

The ciliate *Mesodinium rubrum* and its cryptophyte prey in Antarctic aquatic environments

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Abstract For growth, the mixotrophic ciliate *Mesodinium rubrum* sequesters organelles from ingested prey. Feeding in the field is poorly known; however, isolates of an Antarctic *M. rubrum* strain are maintained in culture on a diet of *Teleaulax*/*Plagioselmis*/*Geminigera*-like cryptophytes, suggesting that cryptophyte presence may be an important factor controlling *M. rubrum* distribution and abundance in nature. We augmented field surveys with published findings to establish the distribution of both *M. rubrum* and a *Geminigera*-like cryptophyte in a range of East Antarctic aquatic environments. We also studied their overwinter abundances in Ace Lake to determine whether a predator–prey relationship existed between the two species in this natural enclosed ecosystem. The ciliate and the cryptophyte co-occurred in the majority of sites sampled which ranged widely in salinity (2.2–150 ‰) and temperature (−3.0–16 °C). We observed a cyclic relationship in species abundances in Ace Lake, implying population growth for *M. rubrum* responded to changed cryptophyte abundance. *Mesodinium rubrum* likely exerts top-down pressure on cryptophyte abundances in natural enclosed ecosystems especially under low-light winter conditions. The ciliate can be considered an apex predator in highly truncated food webs.

Keywords Endosymbiont · *Mesodinium* · Mixotrophic · Trophic relationship

Introduction

The mixotrophic ciliate *Mesodinium rubrum* (Lohmann 1908) obtains much of its carbon requirements for optimum growth through photosynthesis (Johnson and Stoecker 2005). To do so, it must sequester its symbiont organelles from ingested free-living cryptophytes (Gustafson et al. 2000; Johnson et al. 2007)—organelles most often acquired from the Clade B genera *Teleaulax*, *Plagioselmis* and *Geminigera* (Deane et al. 2002; Park et al. 2007). For example, from molecular sequencing, Johnson et al. (2006) identified *Geminigera* cf. *cryophila* (originally called *Teleaulax acuta* in Gustafson et al. 2000) as the cryptophyte endosymbiont to *M. rubrum* in McMurdo Sound, Antarctica. While the feeding behaviour of *M. rubrum* in the field is poorly known (Peterson et al. 2013), its established preference for Clade B cryptophytes suggests that their availability may be an important factor in determining the distribution and abundance of *M. rubrum* in natural environments.

There appear to be a number of factors controlling *M. rubrum* abundance both in culture and in natural environments. Growth of *M. rubrum* populations in culture responded to light intensity, prey (cryptophyte) concentration and type, and also pH (Johnson and Stoecker 2005; Park et al. 2007; Smith and Hansen 2007). Field studies in temperate Chesapeake Bay and the Columbia River showed cryptophyte numbers, water temperature and salinity influenced *M. rubrum* abundance (Johnson et al. 2013; Peterson et al. 2013). Studies of high-latitude lakes revealed that temperature and salinity appeared to be the most important controlling factors (Perriss et al. 1995;

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Gibson et al. 1997), but those Antarctic studies overlooked cryptophyte presence because at the time it was unclear whether *M. rubrum* ever fed. Therefore, one of our objectives was to determine whether the presence of cryptophytes could be considered a factor controlling the distribution of *M. rubrum* in such high-latitude aquatic environments.

The Vestfold Hills form a roughly triangular ice-free coastal oasis of about 400 km² containing a range of fresh-to-hypersaline lakes and bounded by a coastline indented with marine embayments and fjords. The saline lakes are of marine origin having formed as a result of ice-sheet retreat and related changes in sea level following the last deglaciation some 8000 years ago (Gibson 1999). Since then, thirty-four of the saline lakes became permanently chemically stratified (meromictic) while others remained seasonally physically stratified (monomictic) lakes (Gibson 1999). The often simplified microbial biodiversity present in these lakes has been attributed to the severity of the environment, long-term isolation from the sea and progressive stratification, with the species present reflecting their marine origins (Laybourn-Parry and Pearce 2007). Such simplified, often stratified food webs provide an ideal environment in which to investigate relationships between organisms and their evolution (Laybourn-Parry and Pearce 2007).

