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Growth rates of dinoflagellates along the Karachi coast assessed by the size fractionation method

by

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Abstract

The in situ growth rates of dinoflagellates along the Karachi coast off Pakistan was studied by the size fractionated method during winter (February 2006) and summer (May 2007). The growth rate per day ranged from -2.87 to 2.3 d^{-1} (20 species) in winter and from 1.20 to 1.95 d^{-1} (13 species) in summer. Growth rates (μ_{max} d^{-1}) of the dominant species were as follows: *Prorocentrum gracile*, *Prorocentrum minimum*, *Prorocentrum arcuatum* (1.0-1.10), *Protoperidinium steinii* (0.92), *Gonyaulax spinifera* (0.69), *Dinophysis acuminata* (2.3), *Dinophysis caudata* (0.92), *Ceratium lineatum*, *Prorocentrum micans* (1.95), *Gyrodinium* sp. (1.88), *Ceratium furca* (1.70), and *Alexandrium ostenfeldii* (1.34). The declining growth rates were observed for *Pyrophacus stein* (-1.10), *Scrippsiella trochoidea* (-1.61 to -0.82), *Prorocentrum donghaiense* (-1.94) and *Karenia mikimotoi* (-2.48). Our results suggest that a higher temperature induce an increase in dinoflagellate growth rates.

Key words: in situ growth rate, size fractionation method, dinoflagellates, Pakistan

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Introduction

Marine microplankton organisms (20-200 µm size) are the basic food source for macro- and mesoplankton includes phytoplankton, copepods and bacteria which supply the bulk of nutrients in coastal and open waters (Calbet and Landry 1999, Landry and Calbet 2004). Among them, dinoflagellates are not only predominant members of the microplankton community but also important contributors to primary productivity and the production of organic compounds from inorganic substrates (Capriulo 1990, Banse 1992). The microherbivores act as a biotic control for phytoplankton production due to their grazing rates (Jacobson and Anderson 1993, Strom and Buskey 1993, Nakamura et al. 1995, Verity et al. 1993, Strom and Strom 1996). The heterotrophic *Gyrodinium* species feed on chains of diatoms from the Gulf of Mexico during high grazing rates (Strom and Strom 1996) but also on other mixotrophic dinoflagellates species (*Prorocentrum minimum*) (Kim and Jeong, 2004).

Natural phytoplankton populations grow most rapidly in the euphotic zone under light-saturated conditions (Goldman et al. 1979). During the 1980s, the highest growth rates of some phytoplankton classes (e.g. diatoms) were reported to be as high as 2.3 day^{-1} based on chlorophyll *a* (Chl *a*) labeling and dilution techniques (Landry et al. 1984). The doubling time of dinoflagellates can be as short as 1-2 days (Furnas and Mitchell 1997).

Because of this, data collected during the last 30 years have indicated that the in situ growth rates of algal communities may be much higher than 1 day^{-1} in tropical and subtropical waters (Laws et al. 2013). Diffusion chamber techniques (Furnas 1982a), dilution techniques (Landry and Hassett 1982, Garces et al. 2005), ^{14}C-labeling of chlorophyll and carotenoids (Goericke and Welschmeyer 1993), and DNA cytometric analysis (Gisselson et al. 2002) have been used for the assessment of growth rates. These techniques have been used for both field samples (Reguera et al. 1996) and culture experiments (Morton and Tindall 1992, Nakamura et al. 1995, Marasigan et al. 2001, Menden-Deurer et al. 2005, Baek et al. 2007).

Numerous reports are available on estimates of dinoflagellate growth rates from various ocean basins around the world, including the South Bering Sea (Olson and Strom 2002), the Gulf of Mexico (Strom and Strom 1996), the Pacific Ocean (Storm 1991, Perez et al. 2006), the Baltic Sea (Balode 1998), the coastal waters of the USA (Jacobson and Anderson 1993, Strom and Morello 1998), Japan (Nakamura 1995), and Denmark (Hansen 1992). This is the first study to measure growth rates of dinoflagellates in the tropical coastal waters of Pakistan.

Materials and methods

Sample sites

Samples were collected during the winter (08 February, 13 February, 2006) from two stations: Station 1 (STN. 1, 24°49.77' N, 66°57.85' E) inside the Manora Channel and Station 2 (STN. 2, 24°47.93'N, 66°58.87'E) outside the same channel. Another experiment was conducted at the mouth of Manora Channel Station 3 (STN. 3, 24°48.97' N, 66°58.23' E) during the summer (07 May 2007) (Fig. 1).

