Diel vertical migration of *Peridiniopsis niei*, Liu et al., a new species of dinoflagellates in an eutrophic bay of Three-Gorge Reservoir, China

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Abstract In spring, a typical dinoflagellate (*Peridiniopsis niei* Liu et al.) constitutes most of the phytoplankton biomass in most of eutrophic bay of Three-Gorge Reservoir (TGR, China). There are few field observations on vertical migration of the members of the genus *Peridiniopsis*. We studied diel vertical migration of the new species (*Peridiniopsis niei*) at sampling stations A and B in an eutrophic bay (Xiangxi Bay) of TGR during both day and night in March 2007. The present study suggests that vertical migration by *Peridiniopsis niei* is similar in nature to the migration patterns observed for other dinoflagellates. Solar irradiance incident was an important factor regulating the ascent and descent of *Peridiniopsis niei*. The vertical descent of *Peridiniopsis niei* during nighttime was restricted when the thermocline (Temperature gradient $>1°C \cdot m^{-1}$) was present in the station B.

Keywords Diel vertical migration · Dinoflagellate · Thermocline · Incident solar radiation · Nutrient · Stratification

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Introduction

Dinoflagellates are a diverse group of unicellular or colonial eukaryotic microorganisms, which are characterized by regulated motility combined with an ability to photosynthesize (Clegg et al. 2007). As an important functional component of the phytoplankton community, most of the dinoflagellates are capable of using their weak swimming abilities to perform diel vertical migration (DVM), which is a widespread phenomenon in both marine and freshwater habitats, and it has been the focus of most migration studies (Salonen and Rosenberg 2000; Beckmann and Hense 2004; Townsend et al. 2005; Doblin et al. 2006; Yamamoto and Nakahara 2006). In general, DVM behavior is known to facilitate the cells acquiring both high light and high nutrient levels, by maintaining near surface distributions by day and near pycnocline and nutricline depths by night (Ralston et al. 2007; Ross and Sharples 2008). Advantages of DVM behavior can be used to explain the dominance of dinoflagellates in marine and freshwater ecosystem (Salonen and Rosenberg 2000; Clegg et al. 2004; Townsend et al. 2005; Doblin et al. 2006). Most of dinoflagellates with high light and high nutrient affinities frequently become the principal contributor to harmful algal blooms and red tides (Erga et al. 2003; Bearon et al. 2006). Knowledge of DVM is of fundamental importance in explaining dinoflagellates bloom in marine and freshwater habitats and understanding the ecology of dinoflagellates.

In general, variations in DVM behavior of dino-flagellates have been attributed to a large number of driving factors such as light (Kessler et al. 1992; Clegg et al. 2003b), temperature stratification(Clegg et al. 2003a), chemical gradients (Lee et al. 1999; Clegg et al. 2004; Doblin et al. 2006) and salinity (Erga et al. 2003; Clegg et al. 2007). The relative importance and interplay of the various factors that can potentially affect DVM behavior of dinoflagellates show much variation, because aquatic ecosystems, such as ocean, estuaries, bays, lake and reservoirs are very diverse. For example, Erga et al. (2003) concluded that strong haloclines in fjords and coastal waters can prevent phytoplankton flagellates (*Tetraselmis* sp.) in the surface layer from reaching the nutrient-rich deeper layer during the night and therefore play an important regulating role in the bloom dynamics of phytoplankton. In freshwater ecosystems, temperature is the main governing factor with respect to the density of freshwater, and thermocline is the main contributor to the stratification of these waters. Behavioral response of dinoflagellates to temperature gradient has been demonstrated for many phytoplankton flagellates both in situ and/or in experimental columns (Clegg et al. 2003a, 2007). The occurrence of dinoflagellates during temperature stratification is considered to be a result of their ability to conduct DVM down below the thermocline to satisfy their nutrient demand, but some studies (e g., Doblin et al. 2006) also found that cells of flagellates in nutrient-replete columns showed no vertical migration, but they were more dispersed in the upper layer during the dark compared to the light period. However, the knowledge about these aspects remains unknown in most of freshwaters in subtropical and tropical regions, especially from China. Obviously, field observation on DVM phenomenon in those waters is not only of local interest, but relevant for the understanding of DVM behavior of dinoflagellates.