Ace Lake is one of the best studied saline meromictic lakes of the Vestfold Hills (Rankin et al. 1999). The lakes' biota includes an active overwintering population of *M. rubrum*, and a single cryptophyte species (Gibson et al. 1997; Rankin et al. 1999) with molecular affinities to the Clade B cryptophyte (Deane et al. 2002) *Geminigera cryophila* (author's unpublished data) which as stated previously, are the preferred food for *M. rubrum*. The coincidence of the two species in this simplified lake ecosystem makes it possible to study proposed trophic relationships between the species. Therefore, our second objective was to determine whether a predator–prey relationship existed between the cryptophyte and the ciliate in Ace Lake.

We combined published records with results from our own field studies to qualitatively establish the presence of *M. rubrum* and the *Geminigera*-like cryptophyte along a salinity gradient of aquatic ecosystems throughout the Vestfold Hills region. In addition, we quantified *M. rubrum* and cryptophyte abundances in Ace Lake during an austral winter to investigate the possible trophic relationship between two species in that lake.

Materials and methods

Cryptophyte identification

Since first reported in water samples collected from Ace Lake, Vestfold Hills (see references in Rankin et al. 1999),

an asymmetrically shaped, red-pigmented cryptophyte has been observed from a number of lake and marine environments (Scott and van den Hoff 2005). Light microscope (LM) and scanning electron microscope (SEM) observations in this and in previous studies revealed that the Ace Lake cryptophytes morphology (Fig. 1a) was identical across a range of sites including Burton Lake, Ellis Fjord, Bayly Bay, Davis Bay and Fletcher Lake. The cryptophyte has close molecular similarities with *G. cryophila* (authors' unpublished data), yet its morphology is clearly distinguishable from the described Antarctic marine cryptophyte *G. cryophila* (Taylor and Lee 1971; Hill 1991, see Figs. 10.1 c, d in Scott and van den Hoff 2005). While it is possible that more than one cryptophyte species was present in the lakes surveyed, we used the conspicuous morphology and pigmentation of this *Geminigera*-like cryptophyte to positively identify it when it occurred in samples.

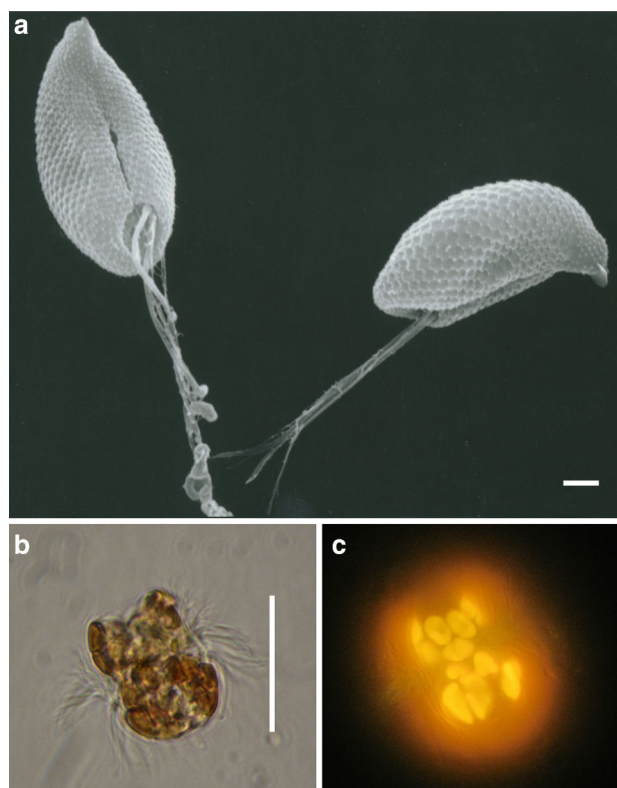


Fig. 1 **a** Scanning electron micrograph of *Geminigera* sp., an unidentified cryptophyte species from Ace Lake, Vestfold Hills, East Antarctica. This cryptophyte has close taxonomic affinities with the Clade B cryptophyte genera *Teleaulax*/*Plagioselmis*/*Geminigera* (Deane et al. 2002), the preferred prey of the ciliate *Mesodinium rubrum* which also occurs in Ace Lake. Bar = 1 µm. **b, c** *Mesodinium rubrum* as viewed by phase contrast (**b**) and epifluorescence microscopy (**c**) of the same cell collected from Ace Lake during the austral winter. The right image (**c**) shows the intracellular distribution of fluorescing (pigment containing) cryptophyte (*Geminigera* sp.) plastids ingested by the ciliate. Bar = 50 µm

Microscopy and cell counts

SEM preparations were made by allowing drops of EM-grade glutaraldehyde-fixed (final concentration of 1 %) water sample to air-dry onto poly-L-lysine-coated cover slips. The cover slips were then dehydrated through a methanol series (10–100 % dry) and sputter-coated with gold, and the preparations examined and protists photographed using a JEOL JSM-840.

