

REVIEW

Mesodinium rubrum: the phytoplankter that wasn't

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ABSTRACT: Recent reports suggest that the potential phototrophic role of plastidic ciliates in marine ecosystems may be considerable. A critical review of the literature demonstrates some confusion surrounding acceptance of the trophic position of even a well-established example of a photosynthetic ciliate, *Mesodinium rubrum*. Despite good evidence of obligate phototrophy from bloom studies, this species has, until recently, been omitted from the majority of routine phytoplankton counts, and has either been assigned to the microzooplankton or completely overlooked. Moreover, problems involved with sampling, enumeration and estimates of productivity for *M. rubrum* are also highlighted from the literature. These principally result from extremes of fragility, motility and vertical aggregation, which are commonly noted for this ciliate. Several recent studies, which have minimized some of these sampling problems and grouped the microplankton into more meaningful ecological categories, suggest that *M. rubrum* has an extremely widespread distribution and can be a very significant member of the phytoplankton. The combination of trophic and methodological difficulties appear to have compounded a serious underestimation of the contribution of *M. rubrum* to the primary productivity of coastal, estuarine and upwelling ecosystems, during both bloom, and perhaps more significantly, non-bloom conditions.

INTRODUCTION

Despite prolonged awareness of the presence of pigmented bodies in pelagic marine ciliates (e.g. Lohmann 1908, Leegard 1920, Kahl 1930–1935), it was not until the late 1960's that a potentially autotrophic role for chloroplast-bearing ciliates was first convincingly demonstrated through studies on blooms of *Mesodinium rubrum** Lohmann (Bakker 1967a, Ryther 1967, Barber et al. 1969), an unidentified oligotrich (Burkholder et al. 1967), and a *Prorodon*-like species (Holm-Hansen et al. 1970).

* The name *Mesodinium rubrum* Lohmann is retained here rather than the more recently proposed *Myrionecta rubra* Jankowski (see Small & Lynn 1985), as many populations exhibit the bifurcate 'oral' tentacles which that description presumes to be lacking (Lindholm et al. 1988). The unique 14 microtubule structure of these oral tentacles has recently been described by Lindholm et al. (1988). *Cylotrichium meunieri* Powers is considered conspecific with *M. rubrum* (Fenchel 1968, Taylor et al. 1971), and photosynthetic forms of *Mesodinium pulex* Claparède et Lachmann are assumed to represent *M. rubrum*. Taxonomic difficulties have been ignored for the purpose of this contribution. However, it is accepted that *M. rubrum* may eventually be shown to represent a species complex, rather than a single species (Lindholm 1985).

Even though the photosynthetic capabilities of these forms, particularly *Mesodinium rubrum*, are now beyond doubt, most research has been carried out during blooms and surprisingly little is understood of their contribution as primary producers to the planktonic community under non-bloom conditions. However, several recent studies have demonstrated *M. rubrum* to be a significant, often dominant phototrophic member of the marine microplankton during certain periods of the year (e.g. Revelante & Gilmartin 1983, 1987, Leppänen & Bruun 1986, Stoecker et al. 1989).

An important ecological role has also been suspected for other chloroplast-bearing ciliates since the studies of Blackburn et al. (1973) and later Mamaeva (1985). Laval-Peuto et al. (1986), Montagnes et al. (1988b), and Lindholm & Mörk (1989) have shown chloroplast retention in a number of ciliates at the morphological and ultrastructural levels, and, with a more physiological approach, Stoecker et al. (1988) demonstrated obligate mixotrophy in the ciliate *Laboea strobila* Lohmann. The ecological role of plastidic ciliates has been fully emphasized in recent studies by Jonsson (1987), Stoecker et al. (1987, 1989) and Laval-Peuto & Rassoulzadegan (1988).

Taylor et al. (1971) and Lindholm (1985) have

reviewed the information relating to bloom occurrence, taxonomic problems and ultrastructure of *Mesodinium rubrum*, but did not consider in detail the relative importance of this species as a primary producer under 'normal' conditions. The present paper reviews literature concerning acceptance of the trophic position of *M. rubrum* under such conditions, with a view to stimulating examination of the role of phototrophic and mixotrophic ciliates generally, for which little ecological information is available.

