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Natural Co-occurrence of *Dinophysis acuminata* (Dinoflagellata) and *Mesodinium rubrum* (Ciliophora) in Thin Layers in a Coastal Inlet

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ABSTRACT. The interdependency of *Dinophysis* spp., *Mesodinium rubrum* and *Teleaulax* spp. has occupied scientists in molecular and ecological domains in recent years. Current knowledge about the predator–prey relationships is based on laboratory investigations. Records on interactions in nature are limited, even though it is known that *Dinophysis acuminata* and *M. rubrum* form population maxima in thin layers associated with thermal stratification. We studied the vertical co-occurrence of these taxa in a stratified coastal inlet in Åland, in the Northern Baltic Sea, SW Finland. Vertical profiles were sampled monthly in the summer of 2008 and observations on diurnal migrational patterns of all species were conducted in September 2008. The population maximum of *D. acuminata* was almost totally confined to thin layers where the depth maximum of *M. rubrum* was present. However, this pattern was only observed early in the morning or at noon. The population maxima of *M. rubrum* and *Teleaulax* spp. overlapped at noon. *Dinophysis acuminata* and *Teleaulax* spp. were restricted to the upper 9 m but *M. rubrum* was found down to 20 m depth. This study offers circumstantial evidence for the interdependency between the three taxa in nature.

Key Words. Co-occurrence, *Dinophysis acuminata*, *Mesodinium rubrum*, stratification, vertical migration.

DINOPHYSIS spp. occur worldwide and produce several toxins causing diarrhetic shellfish poisoning (Lee et al. 1989; van Dolah 2000). The genus is of great economic significance because of the harmful effects on shellfish industry (Yasumoto et al. 1985) and of public interest because of human health issues (Madigan et al. 2006; Vale and de Sampayo 2002). *Dinophysis* spp. are usually background species in the Baltic Sea, occurring at densities from less than 100 to a few thousand cells/L, and cell abundances seldom exceeding 10000 cells/L (H. Hällfors, pers. commun.). These species are usually present at the thermocline at 15–25 m depth in the Baltic Sea (Carpenter et al. 1995; Gisselson et al. 2002). The highest abundances are often associated with salinity and/or thermal density gradient layers (Delmas, Herbland, and Maestrini 1992; Reguera, Bravo, and Fraga 1995).

Dinophysis acuminata Claparède et Lachmann is mixotrophic (Jacobson and Andersen 1994). Phagotrophy is an important aspect of the life history in *Dinophysis* spp. and may be the key in understanding their ecology (Carvalho, Minnhagen, and Granéli 2008). In cultures, *Dinophysis* spp. feed on cells of the phototrophic ciliate *Mesodinium rubrum* (Lohmann) Hamburger & Buddenbrock (= *Myrionecta rubra* Jankowski) (Nagai et al. 2008; Nishitani et al. 2010; Park et al. 2006), which verifies a predator–prey relationship between these organisms. However, data on the co-occurrence of *Dinophysis* spp. and *M. rubrum* in nature are scarce (Rines et al. 2010; Velo-Suárez et al. 2008).

The marine ciliate *M. rubrum* is an important phytoplankter in stratified coastal inlets of the non-tidal Baltic Sea where it can exploit available resources through diurnal vertical migration (DVM) (Crawford and Lindholm 1997; Lindholm and Mörk 1990). *Mesodinium rubrum* often form two vertical depth maxima, one near the surface and another at greater depth, probably relating to light harvesting and nutrient acquisition (Olli and Seppälä 2001; Passow 1991). *Mesodinium rubrum* preys upon cryptophytes (e.g. *Teleaulax acuta*, *Teleaulax amphioxeia*) and sequesters their chloroplasts (Johnson and Stoecker 2005; Nagai et al. 2008) enabling one of the highest primary production rates documented in marine organisms (Smith and Barber 1979). This ciliate can sustain photosynthetic growth without prey for long periods as it enslaves these cryptophytes chloroplasts (Smith and Hansen 2007). However, it needs prey during the growth season (Johnson and Stoecker 2005) and ingests about one prey cell per day or generation (Smith and Hansen 2007).

A new insight generated during recent years is that *D. acuminata* feeds on *M. rubrum,* but there is limited information on their co-occurrence in nature. Inre Verkviken in Northern Åland is a good site for both species (e.g. Crawford and Lindholm 1997; Lindholm 1982; Lindholm and Öhman 1995) and is therefore suitable for studying interactions between *D. acuminata*, *M. rubrum* and cryptophytes. This was already indicated in a previous paper (p. 58 in Lindholm and Mörk 1990). The cryptophytes were ignored in Lindholm and Mörk (1990) but this group is common in the Baltic Sea (Hällfors 2004). We hypothesize that the vertical distribution of the mixotrophic *D. acuminata* is not only determined by light or nutrient acquisition but includes a complementary strategy involving plastid renewal, which is manifested in migration to layers rich in *M. rubrum*.

MATERIALS AND METHODS

Study site. Inre Verkviken is a 20-m-deep, stratified semienclosed brackish inlet in the NW part of Åland, SW Finland. The inlet is connected to the open sea through a 200-m long canal restricting the influx of seawater. Anoxic conditions below 12–15 m during the summer are a prominent feature (Lindholm 1982, 1996). A halocline and a thermocline often coincide strengthening the stratification during the summer (Lindholm 1996).