Experimental design and data analysis

The samples were collected at a depth of 1 m with a 1.7-l Niskin bottle and prescreened through 150 µm and 10 µm mesh nets to remove grazers (Furnas 1982, 1990). Triplicate polycarbonate bottles (acid cleaned) were used for in situ incubations (Furnas 1991). Unfractionated water (Control) was preserved with Lugol's solution, and fractionated water as Fr. A (150 µm) and Fr. B (10 µm) was used to fill the polycarbonate bottles which suspended from floating buoy at the surface water for 24 hr. In the summer of 2007, samples were prescreened only through 150 µm mesh nets (Fr. A); otherwise the procedures were identical in 2006. Water temperature (°C) and salinity were measured with a thermometer and refractometer, respectively. The pH was measured with a pH meter (Hanna H19023, Italy). The community structure was enumerated by using a light inverted microscope to count cells in a settling chamber (Utermöhl 1958). The growth rate (μ d^{-1}) of dinoflagellates was calculated as $\mu = \ln(T_{24}/T_o)/(\Delta t)$, where Δt is the incubation period in days, T_o is the initial cell concentration, and T_{24} is the final cell concentration.

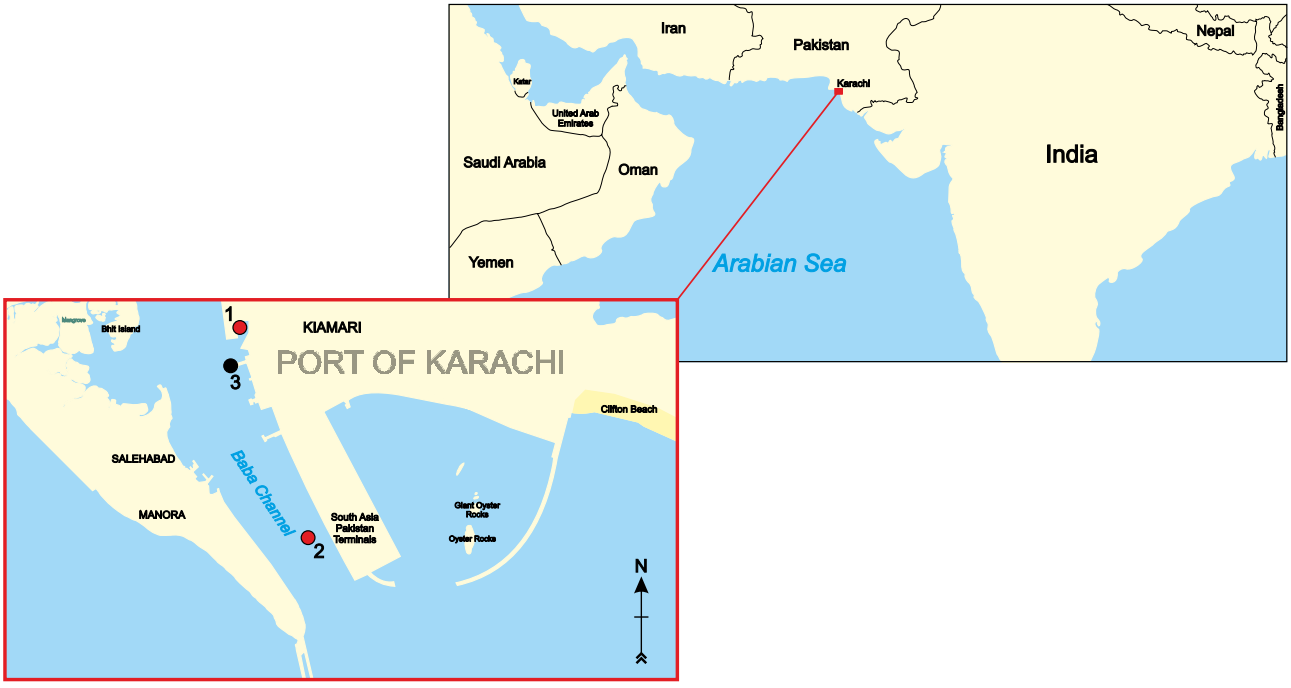

Figure 1

Map of coastal area, Karachi Pakistan and sampling sites STN. 1 and STN. 2 (Red dot) in 2006 and STN. 3 (Black dot) in 2007