In addition to these trophic considerations, a number of important methodological difficulties concerning *Mesodinium rubrum* are also addressed and reviewed, particularly those relating to behavioural, structural, and physiological peculiarities of this curious ciliate.

TROPHIC CONFUSION

Without its capacity to form red-water, *Mesodinium rubrum* could well have long remained unknown as a primary producer (Lindholm 1985).

The pigmented bodies noted by earlier authors (e.g. Lohmann 1908, Leegard 1920) were later identified as chromatophores with associated pyrenoid bodies (Powers 1932, Bary & Stuckey 1950). More recent studies also examined mass occurrences of *Mesodinium rubrum* (Bakker 1966, 1967a, Fonds & Eisma 1967, Ryther 1967, Fenchel 1968, McAlice 1968, Parsons & Blackbourn 1968, Barber et al. 1969, Taylor et al. 1969, 1971), all of which either suspected or verified its photosynthetic ability. Packard et al. (1978), Smith & Barber (1979), and Cabecadas et al. (1983) demonstrated it to be an exceptionally productive phototroph. During a dense oceanic bloom in the upwelling area off the coast of Peru, Smith & Barber (1979) measured values for chlorophyll *a* as high as 1000 $\mu\text{g l}^{-1}$, an assimilation number of 16.8 mg C (mg Chl *a*) $^{-1}\text{h}^{-1}$ and productivity of over 2000 mg C $\text{m}^{-3}\text{h}^{-1}$. Taylor (1982) considered this productivity rate to be the highest aquatic micro-organismal primary productivity on record. He also suggested the association between *M. rubrum* and its cryptomonad symbiont to be the most strongly integrated known, between host and photosynthetic cytotobiont.

Despite this remarkable photosynthetic capacity, it is ironic that confusion has surrounded the phototrophic role of this ciliate under non-bloom conditions. The reasons for this are not clear, since no convincing evidence of heterotrophic feeding has been presented and intact chloroplasts appear to be present throughout the year (Taylor et al. 1971, Lindholm 1985, Crawford pers. obs. Southampton Water). It is possible that the highly variable size distribution (see Leegard 1920, Michanek 1965, Taylor et al. 1971, Lindholm 1985, Montagnes & Lynn 1989, Crawford pers. obs. Southamp-

ton Water) may, in part, have generated taxonomic and thus trophic uncertainty (e.g. see Revelante & Gilmartin 1987). Sorokin (1979, 1981) and Tumantseva (1985) suggested that *Mesodinium rubrum* combines phototrophy with phagotrophy upon bacterioplankton, but provide little clear supporting evidence. This view is not supported by observations that *M. rubrum* lacks a true cytostome (Bary & Stuckey 1950, Taylor et al. 1971, Hibberd 1977, Grain et al. 1982, Lindholm et al. 1988). Bakker (1966, 1967a, b) favoured the idea that *M. rubrum* is a temporary photosynthetic modification of the colourless *Mesodinium pulex* Claparède et Lachmann, with an accompanying degeneration of the cytostome. Tamar (1971) described such a dimorphism in the oral cone of a related species, *Mesodinium fimbriatum* Stokes, however, Taylor et al. (1971) have pointed out that the exceptional thinness of the pellicle of *M. rubrum*, with reduced alveoli, is a major modification unlikely to be accomplished on a short term basis. *M. rubrum* has only been shown to behave heterotrophically in the sense of active amino acid uptake (Smith & Barber 1979), a capability shared by a number of autotrophic forms (e.g. Hellebust 1970). However, it cannot survive in darkness in the laboratory for more than a few days (Taylor et al. 1969, 1971, Lindholm 1985).

Although earlier descriptive microplankton studies (e.g. Leegard 1920) did not specify the trophic mode of *Mesodinium rubrum* at non-bloom densities, some later ones (e.g. Michanek 1965) placed the ciliate within the microzooplankton category. However, despite the developing interest in the photosynthetic ability of *M. rubrum* in the late 1960's, many later studies continued to classify it as a microzooplankton (e.g. Takahashi et al. 1975, Beers et al. 1977a,b, Eriksson et al. 1977, Takahashi & Hoskins 1978). In some instances, this was due to cautious identification to genus level (e.g. Beers & Stewart 1971, Dale & Burkill 1982). Other studies, briefly noting the occurrence of *M. rubrum*, have not specified its trophic position (Parsons et al. 1977, Burkill 1982, Stoecker et al. 1984). The confusion can be emphasised by contrasting the study of Beers et al. (1971), which assigned relatively low numbers of *M. rubrum* to the phytoplankton, with later works by the same author (Beers et al. 1977a, b) placing it within the microzooplankton. A more recent study by Beers et al. (1980) correctly placed *M. rubrum* back with the phytoplankton.