Three-Gorges Reservoir (TGR) located in the mainstream of the Yangtze River (China), is one of the largest man-made lakes in the world, with capacity of 3.93×10^{10} m^3, water level of 175 m, surface area of 1,080 km^2 and watershed area of over 1.00×10^6 km^2 (Wang et al. 1997; Huang et al. 2006). The reservoir includes forty large reservoir-bays (watershed area of each bay >100 km^2), and the surface area of these bays accounts for one-third of the total surface area of the TGR (Cai and Hu 2006; Huang et al. 2006). Based on the estimated residence time, the mainstream

of TGR was still a fully mixed system, and most of the TGR bays may be characterized by well developed stratification (Zheng et al. 2006). Surprisingly, phytoplankton spring blooms often occurred in most reservoir-bays, but there have been no algal blooms reported until now in the main TGR after the reservoir became operational (Cai and Hu 2006). As a new species of freshwater dinoflagellates from China, *Peridiniopsis niei* Liu et al. is often found to bloom during spring in large numbers and color the water brown in the reservoir-bays of the Three-Gorges Reservoir (TGR), China (Cai and Hu 2006; Liu et al. 2008). Theoretically, the typical dinoflagellate *Peridiniopsis niei* with the characteristic of vegetative free-swimming cells, should exhibit active vertical movements in water column, but there is no evidence for DVM behavior of this species from field observation until now. Interspecies differences among dinoflagellates can lead to very different vertical migration strategies and different cell distributions in the water column (Ralston et al. 2007). Field monitoring is thus necessary to understand DVM behavior of *Peridiniopsis niei*.

Xiangxi Bay can be considered as representative of most eutrophic bays of the TGR (Cai and Hu 2006). Monthly monitoring over 2 years revealed mean concentrations of total nitrogen and total phosphorus in Xiangxi Bay of 1.29 mg N L^{-1} and 0.153 mg P L^{-1}, respectively (Cao et al. 2006). Dinoflagellate bloom frequently occurred during warming spring in Xiangxi Bay. The important questions are does *Peridiniopsis niei* perform DVM in the nutrient-rich waters of the bays and does it penetrate the thermocline in the dark? In order to gain a preliminary understanding of the ecology of the organism, we carried out two field observations on vertical distributions of the dominant dinoflagellates (*Peridiniopsis niei*) and their controlling factors during spring of the year 2007 in Xiangxi Bay. The main purpose of paper is to firstly present the results of field observations on diel vertical migration of the new species (*Peridiniopsis niei*) and discuss whether this dinoflagellate perform vertical migrations to the deep nutrient reservoir during the dark periods.

Materials and methods

The field observations were carried out at two sampling stations (A and B) of Xiangxi Bay (Fig. 1). The water

samples for phytoplankton were collected at 2 h intervals during daytime and at 4 h intervals at nighttime using a 5 L Van Dorn sampler. The samples from the station A with ca. 8.5 m depth, at 2 m intervals in water column, and that from the station B with ca. 21 m depth at 2 m intervals in upper water layers (0–6 m) and 5 m intervals in deeper water layers (10–20 m) were taken. The water samples were preserved in situ with standard Lugol's solution in 1.5 L clean plastic bottles. Those samples were concentrated to 30 mL of quantitative subsamples using sedimentation method (Zhang and Huang 1991; Huang et al. 1999). The phytoplankton cells were counted in a Fuchs-Rosenthal counting chamber under an Olympus microscope at $400\times$ magnification. The results were expressed as the number of cells L^{-1}. Water samples for inorganic nutrient (nitrate nitrogen and phosphate phosphorus) were collected in a 300-mL cleaned plastic bottle and were acidified in situ with sulfuric acid. Inorganic nutrients were measured using standard protocols for aquatic ecosystems (Cai 2007). Water temperature (WT) profiles were in situ measured at 1 m intervals along the water column, using a water quality monitoring system (YSI6600EDS, USA), and solar irradiance incident upon water surface (SI, $\mu mol\ s^{-1}$) was obtained from an quantum sensor (Li-192SA, USA). Thermocline depth was defined as the depth where maximum temperature gradient is greater than or equal to $1°C$ per meter (Thackeray et al. 2006; USGS 2008).

