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Ingestion of cryptophyte cells by the marine photosynthetic ciliate *Mesodinium rubrum*

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ABSTRACT: We investigated the mechanism of capturing and ingesting cryptophyte cells by a laboratory strain of the marine photosynthetic ciliate *Mesodinium rubrum* Lohmann 1908 (= *Myrionecta rubra* Jankowski 1976), a cosmopolitan red tide species. When offered cryptophytes as food, *M. rubrum*, originally grown photosynthetically for 2 wk, used its bifurcated oral tentacles to instantly seize prey cells when encountered. Immediately after capturing a prey cell, *M. rubrum* swam in a zigzag pattern (30 to 60 µm long linear paths) for >4 s, without showing the large jumps (with ca. 2000 µm long linear paths) that were usually observed when the predator was not feeding. *M. rubrum* with a cryptophyte attached to its tentacles became motionless while the prey cell was moved to the oral surface of the predator, a process that took <10 s. Engulfment of a captured prey cell by *M. rubrum* occurred through a cytostome-like structure and took ca. 15 s. Once engulfed, the prey was slowly delivered to the posterior end of the ciliate over a period of ca. 63 s. The whole feeding process lasted approximately 92 s. With increasing mean prey concentration, specific growth rates of *M. rubrum* feeding on the cryptophyte increased, with saturation at a mean prey concentration of 44 cells ml^{-1}. The maximum specific growth rate (mixotrophic growth) of *M. rubrum* feeding on the cryptophyte was 0.521 d^{-1}, under continuous illumination of 60 µE m^{-2} s^{-1}, while its growth rate (phototrophic growth) under the same light conditions without added prey was 0.357 d^{-1}. The ingestion rate of *M. rubrum* feeding on cryptophytes increased continuously with increasing prey concentration. The maximum ingestion rate was 8.9 cryptophytes $ciliate^{-1}$ d^{-1}. *M. rubrum* may sometimes exert considerable impact on prey populations.

KEY WORDS: Feeding · Growth rate · Grazing · Life cycle · Phagotrophy · Red tide

INTRODUCTION

Mesodinium rubrum Lohmann 1908 (= *Myrionecta rubra* Jankowski 1976) (Lynn & Small 2002) is a planktonic ciliate that sometimes forms red tides (Powers 1932, Taylor et al. 1971, Lindholm 1985). The nutritional mode of *M. rubrum* has been under debate for a long time, and it is listed as an obligate phototroph (Sieburth et al. 1978) and/or a species with the potential for heterotrophy (Smith & Barber 1979). The inclusion of functional cryptophyte plastids (Barber et al. 1969, Hibberd 1977) as 'incomplete symbionts' (Oakley & Taylor 1978) has also led to the speculation that *M. rubrum* is a potential mixotrophic ciliate (Lindholm & Mörk 1989). Ingestion of cryptophyte cells by *M. rubrum* was first suggested by Hargraves (1991) based on photographic evidence, and the inclusion of cryptophyte cells in the protoplasm of *M. rubrum* was later documented by Gustafson et al. (2000) using data from cytological, epifluorescence microscopy and flow cytometry. The pre-capture behavior and feeding process of *M. rubrum* on cryptophytes, however, have not yet been documented.

To investigate the feeding process of *Mesodinium rubrum* grazing on cryptophytes, we established a culture of *M. rubrum* from coastal waters of Korea and followed the capture and ingestion of prey using a video system. We also measured ingestion rates of *M. rubrum* feeding on cryptophytes as a function of prey concentration.

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The results of the present study provide a basis for understanding the feeding mechanism of *Mesodinium rubrum* grazing on cryptophytes and the impact of such grazing on prey populations.

MATERIALS AND METHODS

Clonal culture of a cryptophyte. The clonal culture of an unidentified cryptophyte (CR-MAL01) was established by isolating single cells from water samples collected at Gomso Bay, Korea (35° 40′ N, 126° 40′ E) in February 2002. The cryptophyte culture was grown at 15°C in enriched f/2 seawater media (Guillard & Ryther 1962) minus silicate under continuous illumination of 25 µE m^{-2} s^{-1} provided by cool-white fluorescent lamps. For feeding experiments, we used cultures in exponential growth phase.

