Ecological behavior of the dinoflagellate *Ceratium furca* in Jangmok harbor of Jinhae Bay, Korea

SEUNG HO BAEK1*, HYEON HO SHIN1, HYUN-WOO CHOI2, SHINJI SHIMODE3, OK MYUNG HWANG1, KYOUNGSOON SHIN1 AND YOUNG-OK KIM1

1KOREA OCEAN RESEARCH AND DEVELOPMENT INSTITUTE, SOUTH SEA INSTITUTE, GEOJE 656-830, REPUBLIC OF KOREA, 2KOREA OCEAN RESEARCH AND DEVELOPMENT INSTITUTE, OCEAN DATA MANAGEMENT TEAM, PO BOX 29, ANSON, REPUBLIC OF KOREA AND 3UNIVERSITY OF TOKYO, ATMOSPHERE AND OCEAN RESEARCH INSTITUTE, CHIBA 277-8564, JAPAN

*CORRESPONDING AUTHOR: baeksh@kordi.re.kr

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The rhythmic migration pattern of the dinoflagellate *Ceratium furca* is a result of ecological adaptation to avoid high irradiance. The high proportions of dividing cells at deeper depths are likely to be an ecological response to maintain their population away from the turbulence in the near-surface layer.

**KEYWORDS:** dinoflagellate; *Ceratium furca*; migration pattern; cell division timing

*Ceratium* is a ubiquitous thecate dinoflagellate genus, slow growing, characteristically found during all seasons and contributing substantially to annual primary production in the world’s oceans (Dodge and Marshall, 1994). *Ceratium furca* is a common bloom-forming species found in coastal waters and the ecological impact caused by blooms has intensified in recent years (Machida et al., 1999). However, there is a paucity of data on ecological parameters of *C. furca* blooms in Asian coastal areas, although ecological and physiological characteristics of *Ceratium* species have been examined by Baek et al. (Baek et al., 2008a,b,c).

Most dinoflagellates have a constant vertical migration pattern and cell division timing. *Ceratium furca* is also known to perform active diel vertical migration (DVM), depending on nutrients and water temperature in both natural (Eppley et al., 1968; Edler and Olsson, 1985) and laboratory conditions (Heaney and Eppley, 1981; Olsson and Granéli, 1991). Recently, Baek et al. (Baek et al., 2009) demonstrated that *C. furca* isolated from Sagami Bay, Japan, exhibits a constant DVM rhythm based on cell division timing, suggesting that such ecological behavior can play an important role in overcoming unfavorable conditions in local environments. According to Edler and Olsson (Edler and Olsson, 1985), different species of dinoflagellates have different ecological abilities. These abilities are possibly linked with their ecological responses for surviving under local environmental conditions. However, the understanding of mechanisms such as DVM pattern and cell division remains limited. Here we investigated the ecological behavior of *C. furca* under environmental conditions in Jangmok harbor of Jinhae Bay, Korea.


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Dinoflagellate blooms usually occur during summer in the coastal areas of the southern sea of Korea (Park et al., 2001), whereas dense blooms of C. furca have not been reported so far. However, in Jangmok harbor, located in the Semi-enclosed Jinhae Bay on the northern side of Geoje Island (35°00'00"N, 128°40'00"E), of the southern sea of Korea, a widespread C. furca red tide was recorded in early summer 2009. The harbor is bounded by natural features, and a manmade structure, rectangular in shape and approximately 1 km wide and 1.5 km long with an opening of 0.5 km. The maximal tidal range in the harbor is approximately 2.2 m and the harbor water is frequently disturbed by shipping traffic. The sampling station was close to the tip of the pier of the South Sea Institute of the Korea Ocean Research and Development Institute, and the mean water depth of the sampling station was about 8.5 m. Field sampling was carried out at three-hourly intervals between 29 July 2009 and 1 August 2009 at 0, 2, 4, 6 and 8 m depths, during the C. furca bloom. In addition, to better understand DVM in relation to cell division, we collected 12 hourly samples from 03:00 to 06:00 AM, based on the experimental methodology of Baek et al. (Baek et al., 2009). During the study period, solar irradiance was also measured at 1 h intervals using a radiometer (LI-190 SA, LI-COR), and irradiance was calculated as μmol m⁻² s⁻¹.