The established single-sample index of dispersion (Morisita's index, MI) was chosen to determine dispersion patterns for dinoflagellate population in water column, as it is independent of both the sample mean and the total number of organisms found in the sample (Thackeray et al. 2006). The index was calculated as:

$$MI = n \times \left(\sum X_i^2 - \sum X_i \right) \Big/ \left(\left(\sum X_i \right)^2 - \sum X_i \right)$$

where X_i is the number of individuals in a given sampling unit (i), and n is the number of sampling units. An index value <1 indicates a uniform distribution, a value >1 indicates an aggregated distribution, and a value $= 1$ indicates a random distribution (Thackeray et al. 2006). Although useful for quantifying the degree of aggregation in biological populations, dispersion indices do not provide any information on the habitat depth of organism. For this reason, the mean residence depth (MRD) is often employed to quantify the average depth of vertical distribution for algal population (Armengol and Miracle 2000; Bezerra-Neto and Pinto-Coelho 2007). The MRD value is calculated according to the equation:

$$MRD = \frac{\sum X_i D_i}{\sum X_i}$$

where X_i is the number of individuals in a given sampling unit (i), and D_i is the depth of sampling units. For testing differences in the vertical distribution of

Fig. 1 Location of sampling sites in Xiangxi Bay of Three-Gorges Reservoir, China
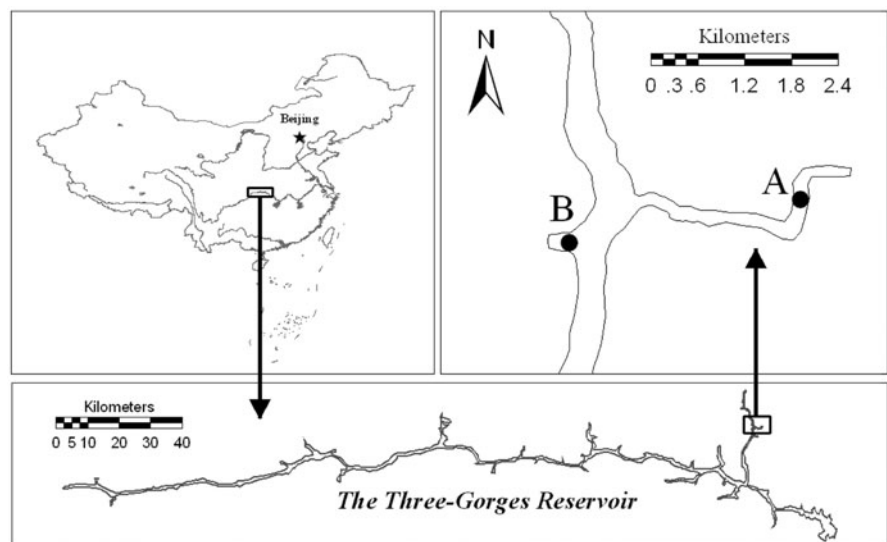
phytoplankton between sampling times, we applied a modified two-sample Kolmogorov–Smirnov test (K–S test) (Solow et al. 2000). Significance levels were estimated by running 1,000 randomizations and calculating the proportion of simulated values greater than the observed value (Zhou et al. 2007). The DVM behavior is determined by significant difference of vertical distribution between daytime and nighttime (Bezerra-Neto and Pinto-Coelho 2007). MI–SI and MRD–SI relationships were derived using linear least squares regression to test the hypothesis that algal populations will become more aggregated in shallower depth with increase in solar irradiance. Prior to analysis, all solar irradiance data were $\log_{10} (X + 1)$ transformed to ensure their homogeneity of variance. Regression analysis was carried out using the software SPSS 13.0.

Results

Solar irradiance incident upon water surface varied greatly in the same trend during the sampling periods, and there were no significant diel differences between both sampling stations (K–S test, $P > 0.05$, Fig. 2). Solar irradiance was at its minimum at early morning, increasing steadily to ca. 1,300 μmol s^{-1} by noon and declined gradually to zero until night (Fig. 2). Water temperature of the A station ranged from 11.26 to 13.87°C, with mean and median values of 12.07 and 11.94°C, respectively, and that of the B station ranged between 11.63 and 15.85°C, with mean and median

values of 12.62 and 12.13°C, respectively. A striking feature of the B station was that maximum temperature gradients at 2200 and 200 hours exceeded 1°C m^{-1} at the depth of 6.9–7.9 m and 5.9–6.9 m, respectively (Fig. 3), while the A station had not maximum temperature gradients >1°C m^{-1} during the 24-h sampling period. The substantial difference between two stations was thus the occurrence of thermocline during nighttime in the B station, but it did not during daytime. Concentrations of DIN in the A and B station varied from 542 to 744 μg L^{-1} and 659 to 1,370 μg L^{-1}, respectively, while that of DIP in the A and B station ranged from 25 to 52 μg L^{-1} and 31 to 206 μg L^{-1}, respectively. For the B station, the concentrations of nutrients above thermocline were obvious higher than that below thermocline (Fig. 4).