The presence of chlorophyll containing plastids was determined by epifluorescence microscopy of glutaraldehyde-fixed or live *M. rubrum* cells collected from Ace Lake. Cell autofluorescence was observed with a Zeiss Axioskop equipped with a blue excitation filter set (487909) consisting of a 450- to 490-nm exciter filter, a 510-nm chromatic beam splitter and a 520-nm barrier filter.

Species distribution in the Vestfold Hills region

Occurrences of a *Geminigera*-like cryptophyte (Fig. 1a) hereafter termed “*Geminigera* sp.” and the ciliate *M. rubrum* (Fig. 1b, c) were determined from qualitative field surveys augmented with records from previously published studies undertaken on the dates listed in Online Resource 1. At field survey sites, a hole was drilled through the ice cover to sample only the underlying oxygenated water column using a depth-graduated hose and a 12-V peristaltic pump. Sufficient water was collected at each site to fill a 25-L⁻¹ plastic jerry can. At chemically stratified (meromictic) sites, water was collected from immediately below the ice cover, then at 2 m and subsequently at 2 m increments to the depth of the chemocline. Water samples were collected at the same depth intervals from physically stratified (monomictic) sites with the exception that the deepest sample was collected from within 1 m of the bottom. The resulting 25-L⁻¹ “whole-lake” water samples were kept in an insulated box to prevent freezing while in transit to the laboratory. Microbes were concentrated by continuous flow centrifugation and fixed with either basic Lugol’s solution or the addition of glutaraldehyde to a final concentration of 2 % prior to species presence/absence examination by LM and SEM.

Temporal abundances in Ace Lake

Ace Lake (Online Resource 2) was sampled fortnightly between 1 July 2004 and 2 December 2004. Water samples were collected from the ice/water interface, then at 2-m intervals from 2 to 12 m depth using a 2.5-L⁻¹ polycarbonate Kemmerer bottle. Lake ice-cover thickness was measured using a graduated pole. Abundances of *Geminigera* sp. and *M. rubrum* cells were determined by settling 10 mL⁻¹ of Lugol’s fixed water sample in plankton

chambers (Hasle 1978) over night. Cells were counted using an inverted light microscope (Leitz Labovert).

Results

Populations of both *M. rubrum* and *Geminigera* sp. were observed by LM and SEM in a range of lake, fjord, coastal embayment and open ocean sites sampled throughout the Vestfold Hills region (Online Resources 1 and 2). Although isolated from the open ocean by ice dams during the austral winter, sites at Bayly Bay, Burton Lake, Fletcher Lake, Rookery Lake, Franzmann Lake, Williams Lake, Deprez Basin and Ellis Fjord had a summer connection to the open ocean (Davis Bay) where populations of both species were observed. However, *Geminigera* sp. was observed but *M. rubrum* was not observed in Bayly Bay and Burton Lake, and *M. rubrum* was observed but *Geminigera* sp. was not observed in Franzmann and Rookery Lakes.

Online Resource 1 shows salinities at sample sites containing both species graded from 2.2 ‰ in near-fresh Watts Lake to 150 ‰ in hypersaline Ekho Lake, and temperatures were between −3.0 °C (Deprez Basin) and 16 °C (Ekho Lake). *Mesodinium rubrum* was observed in the absence of *Geminigera* sp. at lower temperatures in Lake Vereteno (−3.8 °C) and Rookery Lake (−10.8 °C). *Mesodinium rubrum* and *Geminigera* sp. were observed together in 17 of the 32 sites sampled, *M. rubrum* was observed alone at 10 sites, and *Geminigera* sp. was observed alone at five sites.

