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Reproductive ecology of dominant dinoflagellate, *Ceratium furca*, in the coastal area of Sagami Bay

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Abstract — Reproductive ecology of dinoflagellate, *Ceratium furca*, was studied in the coastal area of Sagami Bay. Field samplings and laboratory experiments were conducted to investigate seasonal changes of the field population and effects of temperature, salinity and irradiance on the growth rate of *C. furca*. Abundance of the species increased significantly from April to September and was decreased in November. In particular, the population increased during the spring when the water column was weakly stratified and relatively low nutrient conditions were observed in the surface layer. High growth rates of *C. furca* were observed at the conditions of 20–28°C, 17–34 PSU and 216–800 μE m^{-2} s^{-1} with the highest growth rate (μ=0.72 d^{-1}) being observed at 24°C, 30 PSU and 600 μE m^{-2} s^{-1}. In addition, the growth rates increased gradually with increasing irradiance from 58 to 216 μE m^{-2} s^{-1} in the all salinity conditions, and afterwards the rates reached plateaus between 216 and 796 μE m^{-2} s^{-1}. The field survey and laboratory experiments indicated that the species is distributed throughout the year and adapted to a wide-range of environmental fluctuations such as water temperature, salinity, irradiance and nutrients. These specific characteristics make *C. furca* one of the dominant dinoflagellates in the coastal area.

Key words: dinoflagellate, *Ceratium furca*, growth rate, temperature, salinity, nutrients, light intensity

Introduction

Over the last few decades, magnitude and geographic extent of red tide outbreaks, which are produced by toxic and non-toxic dinoflagellates, have increased (Anderson 1997). Although not all red tides are harmful events, harmful algal blooms (HABs) cause problems on marine environments and resources, such as great economic damage to fisheries (Horner 1997). The harmful algal species has been found throughout the various regions with diverse hydrographic conditions. In general, although studies of toxic species have been conducted over the last few decades, there are few studies of nontoxic red tide species in coastal waters.

The species belonging to genus *Ceratium* frequently dominate coastal phytoplankton communities, and they contribute substantially to annual primary production in coastal water (Nielsen 1991, Dodge and Marshall 1994). Compared with other dinoflagellates, some of the larger species belonging to *Ceratium* may represent an important food source for zooplankton (Nielsen 1991). Moreover, Smetacek (1981) reported that mesozooplankton population was associated with the dynamics of *Ceratium* populations. *Ceratium furca* do not produce toxin, but induces other deleterious impacts through consumption of oxygen as bloom decay, production of scums, or reduction of habitat for fish or shellfish, which frequently caused losses to the aquaculture and tourist industries in many countries (Yin 2003). Recently, extensive blooms of *C. furca* were reported along the Pacific coast of central Japan in 1997 and caused severe damage to the local fisheries (Machida et al.1999).

During many years, the cell division for *Ceratium* species has been estimated in the field and laboratory experiments (Qasim et al. 1973, Elbrächter 1973, Weiler & Chisholm 1976, Weiler & Eppley 1979, Nielsen 1991). In addition, several red-tide dinoflagellates including *Ceratium furca*, which had been previously thought to be phototrophic, are now considered to be mixotrophic (Bockstahler and Coats 1993, Li et al. 1996, Stoecker 1998, Smalley et al. 1999, 2002, 2003). Mixotrophs gain their nutrition through a combination of photosynthesis and uptake of dissolved or particulate organic material. Supplementing their nutrition in this manner could give red-tide dinoflagellates a competitive advantage over strictly photosynthetic organisms, since phagotrophy would enable the mixotrophic species to acquire nutrients and carbon when these essential growth factors are limiting (Li et al. 2000, Smalley and Coats 2002). In particular, ingestion of ciliates by *Ceratium furca* collected from Chesapeake Bay increased with decreasing inorganic phosphate concentrations in field and laboratory experiments (Li et al. 2000, Smalley and Coats 2002, Smalley et al. 2003). However, while the early study of the cell division frequency

to estimate growth of *Ceratium* relied on the original strains of culture, few attempts has been made to evaluate the accuracy of these estimates by using an unbiased measure of increase in cell number. Moreover, although growth rates of *C. furca* have been of interest, its optimal environmental conditions for outbreaks are not clear.

