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## On the ecology of *Mesodinium rubrum* (Lohmann) (Ciliata) in a stagnant brackish basin on Åland, SW Finland

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### Abstract

Phenotypes, distribution and behaviour of *Mesodinium rubrum* (Lohmann) were studied in the stagnant basin Inre Verkviken (salinity about 6‰) on Åland, SW Finland. The organism varied in length from 15 to about 50 µm. The number of cirri varied greatly (33-85) and so did the number of chloroplasts (a few to more than 50). Surface maxima (red water) coinciding with chlorophyll a and productivity maxima were observed in October. Living specimens rich in starch were, however, also found down at 17 m in almost oxygen-free water. The swimming speed of *Mesodinium rubrum* can momentarily exceed 5000 µm s<sup>-1</sup>. Thus the organism has the potential to migrate vertically and take up nutrients from appreciable depths. The organism is highly phototactic and it is easily concentrated in a light gradient. The photosynthetic rate of enriched samples (artificial red water) was much higher than that of the original water samples. The role of *Mesodinium rubrum* in the food web is discussed.

### Introduction

*Mesodinium rubrum* (Lohmann), a ciliate with algal endosymbiosis, has been reported from almost all over the world, often as the cause of red water (TAYLOR et al. 1971). Remarkably high primary productivity values have been measured in connection with *Mesodinium* blooms in the upwelling areas off California and off Peru (PACKARD et al. 1978, SMITH and BARBER 1979). *M. rubrum* is common also in the Baltic Sea (LEEGAARD 1920, MICHANEK 1965) in spite of the low salinity. The organism is extremely euryhaline, its lower salinity limit is 1.5‰ (LINDHOLM 1978).

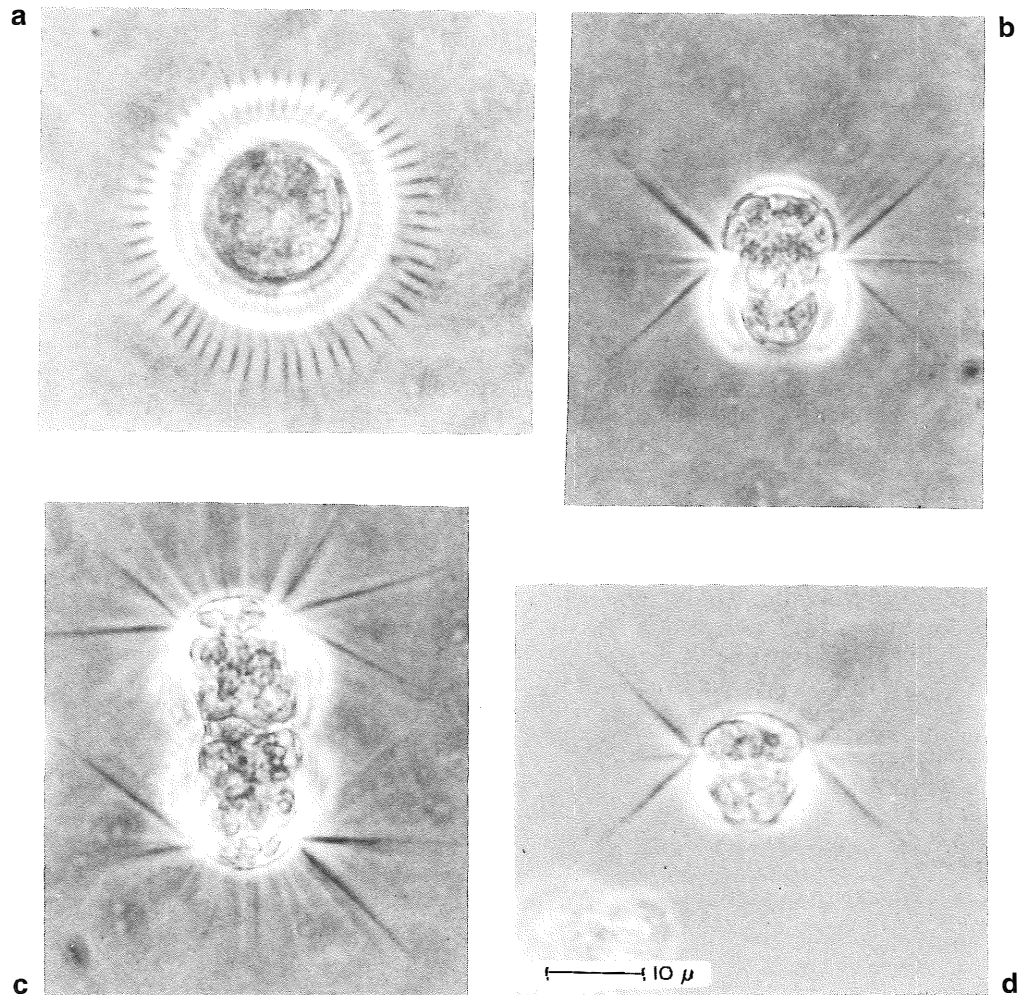
*Mesodinium rubrum* is difficult to observe alive as it is both extremely rapid and very fragile. The size of the organism varies considerably. Two size classes, "forma minor" and "forma major" have been reported from the Baltic Sea (LEEGAARD 1920, MICHANEK 1965). Ultrastructural studies (TAYLOR et al. 1971, HIBBERD 1977, OAKLEY and TAYLOR 1978) indicate that *M. rubrum* may be a complex of two or several species. Few planktologists have, however, studied the living organism. Thus there is limited information on the phenotypes, the physiology and the life cycle of *M. rubrum*.

