INTRODUCTION

Tides and tidal currents have an impact on the ecosystem structure of shallow bays, basically through the grain size distribution (Guerreiro et al. 1966, Raffaelli & Hawkins 1997), thus affecting the nutrient budgets (Mohammed & Johnstone 1995, Kitheka et al. 1996). The physico-chemical properties of water column and sediments, such as temperature, salinity and oxygen conditions, are also influenced by tidal currents (Dayet 1989, Hartet et al. 1992) and therefore by tidal asymmetries and residual circulation, which influence stratification of water column, nutrient balances, and sediment loads (Wallin & Hakanson 1992, Aldridge et al. 1997, Bowers & Al-Barakati 1997, Kitheka 1997, Furukawa 1997, Hamza et al. 2007, Ben Brahim et al. 2010). In many environments, the temporal variability of phytoplankton biomass (and production) is driven by variability of physical forcing that influences vertical mixing, which in turn influences phytoplankton populations at different time scales (Cloern 1991). In fact, tidal influence on bacteria, microphytoplankton and microzooplankton abundance (Morales-Zamorano et al. 1991) and fluctuations of coastal phytoplankton were regulated by different oscillatory modes of the tidal cycle.

Moreover, variations of phytoplankton populations can result from seasonal and interannual variations in water flow (Demers et al. 1986) and from fluctuations in tidal stirring (Sinclair et al. 1981). The identification of the factors that govern the variability of phytoplankton populations are crucial to understand the mechanisms of the species bloom selection within the phytoplankton communities, particularly when this concerns the toxic phytoplankton (Smayda & Reynolds 2001). A basic knowledge of tides and tidal circulation is hence a condition in understanding the intertidal ecosystem of a shallow coast.

The Gulf of Gabès (southern coast of Tunisia), a shallow basin with bathymetry less than 50 m as far as 110 km away from the coast (200 m at 400 km), suffers from the pressure of high urbanization and industrialization rates, as well as the rapidly increasing population growth rates (Hamza-Chaffai et al. 1997, Tayibi et al. 2009). It is subject to increasing eutrophication from both red (Louati et al. 2001) and green tides caused by coastal Ulva rigida replacing the Posidonia oceanica seagrass beds (Ben Brahim et al. 2010). This area, in addition to being known among the most productive areas accounting for approximately 65 % of the country’s fish production (DGPA 2009-2012), is under an intensive anthropogenic pressure due to maritime traffic, phosphate industries, and overfishing. As a result, a decrease in fish production has continually been observed since 1990 (Hamza-Chaffai et al. 1997, 2003).

Since dinoflagellates represent a major part of the eukaryotic primary production in marine ecosystems (Parsons et al. 1984, Schnepf & Elbrachter 1992), the ability of many strains to cause shellfish poisoning and/or to form resting cysts (Wall et al. 1977, Matsuoka et al. 1983) is crucial to understanding the dynamics of dinoflagellates and food availability may be the most important factor regulating seasonal and tidal dynamics of dinoflagellate species.
2009), has led to considerable attention being paid to the diversity and distribution of planktonic dinoflagellates in relation to environmental variables including temperature, salinity, hydrodynamism and nutrients (Wallet et al. 1977, Sinclair et al. 1981). Therefore, a microalgae and biotoxin monitoring program, called the Tunisian national monitoring network of phytoplankton and phycotoxins (REPHY’), has been implemented since 1995 to ensure public safety by establishing tools for early warning of harmful algal bloom events. In this respect, the Gulf of Gabès, which is under environmental pressure (Hamza-Chaffai et al. 1997, Zairi & Rouis 1999), has experienced a substantial proliferation of microalgae and particularly toxic dinoflagellates (Turki et al. 2006). The proliferation of unwanted microalgae has been widely shown to be an increasing problem in both coastal and estuarine environments (Smayda et al. 1997, Leong et al. 2005), causing significant overfishing of demersal resources, and thus degrading benthic habitats (Turki et al. 2006).