Water samples were collected with a bucket (only for the surface layer) and with a 2 L Niskin bottle. Water temperature, salinity and fluorescence values were simultaneously measured with an Ocean Seven 319 CTD (Idronaut). Water samples for nutrient analysis were filtered through GF/F glass fiber filters. The filtered water was placed in a plastic tube and frozen. Samples were thawed at room temperature and kept in the dark for measurements. Nitrate + nitrite (NO₃⁻ + NO₂⁻), ammonium and orthophosphate (PO₄³⁻) concentrations were determined with an auto-analyzer (QUATRO Seal Analyzer, USA) using standard protocols. Total chlorophyll-α (Chl a) concentrations were obtained by filtering seawater samples from all depths. Also, sub-samples from 0, 4 and 8 m were filtered through 20 μm polycarbonate filters and Whatman GF/F glass fiber filters to analyze the Chl a concentration in a > 20 μm size fraction (mainly composed of C. furca). The volume of filtered water for Chl a analysis was 100 mL. Each filter was placed in a 20-ml brown vial and was extracted in 10-mL acetone at 4°C for 24 h. Chl a concentration was determined fluorometrically on a Turner Design fluorometer (Turner-Designs 10-AU).

The population densities of C. furca were immediately determined for each layer using a Sedgwick-Rafter chamber after samples were fixed with 1% Lugol solution. The fixed cells were enumerated separately as follow: non-dividing cells, cells undergoing nuclear division and recently divided cells (Back et al., 2009). The relative proportion of dividing cells was estimated at the different depths.

The cell division proportion at each depth in the water column was compared using the Kruskal–Wallis test. A weighted mean depth (WMD), adapted from Frost and Bollens (Frost and Bollens, 1992), was used to...
examine the diel and tidal vertical migration of *C. furca*. The WMD was calculated as follows:

\[
WMD = \frac{\left( \sum n_i d_i \right)}{\sum n_i}
\]

where \( n_i \) is cell density at depth \( d_i \), taken to be the midpoint of each stratum at each sampling time.

Water temperature in Jangmok harbor ranged from 20.1°C at the bottom to 22.8°C at the surface (Fig. 1a), and salinity showed a reverse pattern to the temperature, ranging from 29.5 to 31.1 psu (Fig. 1b). No significant stratification was observed during the field study. As reported previously, since optimum water temperature for the growth of *C. furca* ranged from 18 to 28°C and significant effects of salinity on growth were not observed (Baek et al., 2008a), the environmental conditions in the study area were considered favorable for the outbreak of blooms of *C. furca*.

There was a large temporal variation in dissolved inorganic nutrients (Fig. 1c–e) during the study period. The highest nitrate + nitrite concentrations were recorded in the surface layers at the beginning of the sampling, varying from 0.02 to 25.2 μM (Fig. 1c). The ammonium concentrations ranged from 0.7 to 6.0 μM (Fig. 1d) and the phosphate concentration was much lower, ranging from the lower limit of detection of 0.01 to 0.27 μM (Fig. 1e). The relatively high cell densities of *C. furca* (> 10 000 cells mL\(^{-1}\)) in the surface layer were observed at relatively low nutrient conditions, especially in relation to nitrate + nitrite concentrations (Figs 1c and 2). This agrees with results from Sagami Bay, where the significant increase in *C. furca* occurred during relatively poor nutrient conditions. *Ceratium furca* has a competitive advantage by adapting to low nutrient conditions through its physiological characteristics of nutrient uptake (Baek et al., 2008b).

*Centratiom furca* maintained very high densities during the study period (Fig. 2). The cells accumulated at the surface and their relative concentrations were characterized by a high time-to-time variability. Other phytoplankton groups in the samples collected were much lower in abundance, and peaks of *C. furca* cell density were significantly correlated with Chl a concentrations; the high Chl a concentrations (> 98 mg m\(^{-3}\)) are considered to be attributed to *C. furca* alone (Fig. 1f and 2). The maximum cell concentration was 10 640 cells mL\(^{-1}\) being observed at 24:00 at the surface on 1 August, while relatively high cell densities were routinely recorded at 6:00 at the surface. The cell densities at the surface seemed to decrease in higher daylight irradiance periods, especially between 09:00 and 15:00, and WMDs of *C. furca* were also deep during these periods (Fig. 3), whereas the WMDs were not correlated with the
tidal cycle \( (P > 0.05) \), indicating that vertical migration is not necessarily related to tidal condition. These results indicate that \( C. \) furca in Jangmok harbor exhibits DVM to avoid strong sunlight. Similarly, Baek et al. (Baek et al., 2008c) observed that decreases in densities of \( C. \) furca in Sagami Bay were also observed during higher daily irradiance periods and Hasle (Hasle, 1954) and Whittington et al. (Whittington et al., 2000) reported that \textit{Ceratium} species migrate downwards from the surface to avoid high-light-induced cell damage. In general, vertical migration has been suggested to be a competitive strategy for phytoplankton under conditions where light and nutrients are spatially separated (Granf and Oliver, 1982). Therefore, dinoflagellates can alter their vertical position in the water column by swimming, which allows them to maintain an optimal depth in terms of light or nutrients. Consequently, the actual duration of high irradiance in the coastal bays is considered to regulate the maintenance of the bloom.

