich and Gayoso, 1999). The growth rate of *T. allenii* reaches saturation at 4, 11, 16 and 20°C under light intensities of 0.8, 3.6, 13.4 and 26.4 μmol/m^{2}s, respectively. Higher values were given for *T. curviseriata* (Popovich and Gayoso, 1999). Similarly, *T. weissflogii* (Grun), a smaller species, was evidenced to be able to grow also in low iron conditions (Strzepek and Price, 2000) whereas another small species, *C. brevis* was reported to continue growing by accumulating iron (Timmermans et al., 2001) at low temperatures and low light conditions by altering their physiologic requirements. Thus, although the influence of iron on growth was not investigated in the scope of this study, it is possible to infer from the aforementioned studies that the growth ability of the species in different nutrient sources under low temperature conditions and low light intensities may be associated with the growth strategies of the species rather than their sizes.

Significantly low temperatures restrict the μ_{max} parameter in *T. nordienskioldii* (Popovich and Gayoso, 1999) and *T. allenii* (this paper). It is however observed that the μ_{max} parameter of *T. pseudonana, T. rotula* and *T. curviseriata* is limited to almost 25°C (Popovich and Gayoso, 1999). Harrison et al. (1993) expressed the changes in temperature/K_L relationship with a positive linear correlation in *C. convolutus* whereas he explained for the *C. concavicornis* that the changes temperature/K_L relationship decreased till 8°C however staying constant at higher temperatures. On the other hand, *T. allenii* exhibited a totally different temperature response at the K_L half-saturation parameter (Figure 5). When the temperature-dependent changes of μ_{max} were examined, it was realized that K_L altered when μ_{max} was constant and μ_{max} altered when K_L was constant in the aforementioned 2 species and in *T. allenii*. Contrary to the other studies (Smayda, 1969; Karentz and Smayda, 1984), *T. allenii* was detected in nature at higher temperatures (19-23.3°C) while it was observed to die above 20°C in laboratory. The temperature of sea water does not fall below 7-8°C throughout the year in Izmir Bay (Sunlu et al., 2006). The growth rate of *T. allenii* would not significantly change with temperature except for extreme conditions. Thus, in autumn and winter it could reduce its affinity to light and become a shade type by possibly causing a bloom. Additionally, an exceptional bloom of it observed in İzmir Bay occurred in fall during 2003 and lasted for 2-3 weeks. According to the autumn 2003 data of the mentioned authors, *T. allenii* was absent from the water column at 25°C during the week 35 whereas its intensity reached to maximum rates following the gradual temperature decrease to 23.1 and 21.3°C, respectively at the weeks 36 and 41. On the other hand, it substantially declined in the water column during the week 44 as a result of the marked decrease of the temperature to 16.1°C. This was not able to be enlightened despite the fact that the decline of the maximum population intensities observed under 16°C in laboratory were resembling the rates measured for natural populations.

The fact that bloom does not continue in winter when light and temperature are suitable indicates that the other environmental parameters could have an influence on the growth rate of the algae. However, the excessive the bloom of *Prorocentrum micans* over the same weeks (Sunlu et al., 2006) may be explained by the possibility of repression on *T. allenii* due to mixotrophic feeding behavior.

When favorable conditions were provided in terms of daylength and light intensity for the growth of this species although it reveals a wide range, different daylight periods and light intensities resulted in diverse outcomes in nutrient uptake rates of this species in nutrient-limited cultures (Laws and Wong, 1978). On the other hand, a light intensity of 6.5 μmol/m^{2}s at 20°C was found to be as the compensation light intensity of the species. It is proposed that in nature and particularly in summer, the light intensities would not be restrictive on the growth capacity of the species. According to the data reported by Sunlu et al. (2006) and Aydın (2004) the limitation of the light intensity on growth ability of the species may be considered not to be influential as much as temperature and nutrients particularly during summer. The photon flux density ranged between 360 - 685 µmol/m^{2}s (on the sea surface) during December, 2003 – February, 2004 under natural conditions.

The maintenance of *T. allenii* all throughout the year demonstrates its capability to reproduce healthily at varying temperatures under low light intensities. However during the annual diatom blooming especially under suitable environmental conditions, it may be considered to be less dominant compared to the other diatom species (Koray, 2004). In light of these characteristics, it is obviously appreciated that *T. allenii* will play a significant role in phytoplanktonic blooms in absence or scarcity of herbivorous zooplankton in the environment. Moreover, *T. nordenskioeldii* was reported by Paasche (1975) to be capable of removing all the detectable silicate from water and grow with around maximum rates in a ca. 0.3 μg atom Si/L presence during the last phases of the diatom bloom. It may be inferred from the above mentioned fact that the silicate levels (8.36 μg atom Si/L) in İzmir Bay would not be growth-limiting for *T. allenii* exhibiting identical cell dimensions, although they might decrease below the detectable rates.

In conclusion, it is evident that the growth limiting effects of light intensity and nitrogenous nutrients (Laws and Wong, 1978; Sunlu et al., 2006) on the excessive reproduction of *T. allenii* distributed in eastern neritic region of Northern Aegean Sea and in Southeastern Black Sea are more important than that of temperature and silicate although a limiting effect of herbivore is also clear on bloom.

ACKNOWLEDGEMENT

This study was funded by Ege University BAP PROJECT (02-SUF-01) Turkey, and it is part of the Doktoral Thesis of H.Göknur ŞİŞMAN AYDIN.

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