In Sagami Bay, *C. furca* is a dominant red tide species; the species appeared from April to September (Baek 2004). After spring diatom bloom, high densities of *C. furca* seem to occur under low nutrient condition, and almost disappear from the water column between the blooms, which have not been known as a regular seasonal occurrence pattern observed in other dinoflagellates. In the present study, natural population of *C. furca* was monitored to clarify relationships between its abundance and environmental factors (water temperature, salinity, nutrients) in the coastal waters of Sagami Bay. In addition to the field investigation, cultured population of *C. furca* was established to examine their optimum growth condition. The experimental results were compared to natural population to discuss their life strategies in the field.

Materials and Methods

Field research

Periodical samplings were conducted monthly from 2000 to 2003 at two coastal stations, St. 40 of 40 m depth and St. 70 of 70 m depth in the north-western part of Sagami Bay, Central Japan (Fig. 1). Sagami Bay faces the Pacific Ocean and its hydrography is primarily related to fluctuations of the Kuroshio Current axis. It is also influenced by the fresh water discharge from Sagami and Sakawa Rivers as well as the water from Tokyo Bay (Hogetsu and Taga 1977). Interaction between the current and river discharges results in stratified waters in the bay. The surface layer consists of a mixture of waters from the Kuroshio Current and fresh waters.

Water samples were taken by a bucket (only for the surface layers) and 6-L Niskin bottles. The sampling depths at the two stations were 0 m, 5 m, 20 m and 35 m depths at St. 40, and 0 m, 5 m, 20 m, 40 m and 65 m at St. 70. Debris and large-size plankters in the collected waters were removed by filtering through a 330 μm mesh on the shipboard immediately after measurements of water temperature with a mercury thermometer. Each filtered water sample was kept in a dark bottle and carried to the laboratory for determination of salinity, inorganic nutrients and phytoplankton abundances including *Ceratium furca*. Salinity (PSU) was measured using an inductive salinometer (Model 601 MK-IV, Watanabe Keiki MFG. Co. Ltd.). Subsamples for the estimation of phytoplankton abundances were immediately fixed with 2.5% glutal aldehyde solution (final concentration) and stored at 4°C in dark condition until cell counts.

Water samples for dissolved inorganic nutrients were filtered through Millipore Milex filters (pore size: 0.45 μm). The filtered water was placed into plastic tubes and kept in a freezer (−20°C) until later measurements of nutrients. The water samples thawed to room temperature, and nitrite+nitrate ($NO_2^-+NO_3^-$), and phosphate (PO_4^{3-}) concentrations were analyzed using a nutrient auto-analyzer (Bran+Luebbe, AACA-II Compact System), following the analytical method of Parsons et al. (1984).

Daily rainfall data from January 2000 to December 2001 were obtained from Manazuru City Office and those from January 2002 to December 2003 were obtained from the Odawara office of the Japan Meteorological Business Support Center.

Photosynthetically active radiation (PAR) was measured daily during the research period with a surface radiometer (Li-190 SA, Li-COR) placed on the roof of the Manazuru Marine Biological Station, Yokohama National University (Fig. 1).

Isolation and culture of *Ceratium furca*

Ceratium furca were isolated from the natural assem-

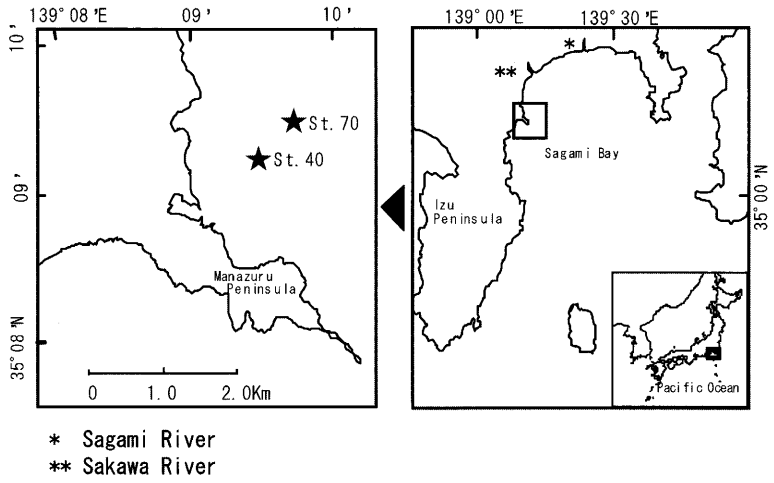

Fig. 1. The sampling stations in Sagami Bay, Japan. Manazuru Marine Station (MMS) of Yokohama National University is also indicated.