Planktonic organisms are subject to strong tidal, diurnal, and seasonal environmental variability in marine areas (Marques et al. 2009), and knowledge of plankton dynamics at different spatial and temporal scales is important for understanding the ecosystem dynamics (Marques et al. 2009, Menéndez et al. 2011). No investigation has been conducted in Tunisia to evaluate tidal control on the nutrients status and phytoplankton community. In order to bridge the existing gap in knowledge of the biotic and abiotic features in the Gulf of Gabès, there is therefore the need to provide useful information on the tidal variations of water nutrients and dinoflagellate population of this area. This study evaluated the influence of low and high tides on nutrients, abundance, species composition, diversity, and distribution of dinoflagellate of the Gulf of Gabès. It also aimed at clarifying the mechanisms of seasonal variation of water-column nutrients and dinoflagellate dynamics, which are affected during tidal cycles in Kerkennah Islands. The tide in the Gulf of Gabès is important and semidiurnal and is the highest on the Tunisian and Mediterranean coasts (Defant 1961), tides can reach 2.3 m during spring (Serbaji 2000). They can reach 30 cm/s near the coast and about 10 cm/s offshore, which is high compared to other areas of the Mediterranean. Tidal flood currents in the Gulf of Gabès are characterized by bifurcations; a main current directs the flow to the north, and another current to the south (Sammari & Gana 1995).

We investigated, firstly, the seasonal variability of dinoflagellate abundance and distribution, and secondly the variability of dinoflagellate abundance and distribution through a tidal cycle particularly between three daily intervals.

MATERIALS AND METHODS

Study area: The station of Cercina is located in the northern Gulf of Gabès and situated on the western coast of Kerkennah Islands, with depths ranging from 3 to 5 m (Fig. 1) and influenced by regional water circulation (Ben Ismail et al. 2010, 2012). This station is directly exposed to the arrival of prevailing cold water from the channels of El Louza (north of Sfax) and warmer water from the channel between Sfax and Kerkennah. Cercina water motion was a system with a semidiurnal tide, showing horizontal displacement of water masses with a periodicity of 12 hours. The horizontal motion generates maxima in tidal current speeds and turbulent mixing with a periodicity of 6 hours. The Islands’ sea bottom morphology is highly complex, characterized by mudholes, marine tide channels and P. oceanica beds of different shapes (Hattour et al. 2010).

Sampling and laboratory procedures: This study was carried out in Kerkennah Islands in 2007. Samples were collected in the months of February, April, July and October, corresponding to the seasons winter, spring, summer and autumn, respectively. Sampling was done in the station of Cercina during 10 days successively and corresponding to spring tide. The tidal amplitude of Kerkennah is ≈ 1.60 m (CAR/ASP2009). Sampling water was collected through 3 hour intervals of the tidal cycle: flood period (T1), slack period (T2) and ebb period (T3). Environmental variables, such as salinity and temperature, were measured in the field concomitantly with phytoplankton sampling. Additionally, nutrients (ammonium, nitrite, nitrate, phosphate, silicate) were analysed in a laboratory with an auto-analyser Luebbe type. Three water sample replicates of one-litre were collected by Kuttner bottle and fixed with formaldehyde (5 %). Microalgae enumeration was performed with an inverted microscope after fixation with Lugol’s solution (final concentration 1 % v/v) and settling for 48 h using the Utermöhl method (Utermöhl 1952). Abundances were expressed in number of cells per litre of sample.

Statistical analysis: The data recorded for the dinoflagellate were submitted to PERmutational Multivariate ANalysis of Variance (PERMANOVA) (Anderson 2005) to analyses differences in abundance between seasons and between the three time intervals of the tidal cycle. PERMANOVA gives the permutation

![Fig. 1. – Map of the study area showing the sampling stations in Cercina.](image-url)
P-value for each test it performs. Data were transformed where necessary to meet the assumption of homogeneity of variances (homogeneity confirmed by non-significant Cochran’s c-test). Student-Newman-Keuls (SNK) test was employed for a posteriori multiple comparisons of means. SIMilarity PERcentage analysis (SIMPER) was used seasonally to identify the contribution of individual species with the pattern of similarity and dissimilarity between the different tidal periods. To link species variability to environmental variables, Pearson’s correlation was applied to physical (temperature and salinity) and chemical (NO$_3^-$, NO$_2^-$, NH$_4^+$, PO$_4^{3-}$, NT, PT and Si(OH)$_4$) variables.

RESULTS

Environmental conditions

The highest value of temperature (27.56 °C) was recorded in summer on the slack period (T2), while the lowest (14.71 °C) in autumn on the ebb period (Fig. 2). Temperature and salinity varied significantly from season to season (ANOVA$_{temperature}$, F = 157.33, n = 36, p < 0.05; ANOVA$_{salinity}$, F = 8.75, n = 36, p < 0.05). Water salinity varied from 42.13 in summer on the ebb period to 35.09 gl$^{-1}$ in spring during the flood period, and showed
an increase in summer and autumn with a remarkable decrease in winter and spring. No significant difference in salinity was detected between the three tidal periods for all seasons, whereas concerning temperature a significant difference was detected only in winter (Table I).