Field sampling. Inre Verkviken was studied once a month during May–September (May 10, June 9, July 11, August 8 and September 9) in the summer of 2008. Water samples were taken at noon at one station at 1-m intervals with a Limnos (Limnos Ltd., Turku, Finland) sampler. Diurnal sampling was conducted in September 2008 (September 9–10) with vertical profiles taken at 1-m intervals at 06:00, 12:00, 18:00, 24:00 and 06:00 h. Light penetration was measured with a LI-COR 188 B Radiometer (LI-COR Inc., Lincoln, NE). Secchi depth was estimated with a white disk 30 cm in diameter. Water temperature was measured with a thermometer in the Limnos sampler.

Water analyses. Hydrographic variables, such as salinity (i.e. conductivity) and oxygen content were analyzed at arrival in the laboratory. Chlorophyll *a* filter and nutrient samples (i.e. nitrate, NO_3) were frozen for later analyses. Chlorophyll *a* was analyzed spectrophotometrically after using 90% acetone for extraction (filtration on 47mm GF-C filters). NO_3 analyses were made according to Grasshoff et al. (1983) and Finnish standard (SFS 3031).

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Cell counts. All phytoplankton samples were preserved with Lugol's solution (Crawford and Lindholm 1997). A Nikon TE 200 (Nikon, Tokyo, Japan) phase contrast microscope and 10 ml chambers were used for cell counting according to the Utermöhl method (Utermöhl 1958). The whole bottom area of the chamber was scanned to enumerate *D. acuminata* and *M. rubrum*. The *Teleaulax/Plagioselmis* group was enumerated in two transects. Cryptophytes are small and difficult to identify after preservation. Therefore, we quantified the cryptophytes including both *Teleaulax* spp. and *Plagioselmis* spp. species. This does not give a correct picture of the vertical distribution of *Teleaulax* spp. but enables us to observe general patterns in their occurrence. Our foremost intention was merely to qualitatively note the presence or absence of cryptophytes, i.e. the enumeration results of this group is statistically less reliable.

Toxin analyses. Toxin analyses were kindly conducted by Katrin Erler at Friedrich Schiller University, Jena, Germany. Samples for the analyses were collected from 1 to 5 m depth in Inre Verkviken on September 10, 2008. All measurements were carried out by liquid chromatography coupled with tandem mass spectrometry and analyzed in the multiple reaction monitoring mode. The PTX-2 content of *D. acuminata* cells was calculated using certified standard substances acquired from the National Research Council in Halifax, Canada.

Statistical analyses. The Pearson correlation coefficient of the vertical distribution of *M. rubrum* and *D. acuminata* was analyzed in GraphPad Prism version 5. *P*-values <0.05 were considered statistically significant. Normal distribution of the data were analyzed with the Kolmogorov–Smirnov test and homogeneity of variances was assessed with Levene's test in Statistical Package for the Social Sciences version 18.0. Correspondence analysis was conducted in the R environment (R Developmental Core Team, 2009). All statistical comparisons between the vertical distributions of the species incorporated only the upper layers (i.e. 0–9 m) because the cell concentration of *D. acuminata* below this was too low for statistically reliable enumeration. Data on *Teleaulax/Plagioselmis* spp. were not included in the statistical analysis because the focus of this study was on interactions between *D. acuminata* and *M. rubrum*. The data set of *Teleaulax/Plagioselmis* spp. was also considered inadequate for sensible statistical analysis. Previously unpublished data from September 1980 and September 1983 were included in the statistical analysis as historical comparison.

RESULTS

There was a marked vertical stratification in terms of both temperature and salinity in Inre Verkviken during the summer of 2008. A thermocline at 6–8 m (Fig. 1A) together with a weak halocline at 4–8 m (Fig. 1D) restrained vertical mixing of the water. The oxygen conditions were good in the upper water mass during the whole summer but became poorer below 8 m in late summer (Fig 1B). In May–August there was an intermediate layer rich in nitrate (Fig. 1C). The surface water at 0–4 m had low concentrations of NO_3 (i.e. 0.0–11.8 μg/L) on all sampling occasions. Deep water rich in NO_3 existed during the whole season except for September when the NO_3-levels fell to almost zero in the whole water column. About 1% of the light at the surface penetrated down to 9 m depth. The Secchi depth was typically around 4 m during the whole season (Fig. 1E). The values of chlorophyll *a* corresponded to the cell concentration of *M. rubrum* (Fig. 1F).

Dinophysis acuminata was almost entirely restricted to the upper 9 m in Inre Verkviken. This was not the case for *M. rubrum*, which migrated down to 20 m in May and June and was found down to 12–15 m depth in August and September (Fig. 2). The vertical occurrence of *M. rubrum* corresponds to the oxygen availability as the population maximum shifted to shallower depths at the end of the summer as oxygen values fell under 2 mg/L below 15 m depth. However, some cells of *M. rubrum* were even found in deep water where the oxygen value was below 0.5 mg/L. No light could be detected at depths below 10 m (Fig. 1).