Algal cell concentrations varied substantially during the observation period and ranged from 0.79×10^6 to 20.2×10^6 cells L^{-1} and 0.17×10^6 to 58.0×10^6 cells L^{-1} in the A and B station, respectively. *Peridiniopsis niei* was the dominant dinoflagellates and accounted for 93.4 and 87.3% of the total abundance in the A and B station, respectively. The total cell number of the dinoflagellates population in the water column of the A station ranged from 14.5×10^6 to 52.5×10^6 cells L^{-1}, with mean and median values of 25.7×10^6 cells L^{-1} and 25.2×10^6 cells L^{-1}, respectively, and that of the B station ranged between 8.7×10^6 and 131.6×10^6 cells L^{-1}, with mean and median values of 42.3×10^6 and 14.8×10^6 cells L^{-1}, respectively (Fig. 3).


Fig. 2 Diel patterns of solar irradiance (SI) during the sampling periods
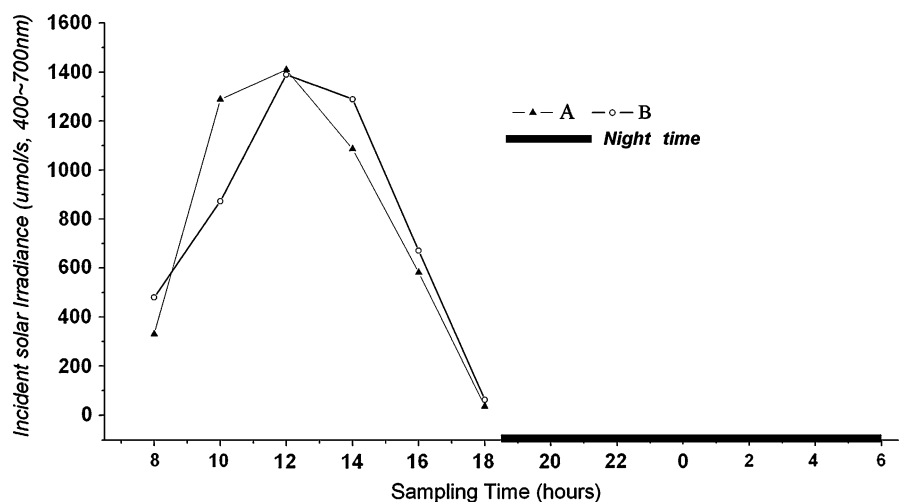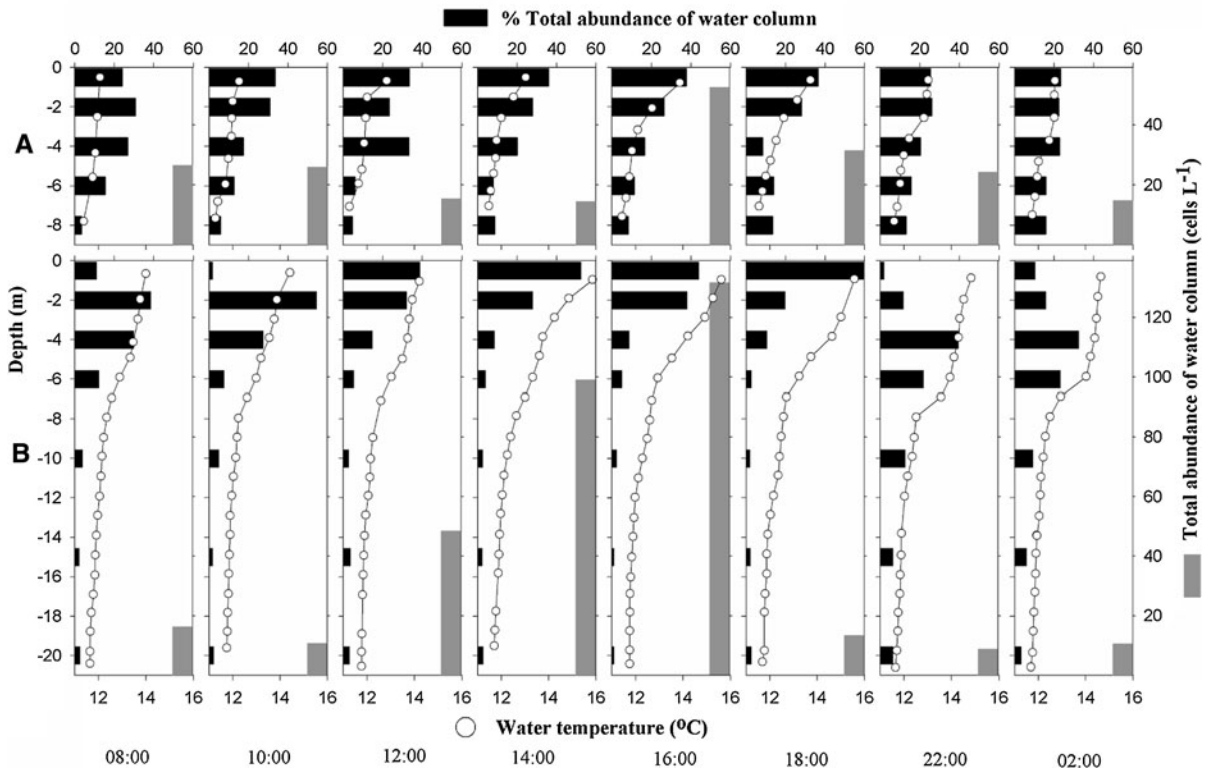