Table 1. Chemical composition of modified T_1 medium. 1 ml of stock solution per 1 liter filtered seawater gives the desired concentration. **H_2SeO_3** was added to the original T_1 medium.

Compound	Concentration (M)
$NaNO_3$	1×10^{-3}
NaH_2PO_4	1×10^{-4}
Fe-EDTA	5×10^{-6}
$ZnSO_4$	1×10^{-6}
$MnCl_2$	1×10^{-5}
$NaMoO_4$	5×10^{-7}
$CoCl_2$	2×10^{-7}
$CuSO_4$	1×10^{-8}
EDTA-Na_2	2.4×10^{-5}
H_2SeO_3	**2×10^{-9}**
Thiamine HCl	5.93×10^{-9}
Biotin	4.1×10^{-9}
Cyanocobalamin	7.38×10^{-6}
Tris HCl buffer (pH 8.0)	5×10^{-3}

blages of Sagami Bay during October 2004, when water temperature and salinity were approximately 22°C and 32.5 PSU, respectively. Each of the isolated *C. furca* cells was washed by serially transferring into 3 droplets of T_1 medium and then put into a 5-ml well of a 12-well tissue culture plate. In the wells, the medium was added with 1 ml of tryptone and yeast extract water to facilitate bioactivity of the cells in the initial culture. Preparation of tryptone and yeast extract water was as follows: 15 g of tryptone and 35 g of yeast were dissolved and suspend in 1 liter of distilled water by heating in a boiling water bath, and then it was autoclaved (15 min. at 121°C). In the preliminary experiments, the cells cultured in T_5 medium (N: 5 μM, P: 0. 5 μM, five times higher concentration of T_1 medium) showed optimum growth as compared with T_1 medium (N: 1 μM, P: 0. 1 μM) (Table 1). Therefore, to acclimate to a laboratory condition, the cells were transferred and cultured in enriched seawater of modified T_5 medium with soil extract at 22°C under the light condition of 180 μE m^{-2} s^{-1} with a 12 L: 12 D cycle (using cool white fluorescent lamps) during a period of one month (Ogata et al. 1987).

Laboratory measurement of growth rate

The growth rates of *C. furca* were determined under different light conditions, salinities and water temperatures. The effect of light, temperature and salinity on the growth rate was examined by three times experiments under the T_5 medium with soil extract in 100-ml triangle flasks. For these experiments, six temperatures (12, 16, 20, 24, 28 and 32°C), six salinities (17, 20, 24, 27, 30 and 34 PSU) and six irradiance regimes (0, 58, 180, 230, 600 and 800 μE m^{-2} s^{-1}) were established. In particular, the cells were incubated at 20,24 and 28°C for the growth rate of the all salinity conditions (17, 20, 24, 27, 30 and 34 PSU) but estimated with only 30 PSU for 12,16 and 32°C. All experiments were conducted for 4 days under a 12L: 12D cycle. Cell density in each treatment was counted under a microscope to estimate the specific growth rate (μ) of *C. furca* by the following equation:

$$\mu=\ln(N_t/N_0)/t$$

Where N_0 and N_t represents the initial and final cell number at the end of the incubation time t (day).

Data analysis

Pearson's correlation analysis was carried out to test the correlations among cell densities of *C. furca* and environmental parameters (temperature, salinity, NO_2+NO_3 and PO_4) in the field. The significance level of $P<0.05$ was used in all statistical analyses.

Results

Environmental factors

Seasonal changes of environmental factors were almost identical at St. 40 with St. 70. Therefore, we showed the result at St. 40 (Fig. 2).

Water temperature varied from 12 to 29°C during the sampling period (Fig. 2b). In each sampling year, the highest temperature was recorded in August or September and the lowest in March. The water column was vertically well mixed from November to March, and gradually stratified thereafter. Salinity varied from 23.0 to 34.7 PSU during the sampling period and low salinities were frequently recorded in summer due to rainfalls (Fig. 2c). In particular, salinity decreased drastically from 34.5 to 24.5 PSU in September 2001 and from 34.5 to 23.0 PSU in August 2003 probably due to heavy rains at 2-4 days before the sampling in both months (Fig. 2a, c). Large amount of rainfalls tended to be recorded from May to October during the every 4 years. In particular, the largest quantity of rainfall during the study period was recorded in 2003. A total rainfall during 5 days before each sampling day was calculated and its vale was in excess of 100 mm by 4 times during the summer seasons (June to September).