The vertical occurrence of *M. rubrum* and *D. acuminata* showed significant correlation over the seasonal scale in the 0–9 m layers (Fig. 2, Table 1). The depth distribution of both species changed during the season except for May and June, which showed somewhat similar depth distributions. Comparable data from 1980 and 1983 also showed significant correlation of depth distributions (Fig. 2, Table 1) and is in line with results from 2008. Despite variable monthly depth distributions, the two species did overlap significantly in every case but in August. The correspondence analysis visualizes the depth distributions during May–September in 2008 and from September 1980 and 1983 (Fig. 3). Comparison of the distance between depth and species in the correspondence analysis graph gives an estimate of the vertical position of the population maxima. As in the correlation analysis, depth distributions in August showed weak signs of resemblance also in the correspondence analysis. However, even in this case the depth maxima of both species was at 8 m (Fig. 2).

The typical *D. acuminata* cell was 45–50 μm in length (Fig. 4) and contained brightly fluorescent orange chloroplasts (Fig. 5). Cells of *D. acuminata* sampled at 1–5 m depth on September 10, 2008 contained pectenotoxin-2 (Table 2).

The vertical occurrence of *D. acuminata* and *M. rubrum* showed significant positive correlation at noon and in early morning (Fig. 6) in the 0–9 m layers (Table 3). During evening and at night the majority of the *M. rubrum* population migrated to deeper layers. At these sampling hours there was a significant negative correlation between the vertical occurrence of *D. acuminata* and *M. rubrum* (Fig. 6). The majority of the *D. acuminata* population occurred at 0–5 m and did not show DVM (Fig. 6), nor did the *Teleaulax/Plagioselmis* group during the 24-h sampling period. The cryptophytes were restricted to the upper 9 m. The population maxima of *M. rubrum* and the cryptophytes overlapped at 1 m depth at noon. The abundances (i.e. 80,000–120,000 cells/L) of *Teleaulax/Plagioselmis* spp. were highest in surface water and by 10 m depth and below none of these cells was observed (Fig. 6).

The correspondence analysis visualizes the distribution of *M. rubrum*: it occurred in the upper layers during daytime and in deeper layers during darker hours (Fig. 7). *Dinophysis acuminata* seemed to be restricted to the upper or midlayers of the water column. Considerable physical interaction between the species was possible at 0–5 m during early morning and at noon. The upper depth maximum of *M. rubrum* shifted to 0–1 m during the second day at noon compared with 3–5 m during the first day at noon. There was a migrational response to this observed in the vertical depth distribution of *D. acuminata* as the position of the population shifted toward the depth maximum of *M. rubrum* the second day at noon (Fig. 7).

DISCUSSION

We hypothesized that *D. acuminata* migrates to layers rich in *M. rubrum* reflecting the observed predator–prey relationship between these two species. Our results suggest that *M. rubrum* may also avoid predation from *D. acuminata* by finding refuge in dark and low-oxygen deep waters (i.e. 10–20 m). The maximum abundance of *D. acuminata* and *M. rubrum* peaked at similar depth layers throughout the season when sampled at noon (0–9 m), except for 1 d out of nine, indicating robustness in our results. We also found that *M. rubrum* performed DVM in Inre Verkviken: it occurred in high densities in surface layers in early morning and at noon and migrated to cold, nutrient rich and oxygen-depleted deep layers by night. However, *M. rubrum* formed two depth maxima