Results

Physico-chemical parameters in winter 2006 and summer 2007

Temperature, salinity and pH were recorded at the designated stations during the winter and summer season (Table 1). In winter, the temperature was 23-25°C at the beginning and at the end of the incubations. The salinity was 35 initially and 40 at the end, and pH was 7.4-7.9 at both stations 1 and 2 (Table 1). At station 3, during summer, the temperature was as high as 32-33°C at the beginning and at the end of the incubation. Salinity was 38, and pH was 7.0.

Table 1

Temperature (°C), salinity and pH value recorded from three stations before incubation (T_o) and after incubation (T_{24}) during winter, February 2006 and summer, May 2007

Exper	Date	Temperature (°C)		Salinity (PSU)		pH	
		T_o	T_{24}	T_o	T_{24}	T_o	T_{24}
1	8 Feb 2006	24	25	35	37	7.4	7.5
2	13 Feb 2006	23	25	40	40	7.7	7.9
3	7 May 2007	32	33	38	38	7.7	7.7

Dinoflagellate community structure and abundance

Dinoflagellate composition and abundance at Station 1 (2006)

The growth rates of 13 species of dinoflagellates were recorded at STN. 1 (Table 2). The cell concentrations ranged from 20 cells to 153 cells l^{-1} before the incubations. The maximum cell concentration was 347 cells l^{-1} recorded at time T_{24} of the control incubation. The cell concentration declined to 180 cells l^{-1} at time T_0 and 260 cells l^{-1} at time T_{24} with 150 µm fractionated samples. The highest cell concentration was recorded for *Prorocentrum micans* and *Dinophysis caudata* (Table 2). In the 10 µm fraction, the only four species were

Table 2

The number of cells l^{-1}, the growth rate GR (μ d^{-1}) measured from unfractionated samples (Control), size-fractionated samples 150 µm (Fr. A) and 10 µm (Fr. B) at station 1

Station 1	Control cells l^{-1}		GR	Fr. A 150 µm cells l^{-1}		GR	Fr. B 10 µm cells l^{-1}		GR
Species	T_o	T_{24}	(μ d^{-1})	T_o	T_{24}	(μ d^{-1})	T_o	T_{24}	(μ d^{-1})
Alexandrium ostenfeldii	33	60	0.59	-	-	-	-	-	-
Ceratium furca	20	13	-0.41	-	-	-	-	-	-
C. lineatum	20	13	-0.41	-	-	-	-	-	-
Dinophysis caudata	100	127	0.24	113	93	-0.19	-	-	-
D. acuminata	20	20	0	-	-	-	-	-	-
Gonyaulax spinifera	40	0	0	20	20	0	-	-	-
Gyrodinium spirale	40	87	0.77	40	20	-0.69	40	113	1.04
Prorocentrum micans	153	347	0.82	180	260	0.37	40	20	0.41
P. gracile	47	127	1.1	127	107	-0.17			
P. arcuatum	53	180	1.22	73	87	0.17	20	40	0.69
P. minimum	27	80	1.1	20	40	1.79	-	-	-
Pyrophacus stein	40	13	-1.1	-	-	-	-	-	-
Scrippsiella trochoide	27	53	0.69	27	0	-0.69	20	20	0.00

Gyrodinium spirale, *P. micans*, *P. arcuatum*, and *Scrippsiella trochoidea*. These were recorded at low cell concentrations of 40 cells l^{-1} at T_0 and 113 cells l^{-1} at T_{24} (Table 2). The highest cell concentration was recorded for *G. spirale*.