Isolation and culturing of *Mesodinium rubrum.* Individual *M. rubrum* cells were isolated from natural assemblages of Gomso Bay during May 2001, when water temperature and salinity were approximately 18°C and 31.5 psu, respectively. Each of the isolated *M. rubrum* cells was washed by serially transferring into 3 droplets of f/2 medium and then put into 2 ml of f/2 medium with 5 prey cells held in a 3 ml well of a 24-well tissue culture plate. The culture plates were incubated at 15°C under continuous illumination of 60 µE m^{-2} s^{-1} provided by cool white fluorescent light. Every 5 to 6 d, cryptophyte prey (CR-MAL01) were added to each 3 ml well containing *M. rubrum*, with the density of cryptophytes adjusted to be 5 times that of the *M. rubrum* cells. Once dense cultures of *M. rubrum* were obtained, they were transferred to 500 ml polycarbonate (PC) bottles containing f/2 medium. Subsequent transfers were made at intervals of 5 to 6 d by placing one-third of a culture in a 500 ml PC bottle into a new PC bottle containing f/2 medium and cryptophytes adjusted to be 5 times that of the *M. rubrum* cells. Experiments were conducted when a large volume of *M. rubrum* culture (MR-MAL01) became available.

Cell dimension and volume. Mean size, surface area and volume of the prey cryptophyte and *Mesodinium rubrum* cells (Table 1) were obtained with an electronic particle counter (Coulter Multisizer II, Coulter Corporation).

Feeding processes. To record the feeding process of *Mesodinium rubrum* on cryptophytes, actively swimming *M. rubrum* cells that had been starved (i.e. grown photosynthetically) for 2 wk were added to 6-well tissue culture plates containing prey. Images of feeding *M. rubrum* were taken continuously over the following 10 h using a Nikon camera and a video camera system (Watec 202B video camera) mounted on an Olympus compound microscope at magnifications of 400× (for the Nikon camera) and 200× (for the video camera).

Ingestion and growth rates. This experiment was designed to measure growth and ingestion rates of *Mesodinium rubrum*, as a function of the prey concentration, when feeding on cryptophytes of 5 different concentrations (0, 75, 1500, 7500, 15 000 cells ml^{-1}). Photosynthetically grown, 2 wk old cultures of *M. rubrum* were diluted with f/2 media in 500 ml PC bottles to obtain experimental cultures at 1500 cells ml^{-1}. The abundances of *M. rubrum* and prey were determined by enumerating cells in three 1 ml Sedgwick-Rafter counting chambers (SRCs).

Initial concentrations of cryptophytes were established using an autopipette by delivering predetermined volumes of cryptophyte culture (CR-MAL01) to the bottles. Duplicate 500 ml PC experimental bottles (mixtures of predator and prey) and duplicate control bottles (prey only) were set up at each predator-prey combination. Duplicate control bottles containing only *Mesodinium rubrum* were also established at 1 predator concentration. All the experimental bottles were kept under continuous illumination of 60 µE m^{-2} s^{-1} of cool white fluorescent and culture-room temperature of 15°C. To determine predator and prey densities at the same time of day (i.e. 16:00 h) from the beginning to the end of the 10 d long experiment, a 5 ml aliquot was removed from each bottle and fixed with 5% Lugol's solution, and all or >200 *M. rubrum* and prey cells in three 1 ml SRCs were enumerated.

The specific growth rate of *Mesodinium rubrum* (µ, d^{-1}) was calculated by averaging the instantaneous growth rates (IGR) for each sampling interval, calculated as:

$$\mathrm{IGR} = \frac{\ln(S_{t_2}/S_{t_1})}{t_2 - t_1} \times 24 \qquad (1)$$

where $t_2 - t_1 = 24$ h and S_{t_1} and S_{t_2} = the concentration of *M. rubrum* at consecutive samplings. The final t_2 for

Table 1. Prey cryptophyte species and ciliate *Mesodinium rubrum* used in the present study. Mean and standard error (SE) of equivalent spherical diameter (ESD) and cell volume were measured by the Coulter Multisizer II electronic particle counter

Species	Strain no.	ESD (µm)	Cell volume (µm^3)	Sampling area (and date)
Unidentified cryptophyte	CR-MAL01	5.3 ± 0.0047	76.1 ± 0.22	Gomso Bay (Feb 8, 2002)
Mesodinium rubrum	MR-MAL01	22.0 ± 0.040	5996 ± 30.0	Gomso Bay (May 31, 2001)

calculation was 72 h, which provided the highest specific growth rate.