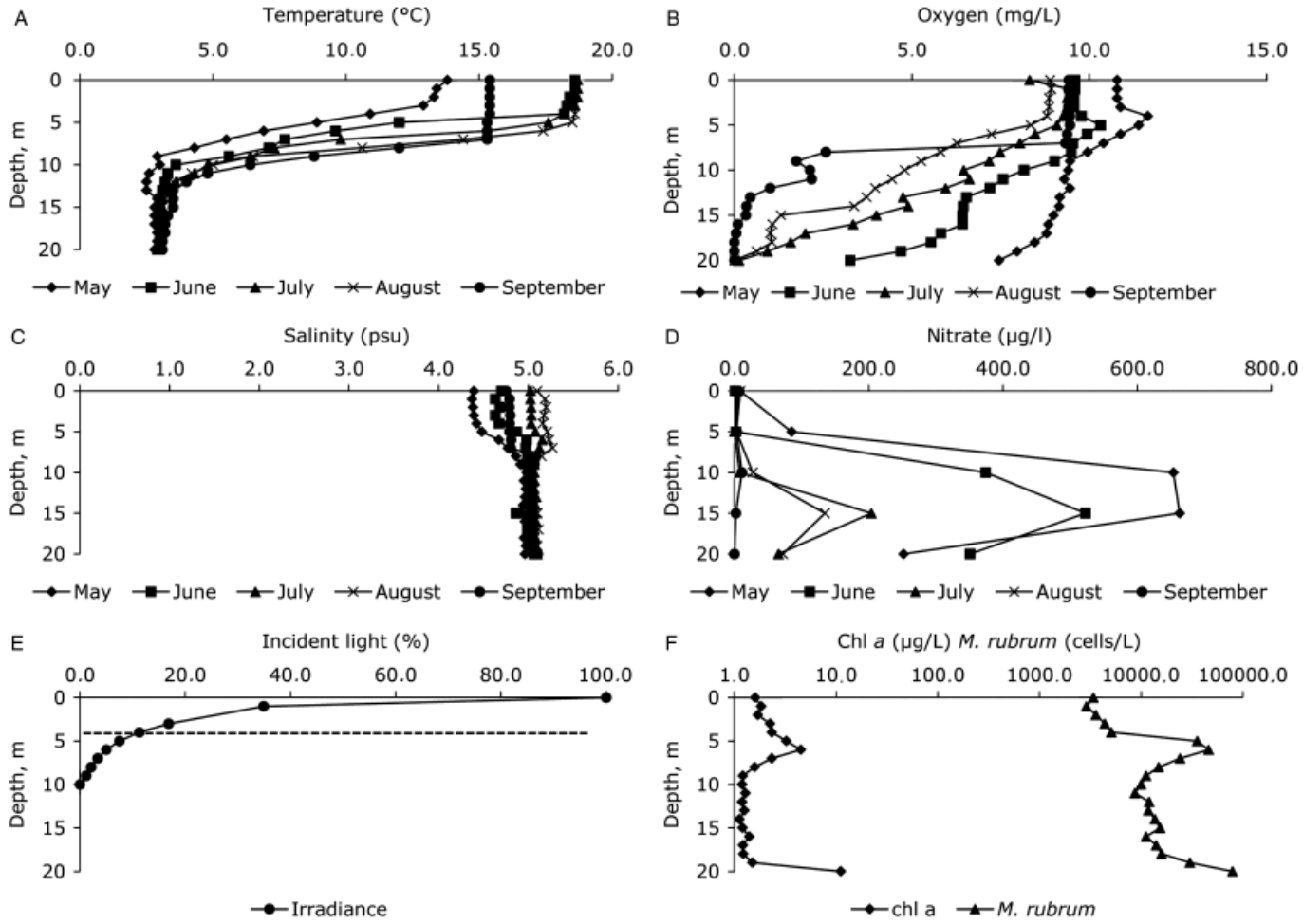

Fig. **1.** Vertical profiles of seasonal variability in hydrographic variables in Inre Verkviken during May–September 2008. **(A)** A thermocline at 6–8 m depth existed throughout the season. **(B)** Oxygen values around 9.0 mg/L existed in the surface water throughout the season; oxygen values fell below 2 mg/L under 15 m depth in August and September. **(C)** An intermediate layer with higher NO_3 concentrations existed in May–August. **(D)** A weak halocline existed at 4–8 m. **(E)** Typical light penetration in Inre Verkviken during May–September 2008. Dashed line depicts the typical Secchi depth. **(F)** Chlorophyll *a* values corresponded to the cell concentrations of *Mesodinium rubrum* at respective depths. Note the logarithmic scale. All sampling was done at noon.

during both day and night. The deeper maximum probably represented cells refueling their nitrate supply as the nitrate concentrations were highest below 10 m depth. The shallow maximum apparently comprised light-obtaining cells. A similar pattern has been shown by Crawford and Lindholm (1997). Our hydrographic data, in terms of the thermo- and the halocline, oxygen conditions, vertical distribution of nitrate, light penetration and chlorophyll *a* values which corresponds heavily with cell concentrations of *M. rubrum* are also in line with the findings of Crawford and Lindholm (1997) and Lindholm and Mörk (1990). This is an indication of stable hydrographic conditions in Inre Verkviken which is known to favor both *M. rubrum* (Figueroa et al. 1998; Passow 1991) and *D. acuminata* (Delmas et al. 1992; Reguera et al. 1995).

The depth distribution of *M. rubrum* at noon was variable, probably because of varying light intensities from day to day. Regardless of this variation—when considering the upper 9 m—most cells of *D. acuminata* were nearly always found in the layers with the highest occurrence of *M. rubrum* at almost every sampling occasion. Our vertical profiles, covering both seasonal and diurnal patterns in species abundance and hydrographic variables, showed that *D. acuminata* was almost totally confined to layers with maximum abundance of *M. rubrum* and with O_2 concentrations above $\sim$ 2.0 mg/L. Both the correlation and the correspondence analyses of the vertical distribution patterns offer circumstantial evidence for the interdependency between *D. acuminata* and *M. rubrum* in nature.

Cryptophytes were present in the surface water throughout the whole season in Inre Verkviken, increasing in abundance from May to August (i.e. 40,000–260,000 cells/L; data not shown). A somewhat lower abundance (i.e. 150,000 cells/L; data not shown) of cryptophytes was observed in the beginning of September, possibly because of intensified predation pressure caused by *M. rubrum*. Encounters between *M. rubrum* and cryptophyte prey were possible in the upper 9 m at noon. The high abundance of cryptophytes probably fulfilled the needs of sporadic plastid renewal in *M. rubrum* during the whole season.

Dinophysis acuminata did not perform vertical diurnal migration in Inre Verkviken. We found no cells below the thermocline, probably because of low oxygen levels. However, the oxygen conditions in the deep water were adequate from May–July, suggesting *D. acuminata* avoided dark depths below 9 m because only $\sim$ 1% of the surface light penetrated this depth and only occasional cells of *D. acuminata* were found at 10 m and below. Despite the shallow occurrence of *D. acuminata*, renewal of plastids