Growth rate of potentially harmful dinoflagellates at Station 1

In unfractionated bottles, the maximum growth rate (1.00 and 1.22 d^{-1}) was recorded for *P. gracile* and *P. arcuatum* and 0.24-0.82 d^{-1} for *Alexandrium ostenfeldii*, *D. caudata*, *S. trochoidea*, and *G. spirale* (Table 2). Negative growth rates ranged between -0.41 d^{-1} and -1.10 d^{-1} for *Pyrophacus stein*, *Ceratium furca*, and *C. fusus*. In the 150 µm fraction, maximum growth rates of 1.79 d^{-1} and 0.37 d^{-1} were recorded for *P. minimum* and *P. micans*, respectively. The lowest growth rates (-0.19 to -0.13 d^{-1}) were recorded for *D. caudata*, *P. gracile*, *S. trochoidea, G. spirale*, and *Gyrodinium* sp. (Table 2). The zero growth was observed for *Pyrophacus stein*, *P. divergens*, and *G. spinifera*. In the 10 µm fraction, the highest growth rate (1.04 d^{-1}) was recorded for *G. spirale*. The high growth rates for *P. micans* and *P. arcuatum* were 0.41-0.51 d^{-1}. The zero growth was observed for *S. trochoidea* (Table 2).

Dinoflagellate composition and abundance at Station 2 (2006)

A total of 19 species were identified from Station 2. The maximum cell concentration was 1267 cells l^{-1} at time T_0 and 1840 cells l^{-1} at time T_{24} in the unfractionated samples (Table 3). The highest cell concentration was recorded for *P. micans* and *D. caudata* at the initial and final time (Table 3). The total cell concentration was 747 cells l^{-1} at T_0 and 1840 cells l^{-1} in the 150 µm fraction. The highest abundance was observed for *P. micans*, *D. caudata*, *P. arcuatum*, and *A. ostenfeldii* at the end point (Table 3). A total of 7 species were identified from the 10 µm size fraction, and the maximum cell concentration (207 cells l^{-1}) was recorded at time T_0 and 120 cells l^{-1} at time T_{24}. The dinoflagellate community was dominated by *G. spirale* and *S. trochoidea* at T_0 when at the maximum cell concentration but the concentration decreased to 80 cells l^{-1} at T_{24} (Table 3).

Growth rate of potentially harmful dinoflagellates at Station 2

In the unfractionated bottles, the maximum growth rates (μ_{max}) of 0.92-1.20 d^{-1} were recorded for *C. furca*, *P. steinii*, and *C. lineatum*. The maximum growth rates of 0.29-0.61 d^{-1} were recorded for

Table 3

The number of cells l^{-1}, the growth rate GR (μ d^{-1}) measured from unfractionated samples (Control), size-fractionated samples 150 µm (Fr. A) and 10 µm (Fr. B) at station 2, 2006

Station 2	Control Cells l^{-1}		GR	Fr. A 150µm Cells l^{-1}		GR	Fr. B 10µm Cells l^{-1}		GR
Species	T_o	T_{24}	(μ d^{-1})	T_o	T_{24}	(μ d^{-1})	T_o	T_{24}	(μ d^{-1})
Alexandrium ostenfeldii	140	167	0.17	287	253	-0.12	80	40	-0.69
Ceratium furca	20	67	1.26	33	73	0.79	-	-	-
C. lineatum	40	33	0.92	40	40	0.00	-	-	-
C. tripose	-	-	-	20	27	0.30	-	-	-
Dinophysis caudata	347	586	0.52	200	503	0.92	-	-	-
D. acuminata	20	27	0.29	7	73	2.39	-	-	-
Gonyaulax spinifera	80	53	-0.41	20	33	0.51	20	40	0.69
Gyrodinium spirale	293	227	-0.26	93	87	-0.07	207	80	-0.95
katodinium glaucum	400	287	-1.87	167	87	-0.65	-	-	-
Karenia mikimotoi	87	40	-0.15	20	20	0.00	150	13	-2.48-
Prorocentrum micans	126	1087	-0.06	747	1840	0.90	20	40	0.69
P. gracile	240	227	0.26	133	247	0.62	-	-	-
P. arcuatum	133	173	-1.25	113	467	1.42	-	-	-
P. donghaiense	140	40	0.41	93	13	-1.95	40	7	1.79
P. minimum	40	60	0.61	27	40	0.41	-	-	-
Protoperidinium stenii	40	73	-0.41	47	87	0.62	-	-	-
P. divergens	20	13	-0.69	20	20	0.00	-	-	-
P. curtipes	40	20	1.25	20	20	0.00	-	-	-
Pyrophacus stein	27	93	-1.61	20	20	0.00	-	-	-
Scrippsiella trochoide	333	67	0.17	233	53	-1.48	133	33	-1.39

D.caudata, *D. acuminata*, *P. minimum*, and *P. steinii* (Table 3). A declining growth rate (-1.87 d^{-1}) was recorded for *Karenia mikimotoi*. The declining growth rates (-1.61 to - 0.69 d^{-1}) were also recorded for *S. trochoidea* and *P. donghaiense*, *P. micans*, *P. divergens* and *P. curtipes* (Table 3).