The nitrite (NO$_2^-$) fluctuated between seasons (ANOVA, $F = 13.48$, $n = 36$, $p < 0.05$) and concentrations ranged between 0.67 µmol l$^{-1}$ in spring to 0.04 µmol l$^{-1}$ in winter. A significant difference was detected between the three tidal periods and the SNK test revealed that the concentrations were high mainly during the slack and the ebb periods for all seasons (Table I). The nitrate (NO$_3^-$) also varied significantly between seasons (ANOVA, $F = 10.73$, $n = 36$, $p < 0.05$) and the highest concentration (1.31 µmol l$^{-1}$) was recorded in summer, while the lowest concentration (0.43 µmol l$^{-1}$) was detected in winter. A significant difference was found between the three tidal periods in winter, spring and summer, where the highest concentration was revealed in the slack and the ebb period. Orthophosphate differed between seasons (ANOVA, $F = 33.17$, $n = 36$, $p < 0.05$) and the highest concentration was recorded in summer (2.03 µmol l$^{-1}$). A significant difference was detected between the three tidal periods only in summer and autumn, where the high concentrations were recorded in the slack and the ebb period. Ammonium concentration varied between seasons (ANOVA, $F = 3.85$, $n = 36$, $p < 0.05$) and the highest concentration was recorded in autumn (8.79 µmol l$^{-1}$). A significant difference was recorded between the tidal periods in winter, spring and autumn, where the highest concentration was observed on the slack and ebb periods. Silicate concentrations fluctuated between seasons (ANOVA, $F = 4.43$, $n = 36$, $p < 0.05$). The concentrations were high in autumn and low in winter, spring and summer. A significant difference was detected between the tidal periods only in autumn and the high concentrations were recorded on the slack and ebb periods.

**Plankton communities**

A specific inventory permitted to identify 64 dinoflagellates in the study area (Table II). The mean abundance of dinoflagellates fluctuated between seasons and showed a significant seasonal variability (ANOVA, $F = 17.67$, $n = 240$, $p < 0.05$). Total dinoflagellate abundances ranged from 5600.20 ± 742.11 cell l$^{-1}$ in spring to 495.90 ± 168.43 cell l$^{-1}$ in winter, showing a remarkable increase in spring and summer (Fig. 3). For each season, significant differences were detected between the three tidal periods (Table III). For all seasons, the abundance of dinoflagellate was high in the slack period (T2).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Salinity</th>
<th>Temperature</th>
<th>NO$_2$</th>
<th>NO$_3$</th>
<th>PO$_4$</th>
<th>Si(OH)$_2$</th>
<th>NH$_4^+$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
<td>F</td>
<td>MS</td>
</tr>
<tr>
<td>a. Winter</td>
<td></td>
<td>Time</td>
<td>0.072</td>
<td>0.097</td>
<td>13.50</td>
<td>0.034</td>
<td>5.92*</td>
<td>1.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual</td>
<td>0.75</td>
<td>1.05</td>
<td>0.01</td>
<td>0.16</td>
<td>0.02</td>
<td>1.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SNK test</td>
<td>T1 &gt; T2 = T3</td>
<td>T1 = T2 &lt; T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td></td>
</tr>
<tr>
<td>b. Spring</td>
<td></td>
<td>Time</td>
<td>15.64</td>
<td>0.16</td>
<td>44.27</td>
<td>0.67</td>
<td>4.61*</td>
<td>1.79</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual</td>
<td>95.87</td>
<td>66.33</td>
<td>0.36</td>
<td>0.42</td>
<td>3.48</td>
<td>1.67</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SNK test</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td></td>
</tr>
<tr>
<td>c. Summer</td>
<td></td>
<td>Time</td>
<td>2.93</td>
<td>1.73</td>
<td>6.55</td>
<td>1.69</td>
<td>5.37*</td>
<td>2.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual</td>
<td>1.69</td>
<td>3.86</td>
<td>0.04</td>
<td>0.26</td>
<td>0.04</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SNK test</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td></td>
</tr>
<tr>
<td>d. Autumn</td>
<td></td>
<td>Time</td>
<td>0.02</td>
<td>0.17</td>
<td>0.07</td>
<td>0.15</td>
<td>3.82*</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Residual</td>
<td>0.11</td>
<td>0.50</td>
<td>0.02</td>
<td>0.19</td>
<td>0.02</td>
<td>4.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>SNK test</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td>T1 &lt; T2 = T3</td>
<td></td>
</tr>
</tbody>
</table>
The main dinoflagellate species contributing repeatedly in tidal period dissimilarity are illustrated in Table IV. The SIMPER test revealed an average dissimilarity among tidal periods for dinoflagellate communities, which are relatively high during spring and summer while dissimilarity is low in autumn and winter (ANOVA, $F = 31.89$, $n = 8$, $p < 0.05$) (Table IV).