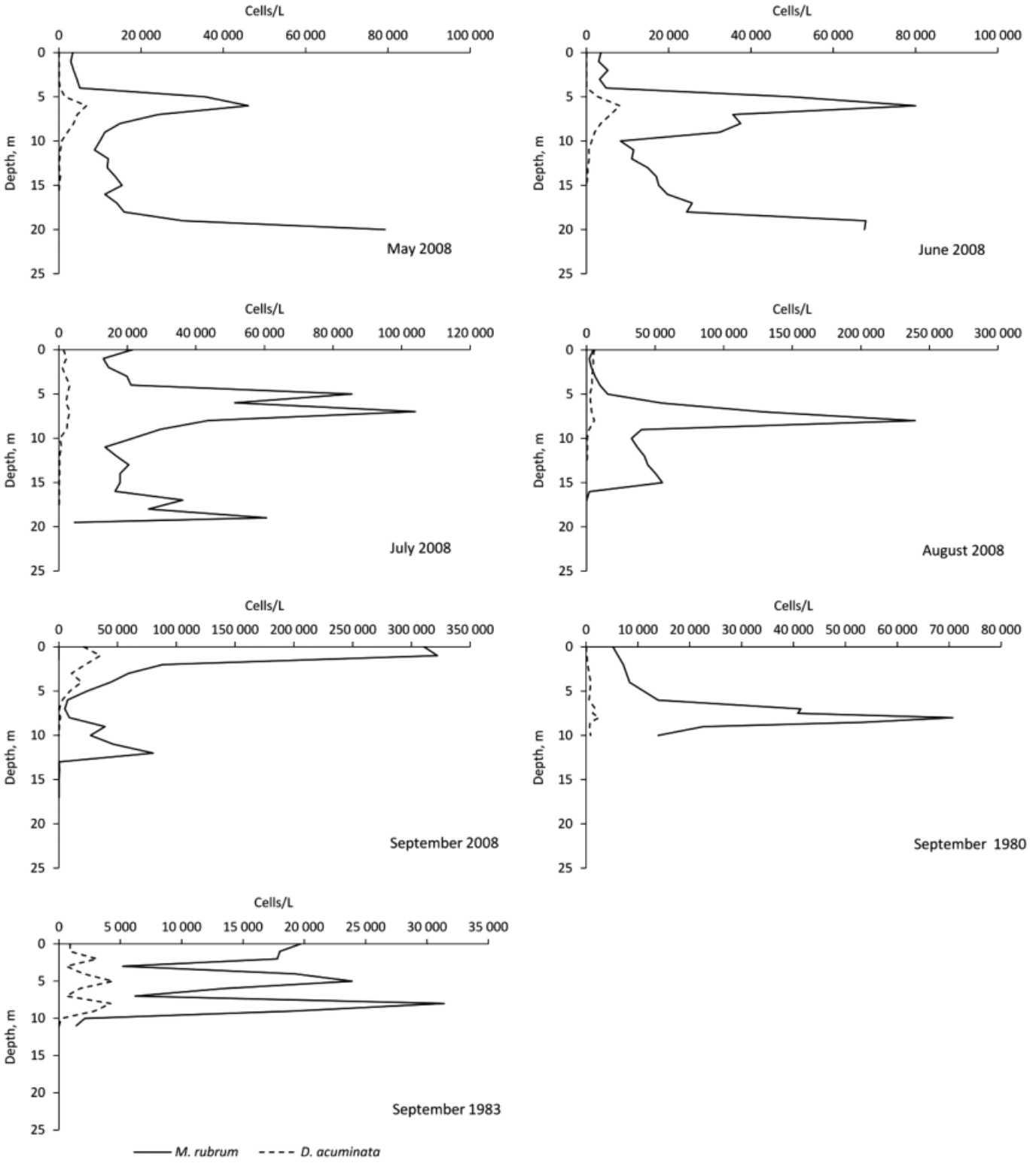

Fig. **2.** Depth distribution of *Dinophysis acuminata* and *Mesodinium rubrum* during May–September 2008. Comparable profiles from September 1980 and 1983. Sampling was done at noon. Please notice the different scales.

was frequently possible because the population overlapped the *M. rubrum* population on a daily basis in the upper layers. Riisgaard and Hansen (2009) suggested that *D. acuminata* needs *M. rubrum* to sustain its photosynthetic growth and that it often is food-limited in nature. Photosynthesis may normally be the primary source of carbon for *D. acuminata*, but when *M. rubrum* is available the growth rate is boosted (Riisgaard and Hansen 2009). Velo-Suárez et al. (2008) observed *D. acuminata* and *M. rubrum* in patches

Table **1.** Correlation values (Pearson's, r, R^2) and P-value indicating the resemblance and significance of the vertical depth distributions of *Dinophysis acuminata* and *Mesodinium rubrum* during May–September 2008 in layers from 0 to 9 m.

Month	r	R^2	P
May	0.82	0.67	0.000
June	0.92	0.85	0.000
July	0.52	0.27	0.049
August	0.23	0.05	0.250
September	0.81	0.66	0.001
September (1980)	0.94	0.88	0.000
September (1983)	0.78	0.61	0.005

Historical comparisons are from September 1980 and 1983.

within the same depth range and proposed this spatial co-occurrence to be a sign of a heterotrophic strategy by the dinoflagellate in nature. Rines et al. (2010) found cells of *Dinophysis fortii* in Monterey Bay, California containing food vacuoles possibly filled with *M. rubrum*. The mixotrophic life strategy of *Dinophysis* spp. may in extreme cases lead to blooms as shown in our study. *Dinophysis acuminata* reached a cell concentration of $>30{,}000$ cells/L in the surface water in September 2008 in Inre Verkviken, which to our knowledge is the highest ever reported concentration in the Baltic Sea.