Fig. 3 The vertical distribution of *Peridiniopsis niei*, vertical variations in water temperature and total abundance of the population in the water column from the A and B station during daytime and nighttime. The abundance at a given depth is expressed as a percentage of the total abundance of the population in the water column
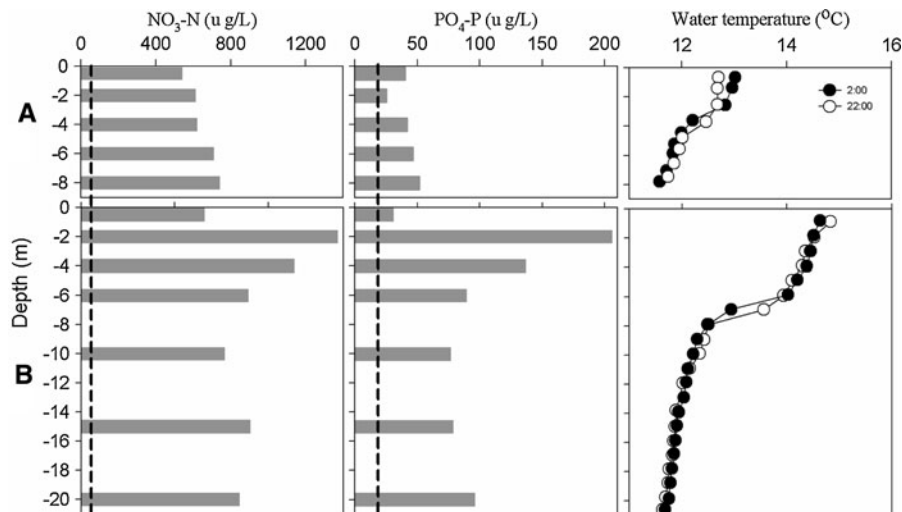

Fig. 4 Vertical profiles of nutrients and water temperature at the A and B station. The *dashed line* indicates the value of nitrate nitrogen and phosphate phosphorus at the beginning of the experiment from Heaney and Eppley (1981)

Diel distribution patterns in the vertical profile of *Peridiniopsis niei* were clearly discernible, but both sampling stations greatly differed (Fig. 4). Furthermore, these analyzed using Morisita's index (Fig. 5). At both stations, *Peridiniopsis niei* appeared to aggregate in shallower water at daytime. At nighttime, *Peridiniopsis*