Figure 4 shows a noteworthy increase of the main dinoflagellate species abundance on the slack and the ebb periods in each season. *Polykrikos kofoidii* showed a
remarkable abundance mainly in the slack period, whereas *Peridinium* sp., *Prorocentrum micans* and *Prorocentrum gracile* showed a notable increase in the ebb period. We noted also an increase of dinoflagellates on the slack period particularly in spring, summer and autumn.

The principal component analysis (PCA) showed a clear correlation between dinoflagellates and nutrients (Fig. 5). The first axis (with 36.37% of variability) showed a positive correlation between dinoflagellate, temperature, nitrite (no2-), nitrate (no3-) and phosphate (Po43-), while negative correlation was found between dinoflagellate, ammonium (nH4+) and silicate (Si(OH)4). The second axis (with 17.39% of variability) showed a correlation of dinoflagellates mainly with nitrite, nitrate and phosphate.

**DISCUSSION**

Our investigation demonstrated a seasonal distribution of the dinoflagellate species related to the tide regime and also to the physico-chemical variables in the Kerkennah Islands. The data-base was performed in order to collect sufficient information related to the dinoflagellate dynamics for the two temporal scales: season and tidal period.

**Table III.** – ANOVA results of seasonal variation effect of dinoflagellates on the three tidal periods (T1 = flood period, T2 = slack period, T3 = ebb period). Bold numbers indicate significant effects.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tidal period</td>
<td>df 2</td>
<td>MS 74.31</td>
<td>F 12.92</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>64.67</td>
<td>8.80</td>
<td>0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>24.63</td>
<td>4.75</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td></td>
<td>38.80</td>
<td>5.82</td>
<td>0.012</td>
</tr>
<tr>
<td>Residual</td>
<td>27</td>
<td>5.75</td>
<td>7.34</td>
<td>5.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.67</td>
</tr>
<tr>
<td>Cochran’s C-test</td>
<td>C = 0.820; p &lt; 0.05</td>
<td>C = 0.539; p &lt; 0.05</td>
<td>C = 0.610; p &lt; 0.05</td>
<td>C = 0.512; p &lt; 0.05</td>
</tr>
<tr>
<td>Transformation</td>
<td>Ln(x+1)</td>
<td>Ln(x+1)</td>
<td>Ln(x+1)</td>
<td>Ln(x+1)</td>
</tr>
<tr>
<td>SNK test</td>
<td>T1 &lt; T2 = T3</td>
<td>T2 &gt; T1 &gt; T3</td>
<td>T2 &gt; T1 = T3</td>
<td>T2 &gt; T1 = T3</td>
</tr>
</tbody>
</table>

**Table IV.** – Summary of the main species contributing to the dissimilarity on the three tidal periods and for each season.