Our observed co-occurrence of *D. acuminata* and *M. rubrum* in nature may be biased because vertical distribution of motile phytoplankton is underpinned by similar hydrographic variables: the most favorable abiotic conditions for photosynthetic growth is at a certain depth at a certain time of day. Such a scenario would force *D. acuminata* and *M. rubrum* to the same depth. However, all species are not found at the same depth in nature and it has actually been shown that *D. acuminata* and *M. rubrum* have

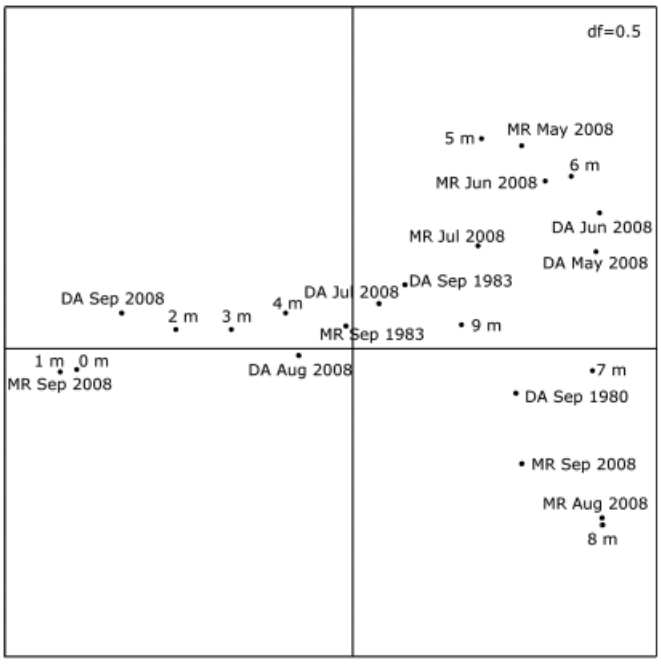

Fig. **3.** Correspondence analysis of seasonal depth distributions of *Dinophysis acuminata* and *Mesodinium rubrum* in 2008. Comparable data for 1980 and 1983. *Dinophysis acuminata* labeled as DA plus present month and year and *M. rubrum* as MR plus present month and year. Note that the data points for ''1 m'' and ''MR Sep 2008'' are overlapped.

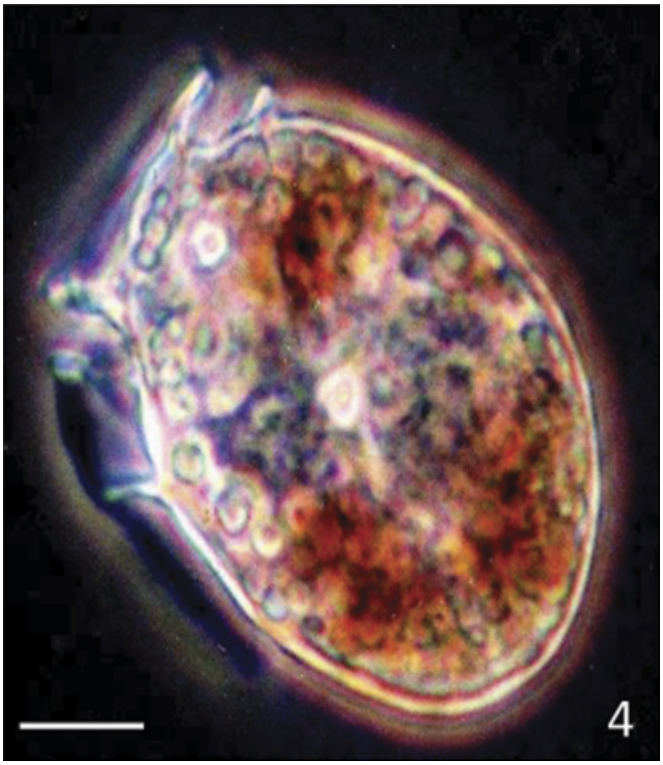

Fig. **4.** Cells of *Dinophysis acuminata* sampled in Inre Verkviken were documented under a light microscope in September 2008. A starved *D. acuminata* with characteristic groups of chloroplasts. Scale bar = 10 μm.