Data for *Mesodinium rubrum* growth rate (GR) were fitted to a Michaelis-Menten equation:

$$\mu = \frac{\mu_{max}(x - x')}{K_{GR} + (x - x')} \quad (2)$$

where μ_{max} = the maximum GR (d^{-1}); x = prey concentration (cells ml^{-1}); x' = threshold prey concentration (the prey concentration where $\mu = 0$); and K_{GR} = the prey concentration sustaining $\frac{1}{2}\ \mu_{max}$. Data were iteratively fitted to the model using DeltaGraph® (Delta Point).

Ingestion rate (IR) was calculated using the equations of Frost (1972) and Heinbokel (1978). Incubation time for calculating ingestion rate was the same as for estimating growth rate. Ingestion rate data were fitted to a Michaelis-Menten equation:

$$IR = \frac{I_{max}(x)}{K_{IR} + (x)} \quad (3)$$

where I_{max} = the maximum IR (cells *Mesodinium*$^{-1}$ d^{-1}); x = prey concentration (cells ml^{-1}), and K_{IR} = the prey concentration sustaining $\frac{1}{2}\ I_{max}$.

RESULTS

Pre-capture behavior and feeding process of *Mesodinium rubrum*

Many video-recorded images were analyzed to determine the time span for each of the 5 steps characterizing the complete feeding process (Table 2). As soon as cryptophytes were introduced into starved cultures of *Mesodinium rubrum* (i.e. those grown photosynthetically for 2 wk), individual ciliates began using their bifurcated oral tentacles to capture prey (Fig. 1A). Once a prey cell was attached to the oral tentacles, *M. rubrum* moved in a zigzag pattern consisting of 30 to 60 µm long linear paths. This behavior (Step I, Table 2) lasted for ca. 4.3 s. During Step I, *M. rubrum* did not make large swimming jumps (ca. 2000 µm long linear path), as is typical of all non-feeding cells. At the end of Step I, *M. rubrum* became 'motionless' for ca. 9.4 s (Step II, Table 2, Fig. 1B,C), during which time the captured prey was carried down to the oral tip of the ciliate. Engulfment of the captured prey cell, a process that took ca. 14.9 s (Step III, Table 2, Fig. 1D–F), always occurred when the cell passed through a hollow cytostome-like structure at the oral end of *M. rubrum*. Once inside the ciliate, the engulfed prey cell was slowly transported to the posterior end of the *M. rubrum* cell (ca. 63.1 s; Steps IV and V, Table 2, Fig. 2). The time required for an engulfed prey cell to reach the equatorial ciliary girdle of *M. rubrum* (ca. 17.1 s; Step IV, Table 2) was shorter than that needed to move the equator of the ciliate to aboral end of the cell (ca. 46.0 s; Step V, Table 2). Thus, the whole feeding procedure took approximately 92 s.

Table 2. Time (s) for each of the 5 feeding steps. Step I: feeding procedure between physical contact of the ciliate's oral tentacles to the prey cell and fixation of the captured prey by the predator; Step II: until the prey cell reaches the ciliate's cytostome; Step III: until the prey disappears from the surface of the ciliate predator; Step IV: until the prey cell meets the equatorial plane of the ciliate's cirri; and Step V: until the prey is delivered to the aboral end of *Mesodinium rubrum*

Feeding step	Mean	SE	No. observation
Step I	4.3	0.96	8
Step II	9.4	2.25	8
Step III	14.9	1.79	9
Step IV	17.1	0.80	3
Step V	46.0	–	1