Fig. 5 Mean residence depth (MRD, *bars*) and the value of Morisita's index (MI, *dotted line*) for *Peridiniopsis niei* from the sites A and B during daytime and nighttime. *Bars* with the *same letters* indicate no significant differences in vertical distribution between sampling times ($P > 0.05$)
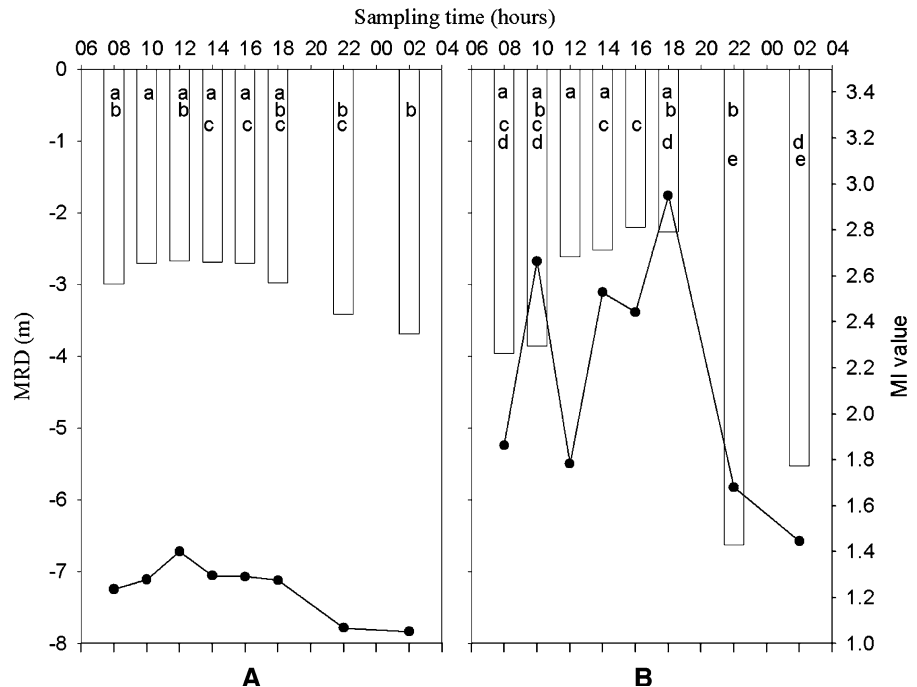
niei populations were randomly redistributed throughout the column in the A station, whereas the organism in the B station avoided the surface layers and moved downward to deeper layers, but mostly aggregated on 4–6 m water layers with maxima in relative abundance (Fig. 3). The linear equations of MI and log-transformed SI were the following (Fig. 6):

$$\text{Station A}: \quad \text{MI} = 1.06 + 0.09 \, \text{Log}_{10}(\text{SI} + 1) \, R^2$$
$$= 0.869, \, P < 0.001, \, n = 8$$

$$\text{Station B}: \quad \text{MI} = 1.25 + 0.22 \, \text{Log}_{10}(\text{SI} + 1) \, R^2$$
$$= 0.283, \, P = 0.178, \, n = 8$$

At the A station, solar irradiance was significantly related to MI and accounted for 86.9% of MI diel variation. However, there was no significant relationship between SI and MI at the B station, where the maximum population of *Peridiniopsis niei* was found at 4.0 m depth during the dark period.

Peridiniopsis niei appeared to perform DVM, as indicated by the significant difference of MRD between daytime and nighttime. The *Peridiniopsis niei* MRD of the A station at daytime (10:00, 14:00 and 16:00) was significantly lower than that at nighttime (2:00) ($P < 0.05$, K–S test, Fig. 5). *Peridiniopsis niei*

had significantly lower MRD at daytime (12:00–16:00) than that at nighttime (22:00 and 2:00) in the B station ($P < 0.05$, K–S test, Fig. 5). The linear equations of MRD and log-transformed SI were the following (Fig. 6):

$$\text{Station A}: \text{MRD} = 3.55 - 0.28 \, \text{Log}_{10}(\text{SI} + 1) \, R^2$$
$$= 0.934, \, P < 0.001, \, n = 8$$

$$\text{Station B}: \text{MRD} = 5.78 - 1.00 \, \text{Log}_{10}(\text{SI} + 1) \, R^2$$
$$= 0.679, \, P < 0.01, \, n = 8$$

Solar irradiance was significantly related to MRD and explained 93.4 and 67.9% of MRD diurnal variation at the A and B station, respectively. This indicates solar irradiance was an important factor influencing vertical migrations of *Peridiniopsis niei*.