Concentrations of nitrate and nitrite ranged from> 0.02 μM on July 2003 to 20.49 μM on August 2003, the mean values during 4 sampling years was 3.06±2.64 μM (Fig. 3d). Phosphate concentrations ranged from>0.02 μM on May 2001 to 1.37 μM on March 2002, the mean values was 0.27±0.20 μM (Fig. 3e).

Seasonal variation of *Ceratium furca* abundance

Ceratium furca were observed at both stations in every study year. The average abundance of the species at St. 70 was lower compared to that at St. 40. Its populations remained at low densities through October to January, and the abundance tended to increase from April to September (Fig. 3). In particular, the species decreased to low densities from

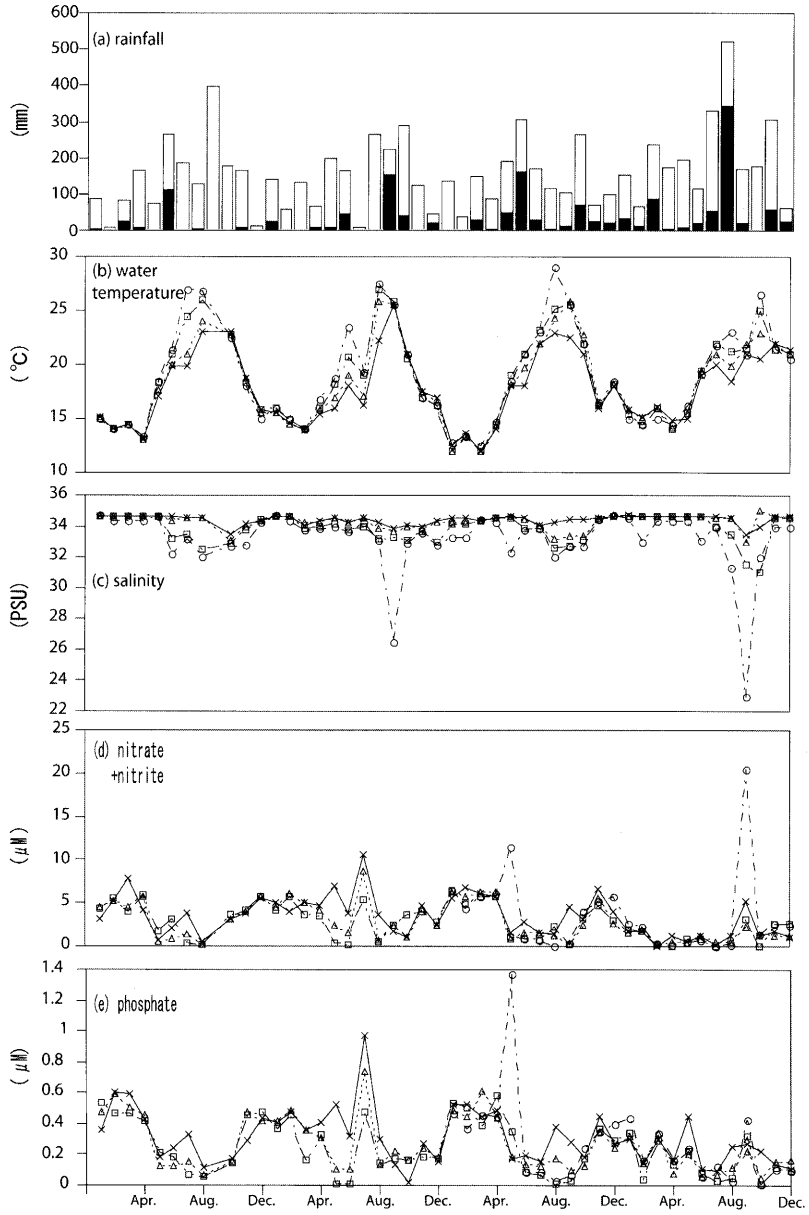

Fig. 2. Seasonal changes of vertical profiles in (a) daily rainfall, (b) water temperature, (c) salinity, (d) nitrate+nitrite and (e) phosphate at the St. 40 from January 2000 to December 2003. Open bars in rainfall (a) indicate monthly averages rainfall. Filled bars indicate total rainfall during 5 days on each sampling date. Open circles, open triangles, open squares and crosses in (b)–(e) indicate 0 m, 5 m, 20 m and 35 m, respectively.