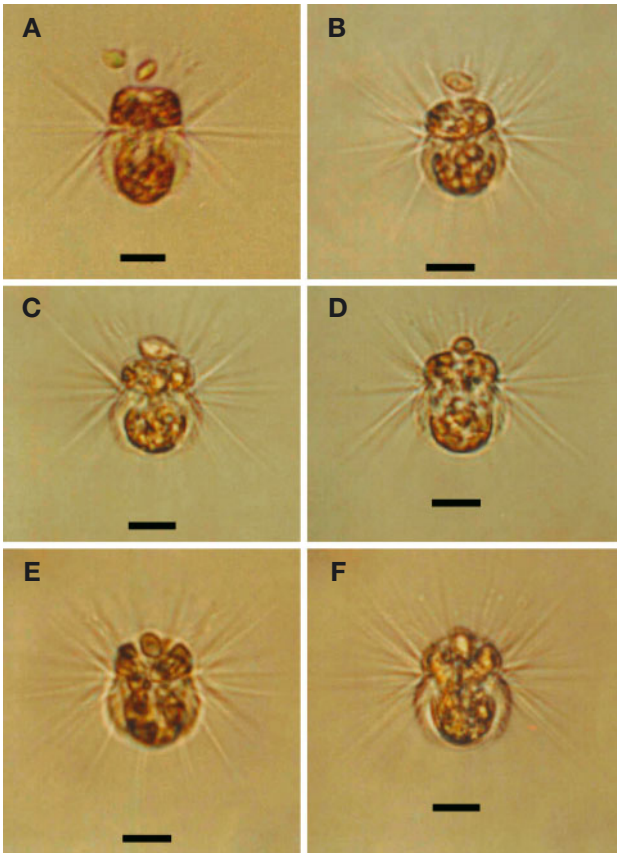

Fig. 1. Feeding process of *Mesodinium rubrum* (MR-MAL01) on a cryptophyte prey (CR-MAL01). (A) *M. rubrum* attacking the prey cell. (B,C) Captured prey cell being carried down to the oral tip of *M. rubrum*. (D–F) *M. rubrum* engulfing the captured prey cell after it has passed through a hollow 'cytostome-like' structure at the oral end. Scale bars = 10 µm

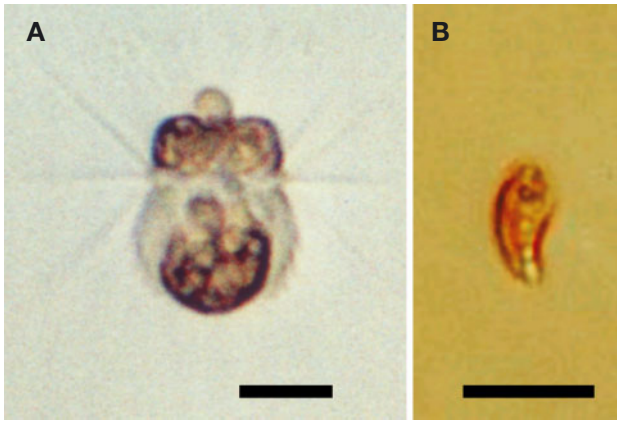

Fig. 2. (A) *Mesodinium rubrum* (MR-MAL01) engulfing (B) a new cryptophyte (CR-MAL01). Prey cells ingested earlier were stacked at the aboral part of *M. rubrum* cell. Scale bars = 10 µm

Growth and ingestion rate of *Mesodinium rubrum*

The growth rate of *Mesodinium rubrum* at low prey concentrations (<1000 cells ml^{-1}) increased sharply relative to basic photosynthetic growth rate (BPGR) (Fig. 3). At prey concentrations >2000 cells ml^{-1}, however, growth of *M. rubrum* rate was saturated. When fitted to the Michaelis-Menten equation, μ_{max} was 0.521 d^{-1}, and K_{GR}, the prey concentration sustaining ½(μ_{max} – BPGR), was calculated to be 44 cells ml^{-1}.

The ingestion rate of *Mesodinium rubrum* feeding on cryptophyte prey continuously increased with increasing prey concentration (Fig. 4). When fitted to a Michaelis-Menten equation, I_{max} was 8.9 cells *Mesodinium*$^{-1}$ d^{-1}, and K_{IR} was calculated to be 26 500 (cells ml^{-1}).

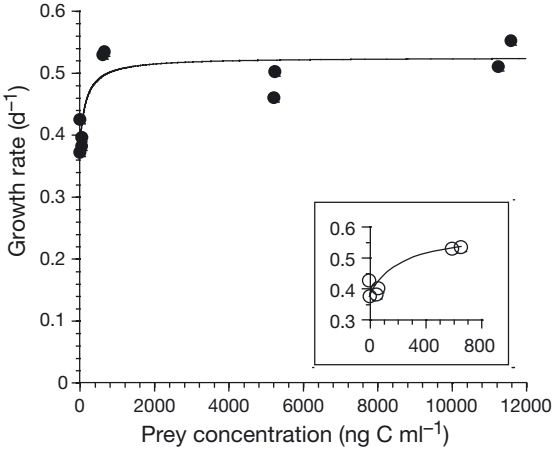

Fig. 3. Specific growth rates (GR) of *Mesodinium rubrum* (MR-MAL01) feeding on cryptophyte (CR-MAL01) as a function of mean prey concentration. The curve is fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. GR (d^{-1}) = 0.52 (x + 96)/[44 + (x + 96)], r^2 = 0.73, where x = mean prey concentration