In our previous study (Baek et al., 2009), the vertical migration of \( C. \) furca to avoid strong sunlight occurred at irradiance levels above 1000 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \). In contrast to the previous result, we observed downward migration of \( C. \) furca from the surface layer even at lower irradiance below 664 \( \mu \text{mol} \text{ m}^{-2} \text{ s}^{-1} \) on 31 July. This difference implies (i) a local adaptation of physiological response to irradiance or (ii) the DVM pattern induced by a specific endogenous rhythm. Weiler and Karl (Weiler and Karl, 1979) showed, by using a laterally illuminated culture, that the pattern of vertical migration in \( C. \) furca was not simply a passive response to diel changes in illumination and phototaxis, but rather under the control of a circadian rhythm. Thus, our result suggests the possibility that the vertical migration of \( C. \) furca is not a simple response to high light intensity and may be under the control of an endogenous rhythm. In other words, the rhythmic migration pattern of \( C. \) furca may be a combination of the endogenous rhythm and an adaptation of the population to avoid strong sunlight.

Kohata and Watanabe (Kohata and Watanabe, 1986) found that the pattern of vertical migration of \textit{Heterosigma akashiwo} is based on the cell division cycle. However, our result here shows that the cell division of \( C. \) furca occurs in the middle and bottom layers during the dense surface bloom periods (between 03:00 and 06:00), which is indicated by WMDs of the proportions of dividing cells (Fig. 3). In addition, the proportions of dividing cells had a positive correlation with depth (Table I). Consequently, \( C. \) furca divides in the deeper layer, irrespective of the DVM pattern, whereas the species moves toward the surface during the dark to light transition after cell division below the surface. The present result raises a question: why the cell division of \( C. \) furca occurs not at the surface but at deeper depth. Recently, Baek et al. (Baek et al., 2009) mentioned that the cell size of \( C. \) furca was significantly reduced during the cell division process, and those divided daughter cells seem to be

**Table I: Statistical results for proportions of Ceratium furca dividing cell collected from 03:00 to 06:00 AM during 3 days in Jinhae Bay**

<table>
<thead>
<tr>
<th>Water layer</th>
<th>N</th>
<th>Mean</th>
<th>SD</th>
<th>U</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper (0 m, 2 m)</td>
<td>18</td>
<td>9.30</td>
<td>10.41</td>
<td>120.5</td>
<td>0.0047</td>
</tr>
<tr>
<td>Lower (4 m, 6 m, 8 m)</td>
<td>27</td>
<td>25.55</td>
<td>26.37</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Significant difference in upper and lower layers values based on Mann–Whitney U-test.
weak. As shown in the pictures in the previous study (see their Fig. 2i and j in Baek et al., 2009), the dividing cells tended to be damaged by physical forces and did not show successfully growth to a normal cell-form under conditions such as shaking incubation bottles or rough pipetting into the bottles. These abnormal cells were frequently observed in laboratory conditions as a result of such physical forces (Baek, personal communication). Under field conditions, high turbulences near the surface is considered to accelerate such cell-damage, which is frequently caused by wave action and disturbance created by winds and passing ships. Margalef (Margalef, 1978) suggested that the different life-forms observed in phytoplankton are functionally interpreted as adaptations to survival in an unstable and turbulent environment. We suggest that the cell division of Ceratium furca in the deeper layer would be able to contribute to the stability in cell-division processes because the turbulence energy decreased with depth. Thus, our result suggests the possibility that Ceratium furca avoids cell division at the surface, although more field and laboratory experiments will be required to clarify the effect of wave disturbances on cell division.

In conjunction with the results of previous studies, our results have revealed the DVM and daily cell division pattern of Ceratium furca, implying an ecological advantage over other algal species under unfavorable environmental conditions such as low nutrient availability, high irradiance and wave disturbance. Such ecological abilities can play an effective role in adaptation to local environmental conditions.

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