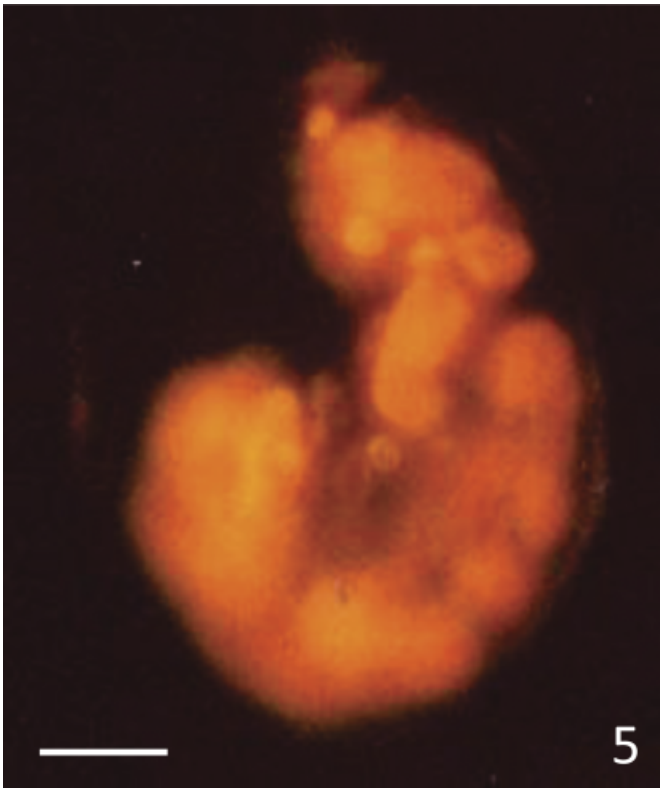

Fig. **5.** Cells of *Dinophysis acuminata* sampled in Inre Verkviken were documented under a epifluorescense microscope in September 2008. A cell of *D. acuminata* with orange fluorescence structures indicating recent active grazing. Scale bar = 10 μm.

Table **2.** Toxin content (pg/cell) of *Dinophysis acuminata* cells at 1–5 m in Inre Verkviken (September 10, 2008).

Depth (m)	PTX-2 (pg/cell)
1	18.68
2	16.15
3	19.10
4	9.34
5	25.27

Table **3.** Correlation values (Pearson's, r, R^2) and P-value indicating the resemblance and significance of the vertical depth distributions (0–9 m) of *Dinophysis acuminata* and *Mesodinium rubrum* during the 24-h sampling series in September 2008.

Sampling hour	r	R^2	P
1200(1)	0.72	0.52	0.006
1800	−0.75	0.56	0.004
2400	−0.57	0.32	0.034
0600	0.70	0.49	0.009
1200(2)	0.82	0.67	0.001

different vertical niche separation strategies (Olli 1999), suggesting that some strong factor was involved in aggregating these species to the same thin layers in Inre Verkviken. The vertical profiles from 1980 and 1983 studied in Inre Verkviken supports the consistency of our observations. Data on co-occurrence of *Dinophysis* spp. and *M. rubrum* can also be found from Leegard (1920) and Välikangas (1926) who studied plankton communities in SW Finland. Rines et al. (2010) hypothesized that aggregation into thin layers is an important part of the ecology of these species and that it should enhance the interactions between them. The