December 2000 and completely disappeared in March 2001. Marked seasonal blooms of the species were observed during the periods from April to August in 2000–2002. However, in 2003, the abundance of *C. furca* was always higher in both summer and winter than those in the previous three years. The blooms occurred differently between the stations, which were observed in February at St. 70 and April at St. 40. During the study period, each bloom of the species did not continue more than one month at both stations.

In the vertical distribution, the maximum densities of the species were observed between the surface and 20 m depth, whose peaks were frequently observed at 5 m depth, and then the abundances sharply decreased with increasing depth at both stations (Figs. 3, 4). The relationship between environmental factors and abundance of *C. furca* during the 4 years are shown in Table 2. The abundance of *C. furca* was not significantly correlated with water temperature and salinity. In contrast, the abundance was negatively correlated with water depth ($r=-0.316$, $p<0.01$), nitrate+nitrite concentrations ($r=-0.374$, $p<0.01$), and phosphate concentration ($r=-0.322$, $p<0.01$).

Specific growth rate

The growth rates of *C. furca* increased with increasing irradiance from 58 to 216 $\mu E\,m^{-2}\,s^{-1}$, and afterwards the rates reached plateaus between 216 and 796 $\mu E\,m^{-2}\,s^{-1}$, in

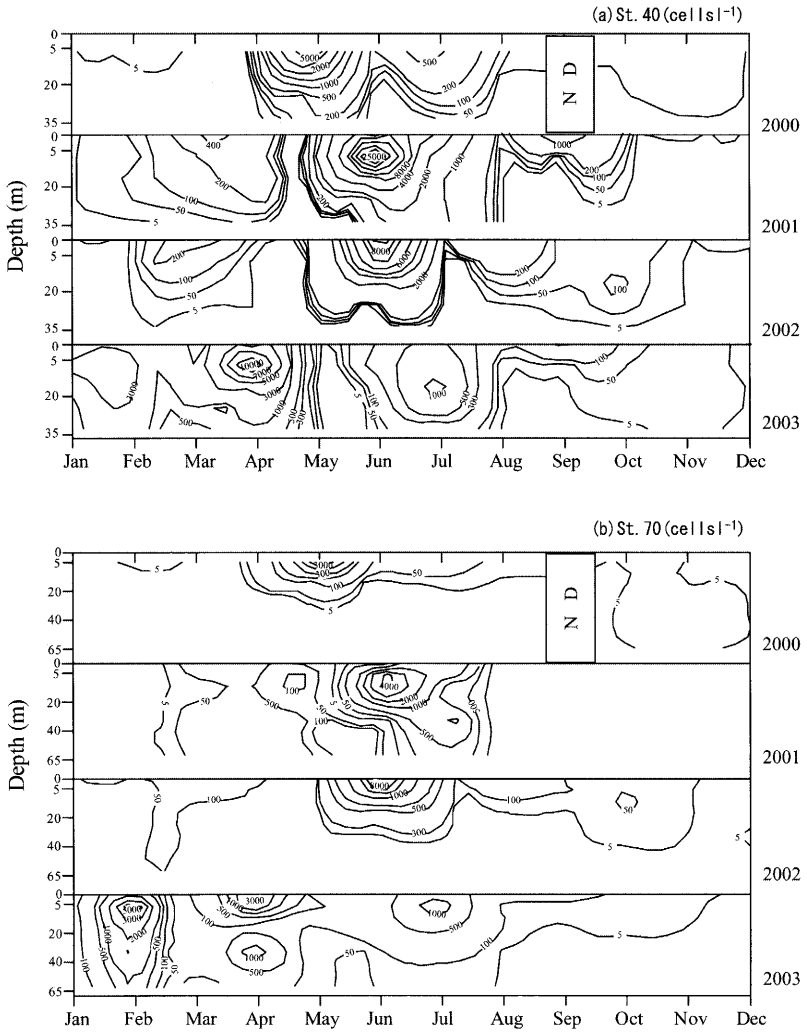

Fig. 3. Seasonal changes of vertical distribution of *Ceratium furca* at St. 40 (a) and St. 70 (b).

Table 2. Correlation coefficients (r) of Pearson's test between environmental factor and abundance of *Ceratium furca* during the 4 years between 2000 and 2003.