Microzooplankton and more general microplankton studies from the late 1970's onwards have gradually acknowledged the autotrophic status of *Mesodinium rubrum* (e.g. Chester 1978, Lindholm 1981, Smetacek 1981, Revelante & Gilmartin 1983, 1987, Andersen & Sørensen 1986, Kivi 1986, Leppänen & Bruun 1986, McManus & Fuhrmann 1986, Sherr et al. 1986, Sanders 1987, Laval-Peuto & Rassoulzadegan 1988, Montagnes

& Lynn 1989, Stoecker et al. 1989). This may have partly resulted from a strong recommendation by Sieburth et al. (1978) that *M. rubrum*, being a functional phototroph, should be classified accordingly.

If the microzooplanktologists have appeared rather slow in releasing *Mesodinium rubrum* from their trophic grouping, then the phytoplanktologists have shown an even greater reluctance in its acceptance. Even now *M. rubrum* is often conspicuously absent from species lists of 'phytoplankton' surveys, even in areas where more specific studies have shown it to be relatively abundant throughout the year. This may in some instances have left *M. rubrum* in an ecological 'vacuum', acknowledged as phototrophic and thus ignored from some heterotrophic ciliate counts (e.g. Smetacek 1981, Kivi 1986), but then perhaps not recognised in corresponding phytoplankton surveys of the same area.

A good example of the complete omission of *Mesodinium rubrum* from routine counts is given by Gieskes & Kraay (1983), in a phytoplankton study of the central North Sea. This study demonstrated an absence of cryptophycean flagellates in cell counts, yet using HPLC pigment 'fingerprinting' they detected relatively high levels of alloxanthin, a pigment diagnostic of that algal class. Extremely low phytoplankton carbon:chlorophyll *a* ratios were also noted, suggesting possible omission of part of the phytoplankton community. Subsequent re-examination by the authors of the Lugol's iodine preserved samples revealed *M. rubrum* in relative abundance (25 to 50 cells ml⁻¹) and in sufficient numbers for its cryptomonad endosymbiont (Parsons & Blackbourn 1968, Barber et al. 1969) to contribute to much of the phytoplankton chlorophyll *a* and alloxanthin. The vast majority of phytoplankton studies do not have the benefit of HPLC as a chemotaxonomic tool. Consequently, significant numbers of *M. rubrum* may well have been ignored on many occasions.

In Southampton Water, UK, *Mesodinium rubrum* has apparently even been missed as the cause of annual red-water. These intense blooms (> 100 µg Chl *a* l⁻¹) have been known since the turn of the century (Royal Commission 1911), and were then assumed to be caused by a peridinean dinoflagellate, although *M. rubrum* was probably to blame (Williams 1980). *M. rubrum* was first noted as the causative species by Williams (1980) and Soulsby et al. (1984), but received no mention in earlier publications on phytoplankton (Savage 1965, 1967), zooplankton (Raymont & Carrie 1964, Barlow & Monteiro 1979), or planktonic oxygen consumption (De Sousa Lima & Williams 1978). This probably resulted both from confusion in its trophic position and inadequate sampling methods, but again emphasizes the potential underestimation of this species.

There are obviously a number of recent exceptions to the failure to include *Mesodinium rubrum* in phytoplankton species lists, for example, Reid et al. (1978) and Cullen et al. (1982) in the southern Californian bight, Blasco et al. (1980, 1981) in the North-West African upwelling, Holligan et al. (1984) in the Gulf of Maine, Cloern et al. (1985) in San Francisco Bay, Mackenzie & Gillespie (1986) and Mackenzie et al. (1986) in New Zealand coastal waters.