Relative abundances for *M. rubrum* and *Geminigera* sp. in ice-covered Ace Lake (Fig. 2) were determined for the austral winter–spring period, 2004. Whole-lake *M. rubrum* abundances ranged between 29 and 204 cells mL⁻¹, and *Geminigera* sp. abundances between 8 and 285 cells mL⁻¹. During the sampling period, the lake’s ice thickness increased from 1.06 m in early July to reach a maximum of 1.53 m by mid-November (Fig. 2). Photosynthetically active radiation (PAR) penetrating the ice cover and water temperatures in this lake are minimal during winter (Rankin et al. 1999). A late-July/August increase in the chlorophyll containing *M. rubrum* population lagged behind the increase in *Geminigera* sp. abundance. Abundance of *Geminigera* sp. then decreased to its winter minimum by mid-September. During August, *M. rubrum* numbers increased threefold to reach late winter levels, remaining relatively high until December when numbers fell again. The small stable population of *Geminigera* sp. that had persisted throughout September and October (late winter) increased (bloomed) in early November. Following the *Geminigera* sp. bloom abundances for both species remained high until the ice cover receded.

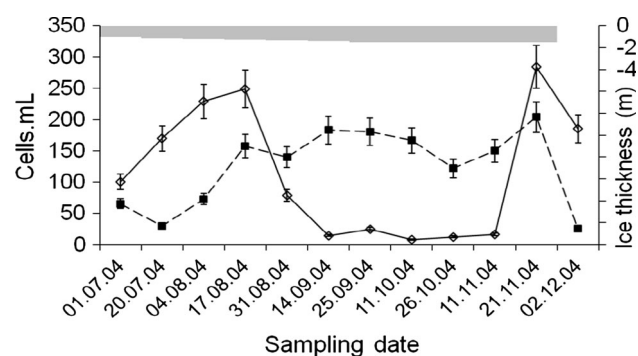


Fig. 2 Temporal changes in abundance estimates (left axis) for the ciliate *Mesodinium rubrum* (solid square and broken line) and its potential prey, *Geminigera* sp. (open diamond and solid line) in Ace Lake, Vestfold Hills, East Antarctica, 2004. Points represent species abundance for the integrated water column extending from the bottom of the ice cover to 12 m depth on each sampling date. Bars = standard error. Grey filled region = ice thickness (right axis)

Discussion

Mesodinium rubrum is the dominant ciliate inhabiting a continuum of saline environments throughout the Vestfold Hills region, East Antarctica (Laybourn-Parry and Pearce 2007, Online Resource 1). We found that this ciliate was capable of tolerating a wide range of polar habitats with salinities from 2.2 to 150 ‰ and temperatures between -10.8 and $+16$ °C. These new data represent a range extension of both environmental parameters beyond those previously reported for *M. rubrum* from Antarctica by Gibson et al. (1997), Perriss and Laybourn-Parry (1997) and Laybourn-Parry and Pearce (2007), with *M. rubrum* occurring in warmer waters with a wider salinity range. The upper temperature value of 16 °C for Antarctic *M. rubrum* is near the ciliates reported global maximum (ca. 20 °C) (Taylor et al. 1971). The cryptophyte we termed “*Geminigera* sp.” occurred across a similarly wide environmental range (-3.0 – 16 °C and 2.2–150 ‰), and this study is the first to report on the temperature and salinity capabilities for this organism.

The majority of the Vestfold Hills saline lakes and their biota are of marine origin (Laybourn-Parry and Pearce 2007). There are two possible explanations for the presence of *M. rubrum* and *Geminigera* sp. in such a wide range of saline lakes: (1) Sea water containing their ancestral marine populations was first isolated from Prydz Bay through glacial processes and isostatic uplift following the last glaciation, and (2) both species are relatively recent introductions into already-established lake ecosystems, their propagules having arrived through processes such as sea spray or faunal dispersal either directly from the ocean or via a stepwise transfer from the ocean through a succession of lakes (Laybourn-Parry and Pearce 2007). For

explanation two to be plausible, extant populations of *Geminigera* sp. and *M. rubrum* living in the nearby open ocean (e.g. Davis Bay) must be physiologically pre-adapted or have the physiological plasticity, to survive transferral from sea water to extreme hypo- or hyper-saline habitats. Both species are known from within oceanic sea-ice environments where they annually experience temperatures as low as -20 °C and changes in salinity associated with the formation and decay of the ice cover (Thomas and Dieckmann 2002). Physiological pre-adaptation could ensure that *M. rubrum* and *Geminigera* sp. not only have the capacity to establish in newly available habitats but are also well equipped to endure certain consequences of global climate variability and change. Already, a shift toward a cryptophyte-dominated phytoplankton community has been observed in the freshening ocean along the Antarctic Peninsula (Moline et al. 2004) where the impacts of Southern Hemisphere polar climate change appear greatest (Ducklow et al. 2013).