### Material and methods

The present study is based mainly on material collected in the fjordlike Inre Verkviken, a stagnant, 20 m deep inlet (area 0.5 km<sup>2</sup>) on Åland, SW Finland. The inlet has brackish water as it is connected by a canal with the Bothnian Sea. The salinity of the surface water was 5.5–6.0‰ during the autumns of 1978 and 1979. In most seasons there is a slight halocline at a depth of 5–12 m. Below the halocline there is a cold, stagnant water mass (salinity about 6.2‰). A complete overturn may occur in November but

stagnation may also last for more than one year. The anoxic deep water contains  $\text{H}_2\text{S}$  and its  $\text{PO}_4\text{-P}$  and  $\text{NH}_4\text{-N}$  concentrations may rise to  $0.5 \text{ mg l}^{-1}$ . The basin as well as most methods have been described earlier (LINDHOLM 1975).

In 1978 and 1979 surface samples were taken directly with plastic bottles, whereas samples for vertical profiles were taken with a Ruttner sampler. Primary productivity was measured with the  $^{14}\text{C}$ -method. Living material, narcotized with MS 222 (Sandoz, Basel, final concentration about 1:10000) was studied with a Wild M 40 inverted microscope and photographed with a Nikon AFM camera. Living organisms were also filmed with a 16 mm movie camera at 32 exposures per second. Live samples were stored in  $+4^\circ\text{C}$  in artificial light; some samples remained rich in *M. rubrum* for more than 2 months. A light trap was used in order to concentrate the organisms (see Fig. 4



**Figure 1**

*Mesodinium rubrum*, living specimens from Inre Verkviiken October 13, 1979. a. End view. b. Side view. c. Specimen undergoing cell division. d. Short individual. Scale same for all.

for details). Water samples for phytoplankton counting were preserved in the field by transferring water to 100 ml bottles containing 4 ml conc. formalin. After addition of some droplets of Lugols solution 10 ml subsamples were used. The counting error should be less than 20 % as more than 100 individuals were counted (e.g. LUND et al. 1958). However, as the organisms are extremely fragile the numbers given may well be underestimated. Chlorophyll a was measured spectrophotometrically using extraction in 90 % acetone (GOLTERMAN et al. 1978). The chlorophyll a filters (Whatman GF/C) were stored deep-frozen for several months before analysis.