<table>
<thead>
<tr>
<th>Season</th>
<th>Period</th>
<th>Av. dissimilarity</th>
<th>Average dissimilarity of the main species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Flood vs slack period</td>
<td>58.18 %</td>
<td>Polykrikos kofoidii (12.54%), Protoperidinum sp. (3.68%), Peridinium sp. (3.50%), Alexandrium sp. (3.46%)</td>
</tr>
<tr>
<td></td>
<td>Ebb vs slack period</td>
<td>57.98 %</td>
<td>Peridinium sp. (14.11%), Polykrikos kofoidii (5.91%), Protocentrum micans (4.05%)</td>
</tr>
<tr>
<td></td>
<td>Flood vs ebb period</td>
<td>66.17 %</td>
<td>Peridinium sp. (17.14%), Polykrikos kofoidii (6.38%)</td>
</tr>
<tr>
<td>Spring</td>
<td>Flood vs slack period</td>
<td>80.05 %</td>
<td>Peridinium sp. (16.78%), Protoperidinum grani (14.23%), Protoperidinum sp. (7.44%), Karenia akashiwa (4.15%)</td>
</tr>
<tr>
<td></td>
<td>Ebb vs slack period</td>
<td>79.87 %</td>
<td>Peridinium sp. (18.93%), Polykrikos kofoidii (8.72%), Protocentrum micans (4.28%)</td>
</tr>
<tr>
<td></td>
<td>Flood vs ebb period</td>
<td>80.73%</td>
<td>Protoperidinum grani (17.63%), Protoperidinum sp. (7.43%), Peridinium sp. (6.50%), Karenia akashiwa (5.94%)</td>
</tr>
<tr>
<td>Summer</td>
<td>Flood vs slack period</td>
<td>78.13%</td>
<td>Oxyphysis marina (6.34%), Alexandrium sp. (5.78%), Scripsiella trochoidea (5.68%), Polykrikos kofoidii (4.32%), Protocentrum micans (4.10%)</td>
</tr>
<tr>
<td></td>
<td>Ebb vs slack period</td>
<td>83.71%</td>
<td>Scripsiella trochoidea (6.10%), Oxyphysis marina (5.91%), Ostreopsis ovata (4.78%), Protocentrum micans (4.52%), Polykrikos kofoidii (4.21%)</td>
</tr>
<tr>
<td></td>
<td>Flood vs ebb period</td>
<td>83.22%</td>
<td>Alexandrium sp. (5.71%), Protocentrum gracile (4.59%), Polykrikos kofoidii (4.43%), Protocentrum micans (4.36%), Peridinium sp. (4.29%)</td>
</tr>
<tr>
<td>Autumn</td>
<td>Flood vs slack period</td>
<td>59.86 %</td>
<td>Protocentrum micans (6.78%), Peridinium sp. (7.71%), Scripsiella trochoidea (6.03%), Alexandrium sp. (6.45%)</td>
</tr>
<tr>
<td></td>
<td>Ebb vs Slack period</td>
<td>66.16%</td>
<td>Protocentrum micans (8.34%), Peridinium sp. (7.98%), Scripsiella trochoidea (6.84%), Alexandrium sp. (6.38%)</td>
</tr>
<tr>
<td></td>
<td>Flood vs ebb period</td>
<td>65.81%</td>
<td>Protocentrum micans (8.16%), Scripsiella trochoidea (6.73%), Polykrikos kofoidii (6.70%)</td>
</tr>
</tbody>
</table>
We found: first, a high abundance of dinoflagellates in spring and summer with maximum abundance occurring in spring and, second, a high abundance of dinoflagellates in the slack period (T2).

Seasonal variation

The distribution of dinoflagellate species in the study area is affected by the variations of physico-chemical variables that in turn are governed by the seasonal dynamics (Alkawri & Ramaiah 2010, Feki-Sahnoun et al. 2014).

The seasonal variability in our study area is largely due to the variation of abiotic factors, since nutrients have been known for controlling the dinoflagellate community structure and biomass (Raymont 1982, Tilman 1988, Gouda & Panigrahy 1996, Sawant et al. 2007). The abundance of dinoflagellates in spring may be triggered by improved light conditions due to a combination of enhanced solar radiation and an increase in nutrients. Similar observations have been reported in previous studies made in other coastal waters (May et al. 2003, Tian et al. 2009, Blauw et al. 2010, 2012). Highest dinoflagellate abundances in spring were associated with an increase in NO$_2^-$, NO$_3^-$, PO$_4^{3-}$, NH$_4^+$ and temperature. The decrease in dinoflagellate abundances during summer may result from rapid depletion of inorganic nutrients. Later in spring and early summer, regenerated silicate appears to stimulate diatom production, concurrent with a developing dinoflagellate population (Kemper 2000, Townsends & Thomas 2002).

Dinoflagellates are generally considered slow growers with a low maximum uptake capacity for dissolved inorganic nutrients (Smyda 1997), which makes them inferior competitors in situations where nutrients are plentiful. Dissolved inorganic nitrogen (nitrate plus nitrite), on the other hand, also eventually runs down, becoming depleted to levels that limit all dinoflagellates growth (Draxler et al. 1985, Horne et al. 1996, Townsend & Thomas 2002).