Though acceptance of the autotrophic role of *Mesodinium rubrum* has improved considerably, problems persist with respect to the use of data from previous studies. In view of the relatively recent interest in ciliate trophic dynamics, considerable use can be made of sparse data, which may have been collected before the trophic modes of individual species were known in detail. For example, in a review of trophic dynamics in the Baltic Sea, Elmgren (1984) suggested that the role of ciliates as grazers of phytoplankton, described by Eriksson et al. (1977), was excessive since *M. rubrum* accounted for one third of the ciliate volume estimated in that study.

Failure to recognise the contribution of phototrophic and mixotrophic forms may also make re-analysis of data from previous studies problematical. Data from the earlier studies of Beers & Stewart (1969a, 1970, 1971) in the waters off southern California and in the eastern tropical Pacific has often been quoted in recent comparisons of heterotrophic ciliate abundances, despite the authors concession of the possibility of other modes of nutrition occurring in some species. In southern Californian coastal waters in March 1976, Reid et al. (1978) found *Mesodinium rubrum* to be an abundant phytoplankton species in the region generally, and the second most important species after *Exuviella* sp. (= *Prorocentrum*) with respect to the chlorophyll maximum. Cullen et al. (1982) also found *M. rubrum* to be abundant in this area in August 1978. However, Goodman et al. (1984) did not mention *M. rubrum* in this region during a study sampling at weekly intervals throughout the spring and summer. Closer examination reveals that this latter statistical study was actually based on a data set collected in 1967 by J. D. H. Strickland's Food Chain Research Group (Eppley et al. 1970, Reid et al. 1970). Although many other factors could be invoked, it would appear unlikely that *M. rubrum* was recorded in routine phytoplankton counts at that time. It is interesting to note that the corresponding microzooplankton contribution (Beers & Stewart 1970) to this study made no particular mention of *M. rubrum* either, though in retrospect the sampling methods (see subsequent sections) may not have been adequate for this species. Other reports do confirm the common occurrence of *M. rubrum* in this region (Lackey & Glendinning 1963, 1965, Lackey 1967, Beers et

al. 1980). Future microplankton studies should adopt more ecologically appropriate categories, as recommended some time ago by Sieburth et al. (1978) and emphasised more recently by Sieburth & Estep (1985).

FIELD SAMPLING LIMITATIONS

Nets

The use of nets is not generally considered to be acceptable for the quantitative study of either phytoplankton (Tangen 1978) or microzooplankton (Beers 1978b). Ciliates are particularly susceptible (e.g. Margalef 1967, Beers & Stewart 1970), due either to physical damage or to cells passing through the mesh. Smetacek (1981) clearly demonstrated the detrimental effect of using nets, upon numerical estimates of non-loricate ciliates in the Kiel Bight. However, nets have been used extensively in semi-quantitative phytoplankton studies (Tangen 1978). The largest cells of *Mesodinium rubrum* occur during blooms and overlap the 'net phytoplankton' size category. This species has been noted by Lindholm (1985) to disintegrate totally in nets and as a consequence net sampling may have led to some erroneous reports of red-tide causal species (Lindholm 1985). The smaller cells of *M. rubrum*, usually encountered outside of bloom conditions, would either pass right through or disintegrate in even the finest nets used. The use of nets cannot therefore be considered acceptable even for semi-quantitative phytoplankton study, in view of the potential role of *M. rubrum* and possibly other ciliates as primary producers.

Pumps

Pump sampling is frequently employed as a means of investigating microplankton distributions. Samples for phytoplankton abundance, in particular, are often taken from the pump outflow for continuously monitored chemical and biological parameters. Beers (1978a) has given a detailed review of the use of pumps for sampling the phytoplankton.

Beers et al. (1967) described a pumping/ concentrating system based on a submersible centrifugal pump, for the quantitative sampling and concentration of microzooplankton and phytoplankton. This has been used in several subsequent studies (e.g. Beers & Stewart 1967, 1969a, b, 1970, 1971) which have contributed significantly to much of the current thinking on the role of ciliates in marine ecosystems. The use of these systems is defended by Beers et al. (1967) and Beers (1978a), who suggest that damage can be reduced to negligible proportions. However, Beers et al. (1967) did