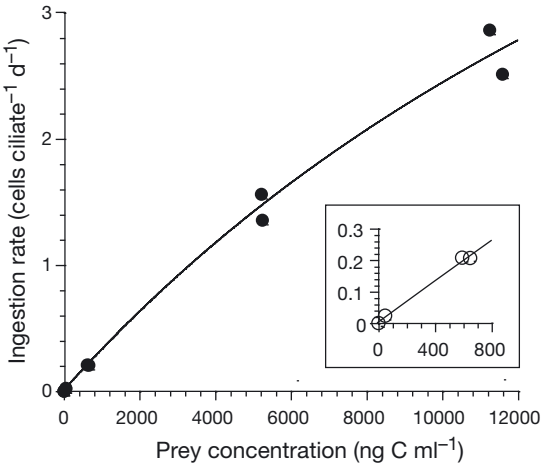

Fig. 4. Ingestion rates (IR) of *Mesodinium rubrum* (MR-MAL01) feeding on cryptophyte (CR-MAL01) as a function of prey mean concentration. The curve is fitted by a Michaelis-Menten equation (Eq. 2) using all treatments in the experiment. IR (prey predator^{-1} d^{-1}) = 8.9 [x/(26 500 + x)], R^2 = 0.989, where x = mean prey concentration

DISCUSSION

Relative to the slow-growing (0.06 to 0.13 d^{-1}) Antarctic isolate of *Mesodinium rubrum* studies by Gustafson et al. (2000), our temperate culture of *M. rubrum* from bloom waters at Gomso Bay, mid-western coast of Korea, was very fast-growing, exhibiting 0.52 d^{-1} for mixotrophic growth and 0.36 d^{-1} for autotrophic growth (Table 3). Feeding of *M. rubrum* on cryptomonads was ascertained by direct microscopic observations and video-recordings following addition of cryptophyte cells to culture of *M. rubrum* starved for 2 wk (= photosynthetically grown). We also measured ingestion rates of our temperate strain of *M. rubrum* (MR-MAL01) when offerred cryptophytes (CR-MAL01) at various concentrations as prey.

Prey ingestion by photosynthetic *Mesodinium rubrum*

Photosynthesis is the main source of nutrition for *Mesodinium rubrum* (Ryther 1967, Stoecker et al. 1991, Lindholm 1992), and thus accounts for this ciliate being classified as a marine phytoplankter (Crawford 1989). Additionally, uptake of dissolved organic compounds is thought to partially satisfy dark respiratory demands of *M. rubrum* (Smith & Barber 1979). Prey ingestion and organelle retaining by *M. rubrum* (Taylor et al. 1969) were clearly shown in a series of 'feeding' experiments using an *M. rubrum* isolate from McMurdo Sound, Antarctica, and its prey, a polar cryptophyte *Teleaulux acuta* (Gustafson et al. 2000). Feeding has not been previously observed in *M.*

Table 3. Carbon requirement for the growth of *Mesodinium rubrum* (GR-C) and contribution by the ingested C (IG-C) through feeding on prey cells. AV(Cp): average density of prey cryptophyte (cells ml^{-1}). Carbon contents of the prey and *M. rubrum* cell were calculated using reported conversion factors: 0.19 pg C μm^{-3} for *M. rubrum* (Putt & Stoecker 1989) and 220 fg C μm^{-3} for cryptophyte cells (Boersheim & Bratbak 1987)

AV(Cp) (cells ml^{-1})	*Mesodinium rubrum* Growth (μ, d^{-1})	*Mesodinium rubrum* C requirement (GR-C ciliate^{-1} d^{-1})	Prey cryptophyte Ingestion (prey ciliate^{-1} d^{-1})	Prey cryptophyte Ingested C (IG-C ciliate^{-1} d^{-1})	Contribution by IG-C % carbon (IG-C/GR-C)	Contribution by IG-C Mean (%)
0	0.372	570.5	0	0	0	0.00
0	0.425	651.8	0	0	0	
50	0.396	607.3	0.021	0.35	0.058	0.06
47	0.382	585.8	0.022	0.37	0.063	
613	0.529	811.3	0.208	3.47	0.428	0.42
658	0.534	818.9	0.205	3.42	0.418	
5240	0.502	769.9	1.356	22.65	2.941	3.32
5213	0.460	705.4	1.562	26.09	3.698	
11247	0.510	782.1	2.864	47.83	6.115	5.54
11587	0.552	846.5	2.514	41.98	4.959	

rubrum (Gustafson et al. 2000), although Hargraves (1991) documented the capture of cryptophytes by a blue-green *Mesodinium* sp. from the Narrow River, Rhode Island, USA.