The fact that nutrients have the greatest influence on dinoflagellate abundance in our study area is clear from the strong positive correlation between their abundance and nitrite, silicate as well as phosphate. It is thus inferable that the wide variation in the abundance of dinoflagellates on an annual scale is largely due to variations in nutrient concentrations.
High temperature and salinity are favourable also for dinoflagellates growth (Bouman et al. 2005, Batlow et al. 2007). Moreover, the change in salinity, pH, nitrogen and phosphate causes variations in their abundance and composition (Yoo 1991). Davies & Ugwumba (2013) revealed that ammonia (NH₃) is one of the nutrients required by phytoplankton for primary productivity. Other nutrients are nitrate, phosphorus, and sulphate. Ammonia is a source of nitrogen and contributes to the fertility of water since nitrogen is an essential plant nutrient. Similar observations were made by Drira et al. (2008) in the same area (Gulf of Gabès, Tunisia) where the high concentration of dinoflagellates may be ascribed to nitrogen inputs in the coastal waters of Gabès. In addition, the phytoplankton density was dependent on nutrient availability (nitrate, nitrite, ammonium, orthophosphates, Total-N, Total-P) and especially on N/P ratios, which seemed to be the deterministic regulator of dinoflagellate dynamics.

Tidal period variation

Environmental forcing by the tidal cycle is an important driver of dinoflagellate variability in Cercina; in fact, dinoflagellate biomass in our study area exhibits variability at small temporal scales over the tidal period. Our results revealed dinoflagellate concentration fluctuations correlated with different tidal periods, and thus with horizontal transport of different water masses. Dinoflagellate concentrations consistently peaked on slack water tide (T2) when the depth reached its maximum, coinciding with the increase in nutrient supply of suspended particulate matter during water motion. Indeed, the abundance of dinoflagellates changes under different tidal conditions, in time scales of hours resulting in a patchy distribution. For example, in spring, dinoflagellate abundance changed in a matter of three hours from < 2000 to > 5000 cell l⁻¹. This notable patchiness may be explained by the strong tidal dynamics. The same result was revealed by Gracia-Escobar et al. (2014) in San Quintín Bay on the Pacific coast of Baja California, Mexico, where diatoms and dinoflagellate abundance changed in a matter of two hours from < 100 to > 800 cell l⁻¹. The same authors revealed also that filamentous cyanobacteria were occasionally present in high numbers (up to 9600 cell l⁻¹) coinciding with the ebbing tide. They attributed the phytoplankton patchiness to the strong tidal conditions.

Besides, the turbidity maximum appears as a transient phenomenon related to tidal currents, dissipating rapidly by sedimentation during current slacks. In fact, turbulence generated by tidal current was the primary control over the transport and distribution of sediments and nutrients in field environments (Anderson & Charters 1982, French et al. 1993).

The results of our statistical analyses indicated that dinoflagellate composition in Kerkennah Islands was strongly affected by tides, and change was significant under the contrasting tidal periods. Our results revealed also that dinoflagellate concentrations decreased during flood and ebb periods (T1 and T3). This timing suggests that microalgae decrease is generated by enhanced tidal mixing due to high current speeds. Thomas & Gibson (1990) showed that turbulence promotes water-column mixing, affecting the amount of stratification, increasing vertical mixing and decreasing the average light field for photosynthetic organisms, and affecting the distribution of nutrients. Ault (2000) demonstrated similar patterns of daily variation for Prorocentrum triestinum, which manifest a diurnal cycle migration. Cell densities of P. triestinum in the water column were high at 0.5 m depth and varied in accordance with photosynthetic yield at a temporal scale of 3 hours. Moreover, turbulence generated by high current tides could be highly significant to dinoflagellate motility by affecting cell trajectories. Our results were in agreement with those of Lauria et al. (1999), which revealed that stability within the water column during slack water periods permits surface aggregation of dinoflagellates, which become homogeneously distributed when turbulence intensifies during ebb and flood currents. The authors found that motile dinoflagellates (Prorocentrum micans and Peridinium trochoideum) aggregated near the water surface during slack water, while they became homogeneously distributed when tidal mixing intensified. Our study agreed with this finding since the highest abundance of Prorocentrum micans and Peridinium sp. was registered mainly during the slack period. The low abundance of dinoflagellate on flood (T1) and ebb (T3) periods and their peak on the slack period (T2), as shown in our results, was observed by Trigueros & Orive (2000) in the Urdaibai estuary (North of Spain) where, to sustain viable populations in shallow, tidally-driven estuaries, phytoplankton organisms have to display swimming strategies to avoid being massively advected by the tidal currents. Given the different swimming and displacement abilities of the different components of the phytoplankton, some flagellates migrate vertically to maintain their populations in an optimal environment. Therefore, this ability to swim actively could give dinoflagellates competitive advantages in terms of net growth rate (Villarino et al. 1995).