note significant damage to the more fragile forms such as the the dinoflagellate *Noctiluca* sp., while Beers et al. (1971) noted damage to aloricate ciliates in unconcentrated samples taken from a pump fitted to the ships hull. Sorokin (1981) has criticized the use of pumps generally, with even the most gentle concentrating procedures, for sampling ciliates, and further suggests that more than 95 % of both naked and loricate forms may be lost by such methods. In view of these criticisms, it appears unlikely that such a delicate species as *Mesodinium rubrum* (Lindholm 1985) could survive these sampling methods without a noticeable effect on cell numbers. Burkill (1982) did observe a significant reduction in the numbers of *M. rubrum* cells using a submersible centrifugal pumping system, whilst numbers of other microplankton species appeared unaffected. However, the centrifugal type pump is considered by Beers (1978a) to be potentially more damaging to plankters, because of the manner in which water is propelled.

Gentle pumping systems may be more promising, though quantitative information is lacking. For instance, Grice et al. (1980) noted a significant population of *Mesodinium rubrum* in a Controlled Ecosystem Pollution Experiment (CEPEX) enclosure in Saanich Inlet, British Columbia, Canada, when sampling with a peristaltic pump. However, such slower intake pumps are more susceptible to the problem of avoidance of the pump intake by the more motile forms (Beers 1978a). Though this problem is usually confined to the larger zooplankton, the well documented swimming capabilities and rheotactic behaviour of *M. rubrum* (Taylor et al. 1971, Lindholm 1985) render it a strong candidate for potential avoidance. Representative sampling of *M. rubrum* using any form of pump system must be considered questionable, at least until adequate quantitative comparisons have been undertaken between different methods. Furthermore, populations of *M. rubrum* enumerated from pumped samples should be considered minimal estimates.

Water bottles

Water bottles are the most widely adopted device for quantitatively investigating the distribution of phytoplankton and probably represent the most effective means of accurately sampling fragile species. A review of the use of water bottles in phytoplankton sampling is given by Venrick (1978).

Although water bottles may be considered potentially to have the least damaging effect on *Mesodinium rubrum*, these devices are not without drawbacks and care must be exercised during sampling. In water samplers such as the 'Van-Dorn', which may incorporate

small 'windows' for the indication of water level, *M. rubrum* could quickly concentrate close to the light source and consequently be undersampled. Although this effect has not been described in a sampling study to date, phototaxis and motility are well documented (Lindholm 1985). This response to light has been effectively utilized by Lindholm (1981) to concentrate *M. rubrum* sampled in low numbers. Similarly, *M. rubrum* has been noted by Cabecadas et al. (1983) to accumulate at the top of a 'Van-Dorn' bottle whilst samples were drawn from the bottom, an effect considered by Lindholm (1985) to result from positive rheotaxis and high swimming speed. Thus, it is recommended that samplers be gently mixed if at all possible, immediately prior to subsampling, which should be done as soon as possible after sample collection.

Vertical distribution and migration

Though the sampling problems described are not insurmountable, and may be minimized, ignorance of the vertical distribution and migration of *Mesodinium rubrum* can lead to gross underestimates of its population density. Whilst this is a general caution for much of the motile plankton, *M. rubrum* is particularly susceptible as a result of its exceptionally high swimming speed (see Lindholm 1985). When hydrodynamical conditions permit, *M. rubrum* forms marked sub-surface and occasionally surface accumulations over extremely restricted depth intervals, both during blooms (Lindholm 1978, Packard et al. 1978, Smith & Barber 1979, Sorokin & Kogelschatz 1979, Cabecadas et al. 1983) and under normal conditions (Takahashi & Hoskins 1978, Lindholm 1981, McManus & Fuhrmann 1986, Dale 1987a). These characteristic vertical distributions have been shown to result from diurnal vertical migration apparently in response to light. It has been known for some time that *M. rubrum* exhibits a strong phototactic response (Bary & Stuckey, 1950). Smith & Barber (1979) further suggested that the diurnal migration resulted from positive phototaxis in increasing light, and negative phototaxis in decreasing light. In the Southampton Water estuary, Soulsby et al. (1984) have also shown an apparently phototactic diurnal migration of *M. rubrum*, while Crawford & Purdie (unpubl.) have evidence of vertical movements of the population in response to tidal motions, superimposed upon this diurnal pattern.