In the 150 µm fraction, the maximum growth rate of 2.3 d^{-1} was observed for *D. acuminata*, and growth rates of 0.92-0.41 d^{-1} were recorded for *D. caudata*, *P. micans*, *C. furca*, *P. gracile*, *P. steinii*, *G. spinifera*, and *P. minimum*. Negative growth rates of (-1.95 to -0.07 d^{-1}) were recorded for *P. donghaiense, S. trochoidea*, *A. ostenfeldii*, *K. glaucum* (-0.65 d^{-1}), and *G. spirale*. The zero growth was observed for *C. lineatum*, *Karenia mikimotoi*, *Gonayaulax spinifera*, *Pyrophacus stein*, *P. divergens*, and *P. curtipes*. In the 10 µm fraction, the maximum growth rate of 0.69 d^{-1} was recorded for *P. micans* and *G. spinifera*, and negative growth rates (-2.48 to -1.79 d^{-1}) were recorded for *K. mikimotoi*, *P. donghaiense*, and *S. trochoidea*. Negative growth rates of -1.38 d^{-1} and -0.69 d^{-1} were recorded for *A. ostenfeldii* and *Gyrodinium* sp., respectively (Table 3).

Total dinoflagellate community and the growth rate at station 3 (2007)

A total of 21 species were identified during the summer season, and the total cell concentration was in the range of 20-1820 cells l^{-1} at T_0 and 20-2860 cells l^{-1} at T_{24} (Table 4). The total growth rate of the community was in the range from -0.86 to 1.95 d^{-1}. The maximum growth rate was recorded for *P. micans*, *C. lineatum*, *Gyrodinium* sp., *C. furca*, *C. fusus*, *P. donghaiense*, *G. verior*, and *P. steinii*. Lower growth rates (-0.82 to -0.63 d^{-1}) were recorded for *Heterocapsa* sp., *G. spinifera*, and *S. trochoidea*. (Table 4).

Discussion

In situ growth rates of dinoflagellates have been reported for the first time from the coastal waters of Pakistan. The present study describes the growth rate of 20 dinoflagellate species during summer and winter months. The maximum growth rate was obtained for *Dinophysis acuminata* (2.3 day^{-1}), and

Table 4

The number of cells l^{-1}, the growth rate GR (μ d^{-1}) of dinoflagellates at station 3 in summer 2007

Station 3	Fr. A 150 µm (cells l^{-1})		GR
	T_o	T_{24}	(μ d^{-1})
Akashiwo sanguinea	20	40	0.69
Alexandrium ostenfeldii	573	2680	1.34
A. tamarense	140	240	0.54
Ceratium furca	40	220	1.70
C. fuscus	40	160	1.39
C. lineatum	40	280	1.95
C. tripose	40	40	0.00
Dinophysis caudata	20	80	1.39
D. miles	20	20	0.00
Gyrodinium sp1	180	1180	1.88
Gyrodinium spirale	161	640	1.39
Gonyaulax spinifera	20	40	-0.69
G. verior	20	80	1.39
Heterocapsa sp	1260	660	-0.63
Kitodinium glaucum	20	40	0.26
Prorocentrum micans	120	840	1.95
P. minimum	135	480	1.23
P. arcuatum	20	20	0.00
P. dongahiense	20	100	1.61
Phyrophacus stein	20	80	1.39
Scrippsiella trochoidea	360	80	-0.82

negative growth rates were -2.87 day^{-1} for *Karenia mikimotoi*.

Moreover, three other species (*P. minimum*, *P. arcuatum*, *P. gracile*) in the control treatments grew at positive rates of 1.0-1.75 d^{-1}. These species grew at moderate rates (0.95 d^{-1}) in fractionated samples (Fr .A, Fr. B) during the winter season and at high rates (>1 d^{-1}) in fractionated samples (Fr. A) during the summer. Using the size fractionation method, samples prescreened through 150 µm and 10 µm nets showed positive growth due to the removal of large grazers and the maximum growth rate was observed for small size dinoflagellates. The estimated rates recorded from Pakistan are high compared to previously reported values from other coastal waters (Garces et al. 1999, Stolte and Garcés 2006, Strom et al. 2007).