<table>
<thead>
<tr>
<th>Correlation coefficient</th>
<th>-0.098</th>
<th>0.636</th>
<th>0.664</th>
<th>-0.622</th>
<th>0.406</th>
<th>0.112</th>
<th>0.685</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>Temperature</td>
<td>NO₂⁻</td>
<td>Si(OH)₄</td>
<td>NO₃⁻</td>
<td>NH₄⁺</td>
<td>PO₄³⁻</td>
<td></td>
</tr>
</tbody>
</table>

| Significance | 0.762 | **0.026** | 0.018 | **0.031** | 0.191 | 0.729 | **0.014** |
The high abundance of the heterotrophic *Polykrikos kofoidii* on the slack period may be explained by its food preference for *Karenia catenata*, suggesting a mechanism of “biocontrol” between these species that may contribute to attenuate a potentially toxic phenomenon under natural conditions (Rodríguez et al. 2005).

Jeong et al. (2010) stated that the mixotrophic Scrippsilla trochoidea is one of the nutrients required by the genus *Polykrikos*, thus the high abundance of *Polykrikos kofoidii* in summer may be related to the high abundance of its favorite prey *Scrippsilla trochoidea*. A study conducted by Davies & Ugwumba (2013) in the Upper Bonny Estu-}

A possible explanation of the increase of *Oxyrrhis marina* in summer during the slack period is the nutrient supply driven by current tide and resuspension by tidal mixing during spring tide. Response of this heterotrophic dinoflagellate feeding on pico-sized prey such as bacterium cell by generating feeding currents using the flagella may be related and favoured by nutrient availability especially the abundance of *Amphidinium carterae*, *Karldinium veneficum* and *Prorocentrum minimum* (Jeong et al. 2010).

Abundance of the mixotrophic *Alexandrium minutum* may be due to its ability to kill potential predators, as has been proven by the finding showing its allelopathy through inhibitory effects on other phytoplankton taxa (Tillmann & John 2002, Lelong et al. 2011), and its toxin production, which is stimulated by water movements and its mixotrophy (Zubkov & Tarran 2008). In addition, abundance may be correlated to nitrogen and phosphorus forms availability (Collos et al. 2007, Abdenadher et al. 2012, Pereira et al. 2012). *Protoperdinium* population dynamics were governed by food availability and likely to be diatom grazers. Olsen et al. (2002) previously showed that *Protoperdinium* population was supported by the bloom of diatoms in autumn in Norway. In contrast, the high abundance of *Protoperdinium granii* in spring in our region was the probable cause of increase in diatoms. In fact, food availability is more important than physical variables (for instance temperature) in regulating population growth in these microplankton grazers (Kjøret et al. 2000).

Finally, different physical forcings, such as tide and current tides, apparently influence dinoflagellate populations in terms of species composition at different time scales in Kerkennah Islands. Tidal influence on dinoflagellate parameters was significant. The high abundance of dinoflagellates was recorded in the slack water period (T2) coinciding with the increase of nutrient supply of suspended particulate matter during water motion, whereas the low abundances were recorded in high tides T1 and T2. To the best of our knowledge, our study took an initial step in our region toward understanding the effects of tide flows on abundance behavior of dinoflagellates. The combination tide and phytoplankton distribution and species composition with other abiotic conditions in future experiments would add further knowledge to the understanding of the role of turbulence in the migratory behavior of dinoflagellates. Variation of dinoflagellate abundance during different tidal periods may not be related only to physical oceanographic conditions. Concentrations of some dinoflagellate species were not related to those of any particular abiotic variables, since we found the same species in every sample throughout the year and interactions between grazers and their preys were among the main factors responsible for the structuring of the dinoflagellate food web. Tides had varied effects on the nutrient status and phytoplankton community (in terms of species composition, diversity, abundance, and distribution). However, abiotic variables were not the only factors governing the dynamics of dinoflagellates.

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