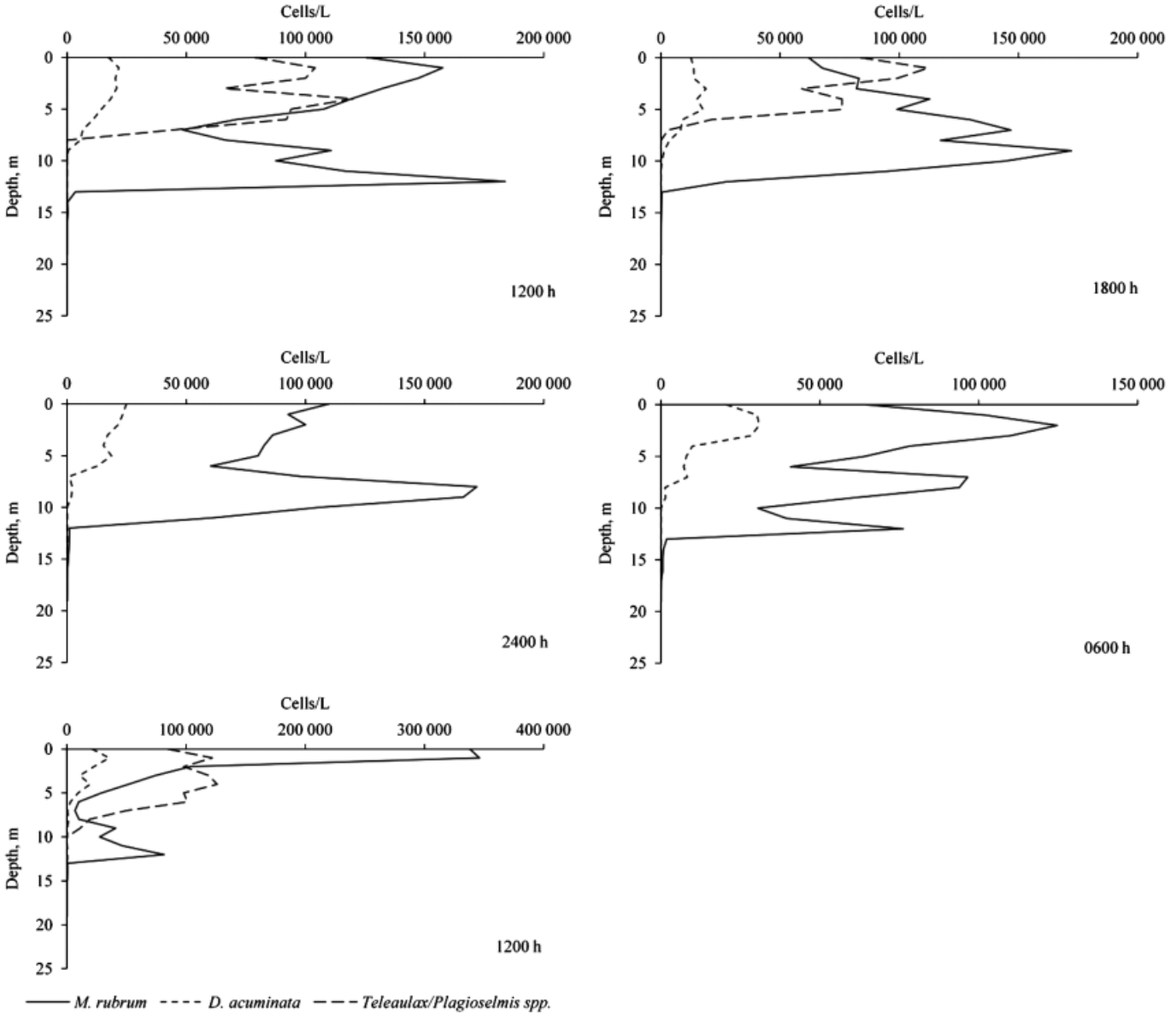

Fig. **6.** Vertical occurrence of *Mesodinium rubrum*, *Dinophysis acuminata* and *Teleaulax/Plagioselmis* spp. during a 24-h sampling series in Inre Verkviken in September 2008. Please notice the different scales.

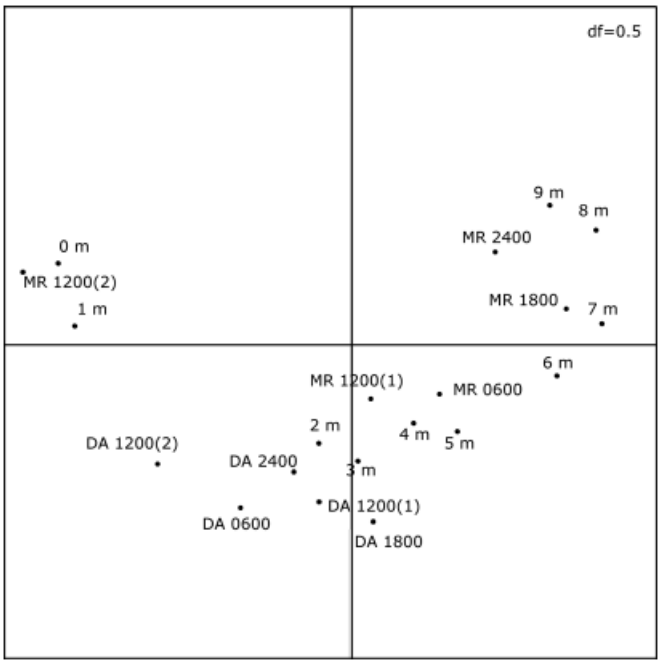

Fig. **7.** Correspondence analysis of the interspecific depth distribution during the 24-h time series examining vertical distributions of *Mesodinium rubrum* and *Dinophysis acuminata* (see Fig. 6). *Dinophysis acuminata* labeled as DA plus present sampling time and *M. rubrum* as MR plus present sampling time. 1200(1) = at noon September 9, 1200(2) = at noon September 10.

same authors emphasized that all three taxa (i.e. *Dinophysis*, *Mesodinium* and *Teleaulax*) have particular migrational patterns, leading the populations may migrate in and out of each other's depth maxima. Population maxima ought to coincide at certain times; this is exactly what we have shown. The population maxima of *M. rubrum* and *D. acuminata* coincided in early morning or at noon and the population maxima of *M. rubrum* and cryptophytes coincided at noon. Cells of *D. acuminata* collected from the thin layers rich in *M. rubrum* were intensively orange in color under an epifluorescense microscope, indicating active grazing (Park et al. 2006; Rines et al. 2010).

Observations that confirmed *Dinophysis* spp. feeding on *M. rubrum* in culture (Park et al. 2006) and that they both contain plastids of cryptophyte origin (Gustafson et al. 2000; Jansson 2004) generated an idea of interdependency between the three taxa. It is currently debated whether the plastids of *Dinophysis* spp. are permanent and originated from cryptophytes or whether they are more short-lived kleptoplastids (i.e. sequestered chloroplasts from cryptophytes via the predation upon *M. rubrum*). Molecular analyses using nucleomorph large subunit rRNA genes and chloroplast markers showed identical sequences for all three species, *Dinophysis* spp., *M. rubrum* and *T. amphioxeia* (Garcia-Cuetos et al. 2010; Nishitani et al. 2010). However, ultrastructural analyses of chloroplasts in the three taxa have resulted in inconsistent interpretations regarding the status of the plastids. Garcia-Cuetos et al. (2010) argued that the plastids in *D. acuminata* are permanent because the arrangement of the thylakoids, the numbers of membranes around the chloroplasts and the arrangement of the pyrenoids are different from chloroplasts in both *M. rubrum* and *T. amphioxeia*. Nishitani et al. (2010) argued that it is possible that the plastids in *Dinophysis* spp. are permanent, kleptoplastids or even both based on molecular and ultrastructural analyses hitherto. It is possible that *Dinophysis* spp. have a permanent plastid of their own but also utilize derived plastids from *Teleaulax* spp. via ingestion of *M. rubrum* (Park et al. 2010). In any case, *Dinophysis* spp. have the highest growth rates in cultures where both *M. rubrum* and *Teleaulax* spp. are present (Nagai et al. 2008), suggesting an interdependency of these three taxa.

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