## Results and discussion

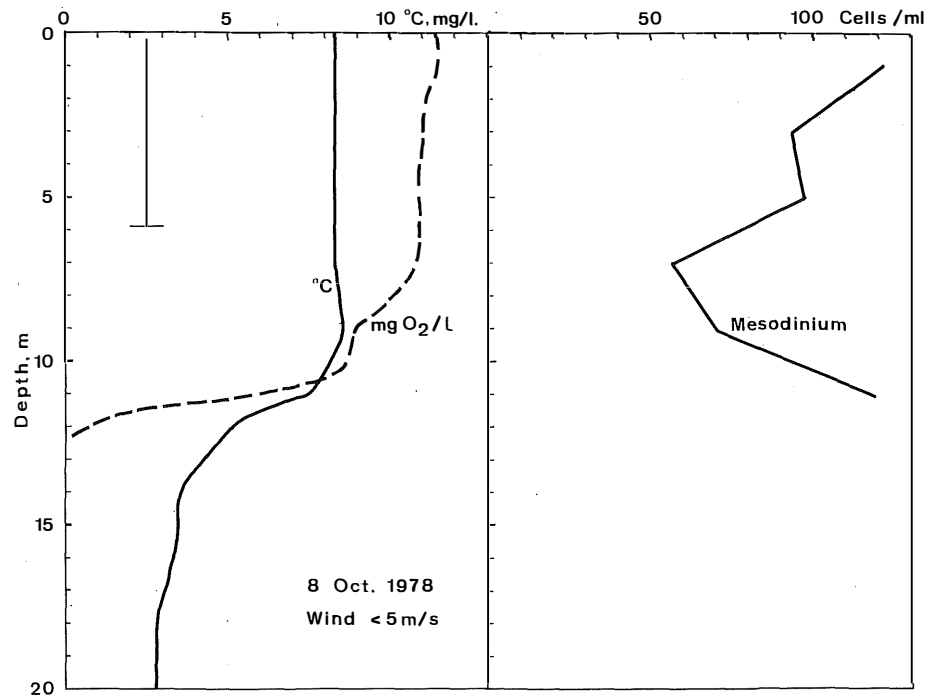
### Phenotypes and behaviour

*Mesodinium rubrum* is pigmented due to an algal endosymbiont visible as a package of chloroplasts. Small *Mesodinium* cells have 10–12 chloroplasts (sometimes fewer), whereas large individuals have 30 or more chloroplasts. Chloroplast numbers and cell length appear to be poor parameters for distinction between different forms of *M. rubrum*. External structures, again, are destroyed by most fixatives. The number of the cirri, which can be counted on photographs of living specimens (Fig. 1 a and b) may be useful. Small individuals of *M. rubrum* usually have 36 cirri (LINDHOLM 1978). Large individuals usually have more than 60 cirri. Thus, “forma minor” and “forma major” sensu LEEGAARD seem to differ with regard to the number of the cirri. However, in the Inre Verkviiken samples taken in October 1979 there were both small and intermediate size cells, showing also intermediate cirral numbers. Thus, the organisms present during my experiments in 1979 were not quite identical with bloom organisms studied earlier (LINDHOLM 1978). A few living specimens have been observed at cell division (Fig. 1 c). Dividing cells have never been recognized in preserved samples. Occasionally very short cells have appeared (Fig. 1 d), which probably represent individuals soon after cell division (TAYLOR et al. 1971: 398). Circumoral tentacles (which should be lacking according to the key of TAYLOR et al. 1971) have been observed in all size classes but not in all individuals. The tentacles are bifurcated and stiff and they are very easily lost. They are usually absent in preserved material, and are seldom reported. Their function is unknown. I have observed living material for hundreds of hours but have never seen the organism ingest particles. Healthy organisms are, however, not easy to study. Typically, *M. rubrum* is at rest for some seconds or less, and then jumps away up to several millimeters. A swimming speed of  $5 \text{ mm s}^{-1}$  was measured by cinematography. This means that the organism can move 100–200 times its body length within one second. *M. rubrum* appears to be five to ten times faster than mosts dinoflagellates.