	Depth	Temperature	Salinity	NO_2 $+NO_3$	PO_4
Temperature	−0.152				
Salinity	0.455*	−0.492*			
NO_2+NO_3	0.249	−0.567*	0.137		
PO_4	0.325*	−0.634*	0.342*	0.776*	
C. furca	−0.316*	0.077	−0.090	−0.374*	−0.322*

* Significant correlations ($P<0.01$).

the all temperature treatments except for 12 and 32°C (Fig. 4a, f). At 12°C, the growth rates were significantly low throughout the all light conditions, although the rates slightly increased with increasing irradiance. In contrast, the growth rates decreased with increasing irradiance at 32°C (Fig. 4f). The growth rates also increased with increasing temperature from 12 to 24°C. On the other hand, in all salinity treatments, high growth rates were observed between 216 and 796 $\mu E\, m^{-2}\, s^{-1}$ and the highest rate was $0.72\, d^{-1}$ at 30 PSU (Fig. 5).

Discussion

Bloom dynamics seem to be driven by interaction between biological and physical processes that occur over a broad range of temporal and spatial scales (Donaghay and Osborn 1997). Morse (1947) reported that *Ceratium furca* reached a significant high density with warm water above the pycnocline at the Patuxent River, Maryland. Donaghay and Osborn (1997) also observed dense populations of *C. furca* mainly near pycnoclines in stratified water columns, because pycnocline has been recognized as a precondition for the development of dinoflagellate populations. Pycnoclines also play an important role in the occurrence of the subsurface population and has often been interpreted as an underlying factor in phytoplankton patchiness (Rasmussen and Richardson, 1989). HABs have frequently been formed dense blooms above pycnoclines at coastal systems induced by

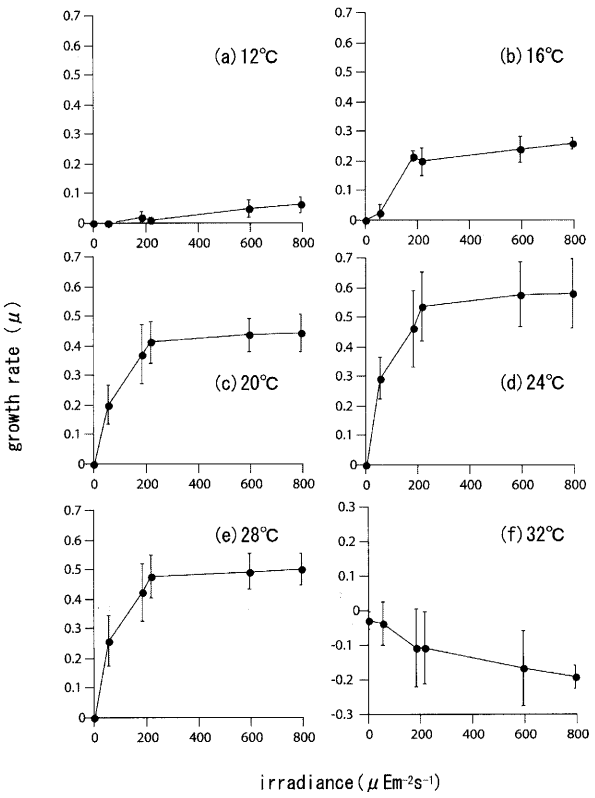

Fig. 4. Changes of growth rates of *Ceratium furca* at different irradiance and temperature conditions.

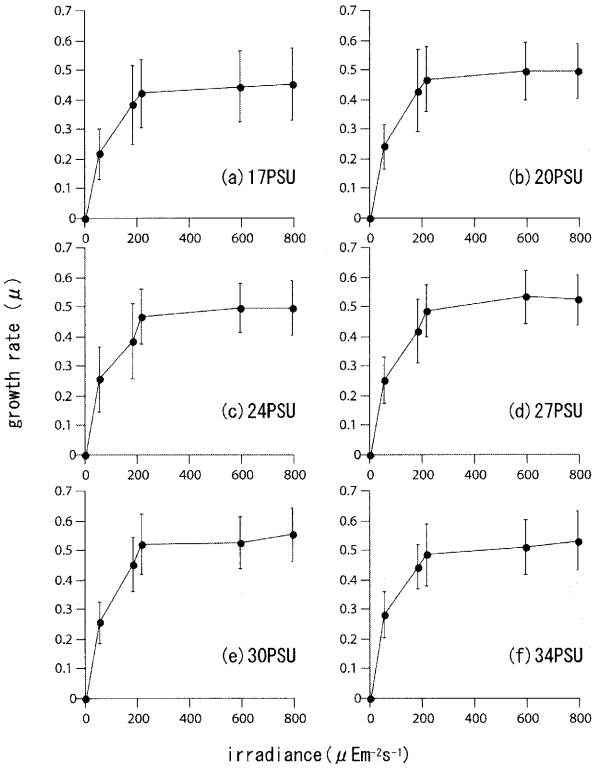

Fig. 5. Changes of growth rates of *Ceratium furca* at different irradiance and salinity conditions.