Discussions

The field observations on the diel vertical distribution of *Peridiniopsis niei* in Xiangxi Bay provide evidence that this population performs diel vertical migration as a specific kind of depth-selection behavior. This statement is based on the significant differences detected between day and night vertical distributions (Fig. 5). It is reasonable to believe that *Peridiniopsis*
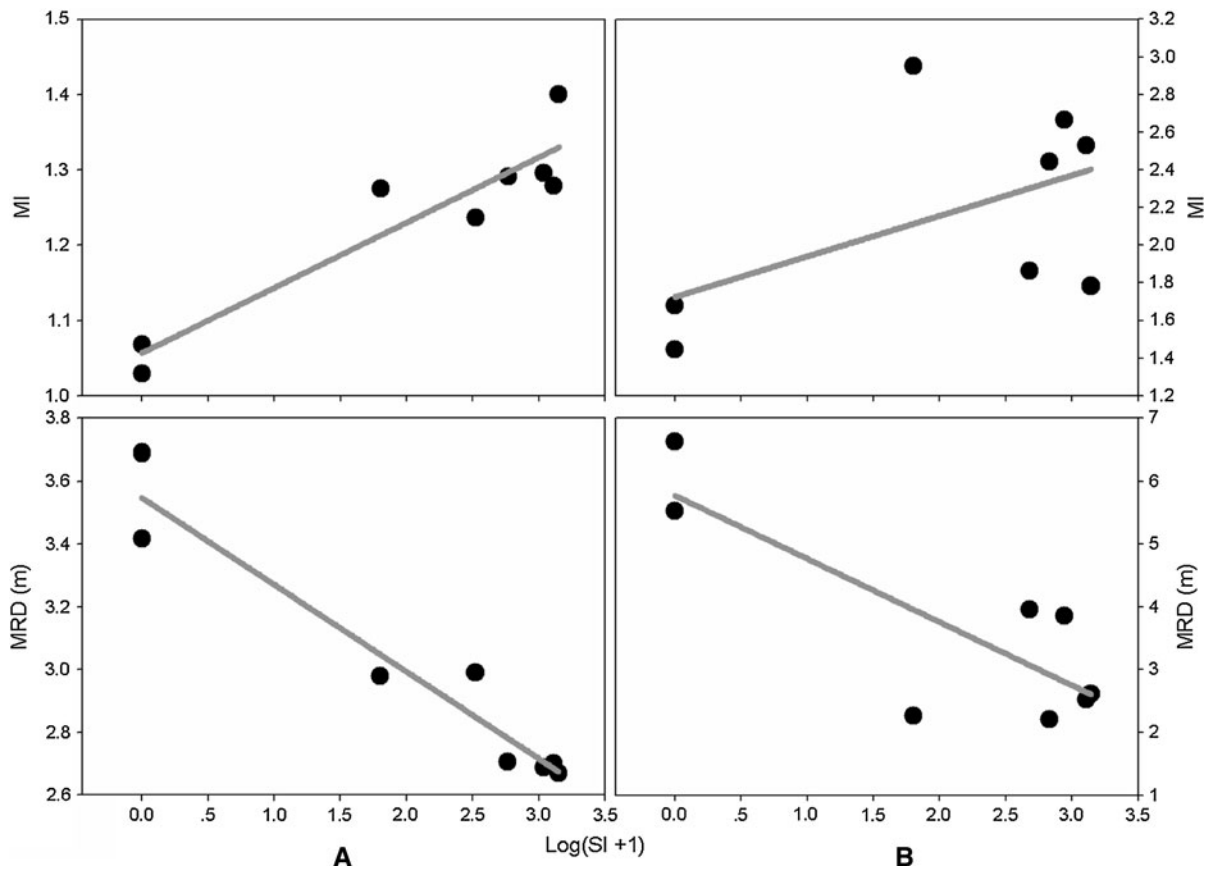
Fig. 6 Regression models of Morisita's index (MI) and mean residence depth (MRD) against $\log(X + 1)$-transformed solar irradiance (SI) at the sites A and B

niei performed an upward movement during around early morning to stay near the surface at most of daytime and a downward movement during around dusk to spend the night in deeper waters. In general, the observed migratory behavior of *Peridiniopsis niei* was characterized by normal vertical migration observed by the majority of the studies dealing with vertical migration of freshwater and marine dinoflagellates, with individuals ascending at dawn and descending at dusk (e.g., Salonen and Rosenberg 2000; Beckmann and Hense 2004; Townsend et al. 2005; Doblin et al. 2006; Yamamoto and Nakahara 2006). Our results indicate that mean residence depth (MRD) of *Peridiniopsis niei* at both stations correlate directly with solar irradiance (Fig. 6). It provides quantitative evidence that the observed migratory behavior of *Peridiniopsis niei* is triggered by solar irradiance.