### Vertical distribution

*Mesodinium rubrum* has been found in Inre Verkviiken during all seasons. The organism is active (swimming rapidly) even in ice-cold water and it occurs even under the ice (both small and large forms). However, concentrations exceeding  $100 \text{ cells ml}^{-1}$  have been observed only in the autumn. The organism is found both at the surface and at greater depths (Fig. 2). Noteworthy is the occurrence of high concentrations of *M. rubrum* close to the oxygen limit which in October 1978 was situated at 12–13 m.

In October 1979 dissolved oxygen was present down to 17 m. On October 13, a calm day, *M. rubrum* had its maximum at the very surface but on October 17, a moderately windy day, there was no surface peak (Fig. 3). One week later, on October 24, a calm, sunny day, *M. rubrum* formed a conspicuous surface maximum (Fig. 3). As earlier, *M. rubrum* was also this time detected at 15–16 m ( $10\text{--}20 \text{ cells ml}^{-1}$ ). Also the individuals



**Figure 2**

Vertical distribution of *Mesodinium rubrum* (both small and large forms) in Inre Verkviiken on October 8, 1978 in relation to the hydrographical conditions. Secchi depth 5.9 m.

occurring at these depths were rich in starch (they were strongly coloured by iodine). As the light supply below 15 m must have been very poor and as there was no sunshine between 11th and 20th of October one can suspect that these organisms had recently migrated from overlying layers, possibly to seek inorganic nutrients.

The chlorophyll a depth distribution showed a pattern much like that of the cell number. Moreover, a surface primary productivity maximum was observed on October 13, but not on October 17 (Fig. 3). Without autoradiographic studies the share of *M. rubrum* cannot, of course, be stated. Experiments made with surface samples on October 17 did, however, strongly indicate that *M. rubrum* was responsible for a significant part of the primary production (Fig. 4); the highest  $^{14}\text{C}$ -uptake rate was found in a reddish fraction when the organisms were allowed to migrate towards the lighted tip of an otherwise darkened, horizontal separation funnel. With the technique used only motile, positively phototactic organisms are enriched at the tip whereas e.g. diatoms tend to sink.

In October 1978 as well as in October 1979 *M. rubrum* was the predominant organism in the surface layer of Inre Verkviiken. Other organisms present in the surface water were *Chaetoceros* spp., *Thalassiosira* sp., *Dinophysis* spp., and small flagellates. At the border of the anoxic zone bacteria and small flagellates predominated. Mainly predatory rotifers (*Synchaeta* spp.) were observed feeding upon *M. rubrum*; when studied in the inverted microscope *M. rubrum* seems to escape from most organisms attacking it.