heavy rainfall, calm sunny weather, influxes of estuarine waters, or interactions between dissimilar water masses (Ryther 1955). At our sampling sites, stratification of the water column gradually developed from spring to summer. Cell numbers of *C. furca* increased near pycnoclines during the spring when the water mass was weakly stratified. Stabilized water column under the stratification formed by pycnocline will have effective function for the population growth of *C. furca* in the field.

Competition for nutrients and water temperature in the water column is often regarded as an important factor in determining phytoplankton succession. In most temperate waters, the spring bloom by diatom occurs at about the coldest part of the year. Phytoplankton assemblages show a regular successional pattern from diatom- to dinoflagellate- dominated by increasing of water temperature (Schrader 1981). Diatoms are able to grow more rapidly than other unicellular algae under high nutrient condition during spring in the temperate waters (Jitts et al. 1965, Thomas et al. 1978, Kanda et al. 2003). On the other hand, dinoflagellates may dominate with relatively high temperature under enhanced oceanographically stable conditions because they have advantages in nutrient competition by moving vertically in the water column (Thomas and Gibson 1990, Donaghay and Osborn 1997). In particular, reproduction of dinoflagellates was greatly influenced by water temperature and high temperatures over 20°C are beneficial for their remarkable growth (Nordli 1953, Dodge and Marshall 1994). In addition, diatoms have much larger K_s (half- saturation constant) values for phosphate and nitrate as compared to dinoflagellates (Qasim et al. 1973). For this reason, dinoflagellates are usually the most numerous in the low nutrient conditions and high temperature during summer season. Similarly, in this study, high abundances of dinoflagellates *C. furca* were also observed abundantly under the low nutrient concentrations and there were significant negative correlations between the density of the species and nutrient concentrations, namely nitrate+nitrite and phosphate (Table 2). Isolated stocks of *C. furca* from the natural phytoplankton assemblages were cultured successfully with T_1 medium under very low nutrients level (on molar basis nitrate≤1.0 and phosphate≤0.1) of blooming period of at the study sites. Therefore, *C. furca* could be developed under low nutrient conditions after diatom blooms.

The present result from the laboratory experiment of *C. furca* provided clues to our understanding of their physiological feature and life strategies. The growth rate of *C. furca* increased with increasing light intensity and did not largely change among all salinity treatments. Our experiments indicated that *C. furca* was able to tolerate in the wide range of salinity (17 to 34 PSU) and of temperature variation (12 to 28°C), with higher growth rates under the condition of 20–28°C (Figs. 4 and 5). Although *C. furca* is a cosmopolitan species and reported values of its optimum salinity and temperature vary greatly, Nordli (1953) reported the most

rapid growth of *C. furca* in the field conditions at 24°C and 20–25 PSU, which well agrees with the present study. Our results suggest that this species is adapted to wide ranges of temperature and salinity conditions. Compared with other phytoplankton species, *C. furca* probably have a wide adaptability for salinity range (17–34 PSU), which could be induced by large amounts of freshwater inputs by the rainfalls (>100 mm) and by the river inflow. A clear river effect on dynamics of phytoplankton biomass and production, which induced by heavy rain during spring and summer seasons, has been recorded in our research field (Satoh et al. 2000). Smalley and Coats (2002) reported that *C. furca* seemed to be restricted to >10 PSU water and was most abundant at ca. 14 PSU in the Chesapeake Bay. In Laguna de Sontecomapan, Mexico, *C. furca* was found in waters with salinities ranging from 13 to 35 PSU in the estuarine and inshore of tropical zone (Guerra- Martinez and Lara- Villa 1996). In our study site, red tides of *C. furca* and *C. fusus* were simultaneous observed in high water temperature (>24°C) and relatively low surface salinity (24 PSU) in August 2003 (Kanagawa Prefecture fishery institute, 2003). Many of coastal phytoplankton seems to be well adapted to external environmental changes. However, *Ceratium* species such as *C. furca* and *C. fusus* had fatal damage below 14 PSU in our study field (Baek 2004). These salinity adaptations may be due to different physiological tolerance to salinity, which were caused by different geographic environmental conditions such as rainfall and/or large amount of fresh water discharge into the study area. In Sagami Bay, their high reproduction was observed under the relatively low salinity condition in the summer season and they had fatal damage from very low salinity (<14 PSU). Qasim et al. (1972) suggested that *C. furca* and *Dinophysis miles* showed a wide adaptability to salinity change and their maximum photosynthesis rates occur at low salinities. Thus, drastic salinity change probably plays an important ecological factor controlling their abundance in the coastal area.