The *Peridiniopsis niei* populations at both stations were characterized by marked vertical spatial heterogeneity during daytime, showing consistently aggregated patterns, as measured by a dispersion index approach. At nighttime, vertical distribution patterns of the dinoflagellates population displayed obvious difference between both stations. This dinoflagellates were found to be dispersed throughout the water column of the A station, while the populations became re-aggregated above thermocline at the B station. The sharpness of this thermocline is due to daytime surface heating up to 1800 hours and subsequent surface cooling by 2200 hours, which generates a sharp thermocline at depth over night. The thermocline at the B station appears to restrict vertical descent at night. Heaney and Talling (1980) also pointed out that the vertical descent of *Ceratium* at night was restricted when a thermocline was present, and the same behavior

has been described by Frempong (1984). Such a phenomenon was also observed in the present study for *Peridiniopsis niei*. Diel variations in dispersion at the A station were correlated with solar irradiance, but it did not at the B station, as further detected by the regression analysis between solar irradiance and Morisita's index. It is thus reasonable to believe that the vertical descent of *Peridiniopsis niei* was prevented when a thermocline was present during the dark period in the B station.

The restriction of vertical descent by the thermocline is largely due to the abundance of nutrients at the waters above thermocline, as indicated by the work of Heaney and Eppley (1981) and Olsson and Graneli (1991). Some dinoflagellates with insufficient nutrients penetrated below thermocline, and had access to subthermocline nutrient pools during the dark period, while the vertical descent of those populations with sufficient nutrient was restricted by temperature gradients, as suggested by most of studies (e.g., Clegg et al. 2003a; Heaney and Eppley 1981; Juliette et al. 2005; Olsson and Graneli 1991 Ross and Sharples 2008). For example, Heaney and Eppley (1981) found that steeper thermocline (ca. 0.8°C 0.1 m^{-1}) resulted in accumulations of the dinoflagellates (*Gonyaulax polyedra* and *Ceratium furca*) in such a thermocline region when the populations had sufficient nitrate nitrogen (ca. 56.0 μg L^{-1}) and phosphate phosphorus (ca. 18.6 μg L^{-1}) at the beginning of their experiment, while both dinoflagellates performed a more complete descent through the thermocline when both nitrate nitrogen and phosphate phosphorus had been depleted, and were less than 2.10 and 4.6 μg L^{-1}, respectively. Olsson and Graneli (1991) also found that three coexisting dinoflagellates (*Prorocentrum minimum*, *Prorocentrum micans* and *Ceratium furca*) were able to migrate through the strong artificial thermoclines in their experiment, which had low nitrate nitrogen (ca. 29.0 μg L^{-1}) and phosphate phosphorus (ca. 2.2 μg L^{-1}). Thus, the dinoflagellates appear to penetrate a thermocline less when they are nutrient replete than when nutrient deprived. In Xiangxi Bay, the concentrations of total N and total P already exceeded the threshold value of eutrophic state (Cai and Hu 2006). The nutrient profiles of the present study showed that the waters above thermocline at the B station had sufficient nitrate nitrogen and phosphate phosphorus (Fig. 4). The nutrient

concentrations were much higher than that of the beginning of the experiment from Heaney and Eppley (1981). We can thus conclude that *Peridiniopsis niei* did perform vertical migrations in the daytime but did not penetrate the thermocline in the dark because nutrient levels in the eutrophic waters were more than adequate to meet its nutrient demands.

Conclusion

In conclusion, strong DVM patterns were found for *Peridiniopsis niei* in a representative of most eutrophic bays of TGR. Solar irradiance incident was an important factor influencing vertical migrations of *Peridiniopsis niei*, and the ascent starts before sunrise and descent before sunset. In addition, the temperature gradient during the dark period can act as a barrier to downward migration of *Peridiniopsis niei* in the eutrophic bay.

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