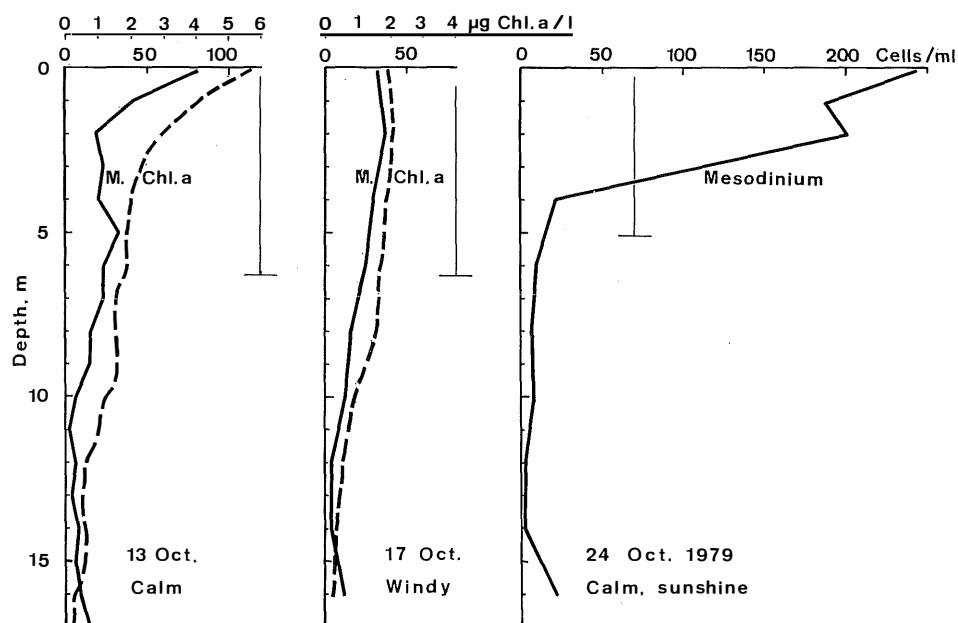


Figure 3

Vertical distribution of *Mesodinium rubrum* (small and intermediate size cells) on three days in October 1979. Dotted lines = chlorophyll *a* content ( $\mu\text{g l}^{-1}$ ) on October 13 and 17.

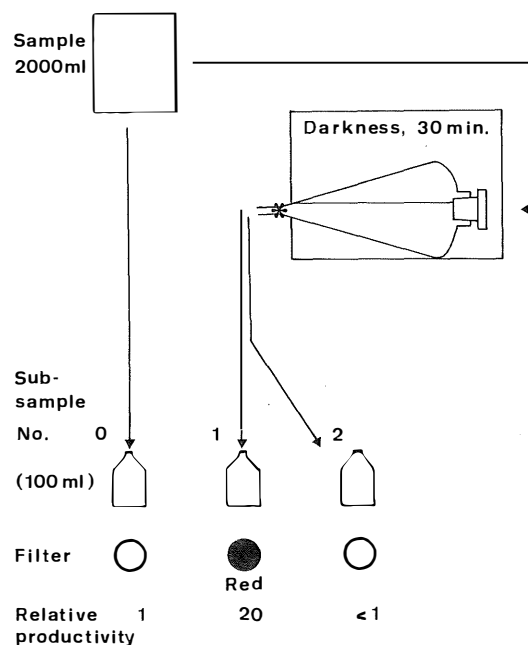


Figure 4

A light trap (separation funnel) for concentrating *Mesodinium rubrum*. After 30 min. one reddish sample with greatly enhanced primary productivity can be withdrawn.

*M. rubrum* imparts a reddish or greenish colour to the water when present in concentrations above ca. 200 cells ml<sup>-1</sup>. When the concentration exceeds about 50 cells ml<sup>-1</sup> it gives a reddish or brownish colour to membrane filters already when a 100 ml sample (fresh!) is filtered.

The ciliate *Mesodinium rubrum* is really marvellous. It is an outstanding primary producer – a phytoplankton (SIEBURTH et al. 1978, PACKARD et al. 1978, SMITH and BARBER 1979), a euryhaline and eurythermous bloom-forming organism of worldwide occurrence. Its peculiar symbiosis makes it an organism of great cytological and evolutionary interest (TAYLOR 1974, HIBBERD 1977, OAKLEY and TAYLOR 1978). Moreover, being unusually motile (being able to escape most grazing organisms) but at the same time extremely fragile, this single organism (or species complex?) drastically illustrates many intricate methodological problems. The ecology of *M. rubrum* is also fascinating. How does it form blooms and why does it become so abundant in the autumn? The organism may be abundant in the whole water column (LINDHOLM 1978) but surface blooms may also be produced by active movements especially during calm weather. At the surface the organism finds optimum conditions for photosynthesis. *M. rubrum* can also migrate vertically (SMITH and BARBER 1979). The organism is rapid enough to make even long diurnal vertical migrations. As inorganic nutrients are likely to be in shortage above the thermocline and the halocline vertical migration implies a great advantage. Also, when there is no stratification rapid swimming is useful; motile primary producers can then best maintain themselves within the euphotic zone and survive. Most *Mesodinium* blooms have been observed in warm water (TAYLOR et al. 1971). However, in the Finnish archipelago *M. rubrum* appears to grow well also in cold water and even under relatively poor light conditions. Thus, many different adaptations enable *M. rubrum* to form blooms.

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