Several physical factors, such as winds, current, tidal flows, and density gradients, have been suggested to play important roles in the regulation of phytoplankton populations, which may act to concentrate phytoplankton cells in specific areas (Steidinger 1973). The populations of *C. furca* developed gradually from spring to early summer when nutrient concentrations were relatively low in our research area. Marked seasonal blooms of the species were observed from May to August during the research period of 2000–2002. However, in the year of 2003, a remarkable outbreak of *C. furca* and other *Ceratium* species such as *C. fusus* was observed from January to February, which started earliest as compared to previous three years. Since physical environmental factors (salinity, temperature and nutrients) that we measured did not change greatly between the early spring in 2003 and the previous three years (Fig. 2b–e), those factors seem not to have any important roles in breakout of the populations of these species in February 2003. Water current has been suggested as a key role in distribution of *Ceratium* species as well as water temperature (Dodge and Marshall 1994). As mentioned, the Kuroshio branch brings warm water into the Sagami Bay (Iwata 1989). In January 2003, the axis of the Kuroshio Current approached closely to the Izu peninsula in this year (Kanagawa Prefecture fishery institute 2003), which might have brought the species originated from southward region of the Pacific Ocean into Sagami Bay (Kanda 2003). Machida et al. (1999) reported that *C. furca* occurred as extensive red tides from Wakayama to Ibaraki Perfecture along the Pacific coast of central in Japan during March to July in 1997. During this red tide period, water temperature varied from 13 to 20°C, which was similar to those in this study. Therefore, relatively low temperature around 14 to 15°C in February 2003, the populations was possible to develop enough in the water columns, if the species could be introduced from out side of the bay and survive in the field conditions.

Cell numbers of *C. furca* were decreased gradually from autumn to winter season. Two possible cues of the decrease of the species could be discussed as follows: (1) breakdown of summer stratification with decreased temperature and (2) due to the shortage of photoperiod (day length) after October. Several authors suggested that water temperature clearly influenced generation time for *Ceratium* species (Nordli 1953, Elbrachter 1973, Weiler and Eppley 1979, Nielsen 1991, Dodge and Marshall 1994). Weiler and Eppley (1979) also reported that photoperiod markedly effected on cell division time of *Ceratium* species. Our results indicate that the growth rate of *C. furca* is limited below 16°C with continuous low irradiance. From the laboratory experiments, the growth rates of *C. furca* at 16°C of water temperature were estimated ca. 0.2–0.25 d^{-1}. Additionally, the species was frequently observed through the water columns during winter season of water temperature below 15°C. Although doubling time of *C. furca* in the field might be presumed to be shorter than that of the laboratory, the reduction of the field populations during this season may be due to vertical and horizontal diffusion of the population, which were induced by vertical water mixing after breakdown of stratification in the low temperature seasons.

The dinoflagellates *Cochlodinium ploykrikoides* and *Ceratium furca* have recently been recognized as dominant red tide species in the eastern Asian areas (Machida et al. 1999, Lu 2003, Lirdwitayaprasit 2003, Suh et al. 2003, Yin 2003) and the ecological damage of coastal area caused by them have more and more increased. Although toxin producing HAB species such as *Cochlodinium* and *Alexandrium* are still hazardous even in very low densities, non-toxic species such as *C. furca* with explosive break out has also high risk in the coastal management. Continuous monitoring on their field population and environmental conditions will contribute

to better understanding of the physiological responses by red tides species in early stages of bloom. Progress in the interpretation of the ecological implications of these species characters will give important information to construct and parameterize models to predict explosive breakout of HABs such as *C. furca* in the coastal area of East Asian waters.

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