Growth rates are influenced by various environmental factors, such as nutrients (Calbet and Landry 2004, Wang et al. 2007), dissolved inorganic carbon (DIC), dissolved oxygen (DO), and prey composition (Jeong et al. 2001, Kim and Jeong, 2004). Nitrogen is a nutrient which can enhance the growth rate of dinoflagellates rather than stimulate the biomass (Calbet and Landry 2004), and some phytoplankton species have been reported to have low growth rates at low temperatures, and low light in Antarctic waters (Sommer 1989). Sometimes, nutrients can be a non-limiting factor for the phytoplankton growth and the growth rate can be increased due to high temperature and pH values (Alam et al. 2001). Most of the phytoplankton species had higher growth rates >2 day^{-1} at temperatures of 15-20°C (Bonin et al. 1986). Temperature is an important factor which increases the phytoplankton growth rates in culture and field experiments. In culture, species of toxic dinoflagellates had the maximum growth at high temperatures of 20-25°C (Cannon 1993, Jensus and Moestrup 1997, Baek et al. 2007). Our values for growth rates of toxic species at 33°C in situ were 1.20-1.95 d^{-1} during the summer (Table 4). The value of the growth rate of *D. acuminata* in the present study is much higher than the rate of 0.95 d^{-1} reported from Korean waters (Park et al. 2006). These high growth rates can be due to the absence of grazers (Hansen et al. 1997) or may be due to different prey species (Jeong et al. 2001). Most of the heterotrophic dinoflagellate species such as *Polykrikoides kofoidii* feed on prey species to obtain the maximum growth (Jeong et al. 2001). This growth rate is higher than that of *Dinophysis* species reported from the Baltic Sea (0.1 to 0.4 d^{-1}; Garces et al. 1997) and Japan (0.2 to 0.7 d^{-1}; Chang and Carpenter 1991). The growth rate of *D. caudata* is within the range of values reported from Japanese waters (1.03 d^{-1}; Nishitani et al. 2007). The growth rate of *C. furca* is higher compared to rates reported from other coastal waters of many countries (0.90 d^{-1}; Chang and Carpenter 1985; 0.59 d^{-1}; Baek et al. 2002; 0.37 d^{-1}; Garces et al. 1999). The growth rates for two other species, *P. minimum* and *C. lineatum*, were positive in both the summer and winter and the growth rate of *S. trochoidea* was negative in both seasons (Table 3 and 4). The lowest in situ growth rate was recorded for *K. mikimotoi*. This species grows very slowly in culture (Gentien et al. 2007). The negative growth rates shown by all species (Table 2-4) may be due to the dominance or competition and allelopathy among other algal species and grazing by mixotrophic species or may reflect a need for more time (2 days to 2 weeks) required for replication (Hansen et al. 1997, Menden-Deurar et al. 2005). Growth rates may also be constrained by the incubation enclosure and light penetration. Actually, the time of seawater being enclosed in the bottle closely correlates to the deviation of particulate material from its natural

state. Short times or large containers are thought to minimize the containment effect. The low growth rates may also be linked to physical processes as opposed to biological processes in the formation of red tides within upwelling systems. Prescreening the sample through 150 µm and 10 µm removed major grazers. Alternatively, the filtered seawater may be used to physically reduce the number of grazers per unit volume (i.e. dilution experiments) – assuming that the grazing rate is regulated by the encounter rate between grazers and prey (concentration) (Furnas 1982). Size fractionated the populations, even through 10 µm, will probably not remove many of the small flagellates that graze on very small picoplankton and bacteria. We assumed that this treatment does not have much of an effect if small organisms (10 µm) were not major contributors to overall grazing pressure. It is important to develop culture experiments to determine the growth rates of dinoflagellates in different environmental regimes and to conduct further research focused on prey concentration and grazing experiments.

In conclusion, the high temperature conditions in Pakistani coastal waters increases the growth rate of dinoflagellates. This is the first growth rate experiment in coastal waters of Pakistan that used size fractionation and incubation methods. Incubation in bottles can be harmful to organisms due to specific grazers, although a positive growth rate close to the theoretical maximum suggests that the incubation method did not reduce the dinoflagellate growth.

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