Molecular studies of the Antarctic *M. rubrum* have identified its endosymbiont as the cryptophyte *Geminigera* cf. *cryophila* (Johnson et al. 2006; Park et al. 2007). Only a single cryptophyte species (Fig. 1a) is known from the Ace Lake study site (see references in Rankin et al. 1999), and that cryptophyte has close phylogenetic affinities to *G. cryophila* (authors’ unpublished data). Moreover, it is the most likely source of the pigmentation observed using epifluorescence microscopy of live and fixed *M. rubrum* (Fig. 1b, c) collected from Ace Lake during winter. Those observations plus the cyclic changes in abundance for the two organisms over time (Fig. 2) lead us to conclude that a predator–prey relationship existed between the two species in Ace Lake during the study period. These field data support the proposal by Park et al. (2007) and Stoecker et al. (2009) that a predator–prey relationship should exist between these species and improve our understanding of the feeding relationship between these two organisms in nature.

Responses by the Ace Lake *M. rubrum* population to changed *Geminigera* sp. abundance were clear (Fig. 2). During early winter (July–August), the lake’s *M. rubrum* population responded positively to cryptophyte availability. Previous empirical evidence shows that growth for *M. rubrum* in culture also increased when fed cryptophytes (Johnson and Stoecker 2005; Park et al. 2007). We also observed growth of *M. rubrum* in Ace Lake slowed during winter and then remained steady for an extended period as *Geminigera* sp. numbers decreased and stabilised at their own minimum. Johnson and Stoecker (2005) showed that growth rates for *M. rubrum* also slowed or ceased in cryptophyte starved cultures and that their populations could remain relatively stable for extended periods without ingesting new prey. Overall, our observations in a natural

lake ecosystem are similar to previous laboratory studies, suggesting that *Geminigera* sp. abundance is implicated in *M. rubrum* population changes in polar ecosystems.

As stated above, the Ace Lake *M. rubrum* population remained stable for an extended period over the austral winter when *Geminigera* sp. availability was minimal and ice cover was thickest (Fig. 2). Moreover, overwintering cells of *M. rubrum* remained active and contained chlorophyll (Fig. 1c) when lake water temperatures and incoming PAR were lowest (Rankin et al. 1999). Moeller et al. (2011) showed that *M. rubrum* has the capacity to function phototrophically in low-light conditions, leading them to suggest that *M. rubrum* possesses a resilient photosynthetic apparatus that has an extraordinary capacity to acclimate to extremely low irradiances such as those found in waters beneath ice cover in Ace Lake. This is indeed the case but the ciliates' extraordinary photosynthetic capacity has been acquired by theft (Gustafson et al. 2000) through the sequestration of plastids from Clade B cryptophytes such as *Geminigera* cf. *cryophila* (Johnson et al. 2006). One distinguishing feature of Clade B cryptophyte plastids is the presence of a unique ancillary pigment, the biliprotein Cr-phycoerythrin 545 (Deane et al. 2002). The expression of this pigment is enhanced at low-light levels (Wilk et al. 1999) and well adapted to harvesting downwelling irradiance in the 450- to 550-nm wavelength region (the greenish-yellow part of the light spectrum) that dominates the light field beneath first-year ice, including the waters of Ace Lake (Maykut and Grenfell 1975; Gibson et al. 1997). The *Geminigera*-like red-pigmented cryptophyte from Ace Lake also contains the biliprotein Cr-phycoerythrin 545 (Scott and van den Hoff 2005; authors unpublished data), providing the lakes *M. rubrum* population with an excellent pre-adapted overwintering survival mechanism that could supplement starch storage and encystment (Bell and Laybourn-Parry 1999a).

Unexpectedly, a *M. rubrum* but no *Geminigera* sp. population was observed in ten of the study sites (Online Resource 1). Given the proposed trophic relationship between *M. rubrum* and Clade B cryptophytes (Park et al. 2007, this study), we expected that all sites with *M. rubrum* would, in principle, contain *Geminigera* sp. Our result may be an artefact caused by differences in sample concentration procedures or because *Geminigera* sp. abundance was below detection levels either at the time or depth of sampling. Alternatively, the disparity is real, and *M. rubrum* populations lacking the availability of *Geminigera* sp. may feed on different living prey or non-living particles such as those ingested by other mixotrophic protists (Sanders 1991; Myung et al. 2006). Based on the ciliates' trophic preferences, we speculate that populations of *Geminigera* sp.

will, in the future, be found at all sites where *M. rubrum* was observed in the Vestfold Hills lakes.

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