Under the experimental conditions used here, feeding on cryptophyte prey contributed only partial resources for growth of *Mesodinium rubrum.* The mean specific growth rate of *M. rubrum* was 0.40 d^{-1} in experimental bottles without added cryptophytes (=BPGR), and growth of *M. rubrum* was not limited by prey availability in the experimental bottles with an initial prey density of 1370 cells ml^{-1} (Fig. 3). When specific growth rates of *M. rubrum* were fitted to a Michaelis-Menten equation, μ_{max} was 0.521 d^{-1}, and the specific growth rate at prey concentration '0' was estimated to be 0.357 d^{-1}.

The contribution of the ingested prey to the C requirement for growth of *Mesodinium rubrum* was not greater than 6% in our experiments (Table 3). Therefore, phagotrophism of *M. rubrum* may be required for something other than meeting its major nutritional demands. Newly retained chloroplasts may be kept functionally active inside a *M. rubrum* cell for only a few generations (see Fig. 1a,b in Gustafson et al. 2000). Regular uptake of prey organelles is needed to sustain growth, because the chloroplasts of the mother cell are simply halved into 2 fractions for the 2 new daughter cells during cell division of *M. rubrum* (Lindolm et al. 1998, see Fig. 3a in Gustafson et al. 2000). One can thus speculate that *M. rubrum* needs to ingest cryptophyte prey once every few generations. Such prey ingestion events may be short lived, requiring less than 30 min (90 s for each prey cell, Table 2) to obtain 20 new chloroplasts (Hargraves 1991). Thus, we hypothesize that feeding is not a regular process for acquiring major nutrition, but rather an infrequent life cycle event providing *M. rubrum* a way to acquire chloroplasts.

Impact of *Mesodinium rubrum* predation on cryptophyte populations and its ecological implications

K_{IR} (4.5 prey *Mesodinium rubrum*$^{-1}$ d^{-1}) was calculated to be 26 500 cells ml^{-1}, which is ca. 2 times that of the maximum initial prey concentration (13 000 cells ml^{-1}, Fig. 4) in our feeding experiment. The mean IR in duplicate experimental bottles with the maximum initial prey concentration was 2.7 prey *M. rubrum*$^{-1}$ d^{-1} (Fig. 4). Mean prey concentration in those bottles declined to 1220 and 13 cells ml^{-1} after 5 and 10 d, respectively, while the mean predator density increased from 1430 ciliates ml^{-1} to 15 720 and 16 530 ciliates ml^{-1} after 5 and 10 d, respectively (H. S. Kim unpubl. data). Therefore, *M. rubrum* was able to control the cryptophyte populations in our experiment, reducing prey density to an extremely low concentration within 10 d. The maximum concentrations of natural populations of *M. rubrum* (1700 to 5020 ciliates ml^{-1}) and cryptophytes (2700 to 7900 cells ml^{-1}) in Gomso Bay and the adjacent Keum River Estuary, Korea (W. Yih unpubl. data), correspond well with the prey and predator concentrations used in our feeding experiment. Thus, it seems likely that the natural *M. rubrum* populations in Gomso Bay and Keum River Estuary (Yih & Shim 1997) sometimes exert considerable impact on cryptophyte prey populations.

Cryptomonads are known to be ingested by the notorious *Pfiesteria* spp. (Burkholder & Glasgow 1997) and other dinoflagellates including *Amphidinium latum* (Horiguch & Pienaar 1992), *Amphidinium poecilochroum* (Larsen 1988), *Prorocentrum minimum* (Stoecker et al. 1997), *Gymnodinium acidotum* (Fields & Rhodes 1991), *Gymnodinium* '*gracilentum*' (Skovgaard 1998), and *Gyrodinium galatheanum* (Li et al. 1996, 2000). Many of these dinoflagellates retain chloroplasts of their cryptophyte prey, rendering cryptophytes a preferred source of kleptochloroplast among dinoflagellates

(Eriksen et al. 2002) and other protists like *Mesodinium rubrum* (Gustafson et al. 2000). Thus, one might speculate that the multi-species competition for the 'common food organism,' cryptophytes, may affect patterns of succession in natural communities of planktonic protists. The complexity of trophic interactions associated with *M. rubrum* become even more complicated by recent reports that mixotrophic cryptophyte species feed on bacterioplankton (Roberts & Laybourn-Parry 1999).

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