These migrations can lead to a vertical distribution in which the vast majority of the daytime population may be concentrated close to the surface. Although more pronounced during blooms, sub-surface maxima are a regular feature of the population in Southampton Water, except during strong winds (Crawford pers.

obs.). Takahashi & Hoskins (1978) found an average of > 65 % (mostly > 90 %) of the *Mesodinium rubrum* population to be concentrated in the top 5 m throughout the winter in Saanich Inlet, British Columbia. In the Peru upwelling zone, *M. rubrum* has been shown to migrate vertically by as much as 30 to 40 m, commencing at dawn and arriving at the surface by late morning (Smith & Barber 1979, Sorokin 1979, Sorokin & Kogelschatz 1979, Barber & Smith 1981). This migration was monitored by Smith & Barber (1979) as a dense band of chlorophyll, about $60 \mu\text{g l}^{-1}$ Chl *a*, while 10 m above and below this layer the chlorophyll concentration was $2 \mu\text{g l}^{-1}$. Chlorophyll concentrations did reach $1000 \mu\text{g l}^{-1}$ in a 10 to 20 cm thick layer (Smith & Barber 1979). Dale (1987a) demonstrated that the abundance maximum of *M. rubrum* in Lindåspollene, Norway, underwent a diurnal vertical migration from between 2 and 5 m depth during the day to 15 m at night. Vertical migration of *M. rubrum* has also been observed in Lindåspollene by Dale (1987b, 1988), and in New Zealand coastal waters by Mackenzie & Gillespie (1986) and Mackenzie et al. (1986). In the North Sea, Baars & Franz (1984) speculated that a diurnal fluctuation in surface chlorophyll could have been due to an internal rhythm of the symbiotic association in *M. rubrum*, which was abundant at the time. This fluctuation could equally have been caused by vertical migration of this species.

Given such distributions and migration, the depth intervals of bottle or pump sampling usually adopted in phytoplankton or microzooplankton studies (e.g. surface and 10 or 5 m intervals) could seriously underestimate the contribution of this species to the community. For instance Revelante & Gilmartin (1987) found *Mesodinium rubrum* to be an important species in the Damariscotta Estuary, Gulf of Maine, but sampling with a water bottle at the surface, 7, 15, and 22 m, could have significantly underestimated the population. Similarly, Montagnes & Lynn (1989) and Stoecker et al. (1989) sampled at ca 10 m intervals during examinations of the role in productivity of *M. rubrum* in other regions of the Gulf of Maine.

Smith & Barber (1979) suggested that the contribution to productivity of *Mesodinium rubrum*, even during blooms, could also be seriously underestimated, since at sea, samples for physiological rate incubations are often taken from the surface in the early morning before *M. rubrum* has completed its upward migration (see also Mackenzie et al. 1986). In situ fluorometry can overcome some of the problems of describing vertical distributions (e.g. Soulsby et al. 1984), but this can only be employed to give information on a single species during periods of total dominance, as encountered during blooms.

Some studies have taken integrated samples from

pump intakes lowered over given depth ranges. Although this could potentially give a more accurate estimation of the total population in the water column, the procedure is nevertheless subject to the limitations of pumping samples already described. The potentially distorting effect of sampling upon determinations of the vertical distribution of *Mesodinium rubrum*, cannot be overstated. During design of field sampling programs, particular attention must be given to sample depth interval, time of day, and state of tide.

Horizontal distribution

The extremely inhomogenous horizontal distribution of *Mesodinium rubrum* is a further complication hindering sampling of this species. Blooms of *M. rubrum* have been noted to occur in irregular patches or clouds during calm conditions (Fenchel 1968, Packard et al. 1978), and aligned in streaks or 'windrows' when wind speed increases (Powers 1932, Packard et al. 1978). In a dynamic environment such as the Southampton Water estuary, streaks and patches of red-water caused by *M. rubrum* can be advected rapidly past the sampling station, on time and distance scales of seconds and metres respectively (Crawford pers. obs.). Clearly this presents considerable problems for representative sampling.

The potential of remotely sensed imagery for providing a more synoptic insight into the horizontal distribution and dynamics of blooms of *Mesodinium rubrum* appears impressive. In addition to providing some of the highest chlorophyll concentrations encountered in the marine environment, the cryptomonad endosymbiont of *M. rubrum* also possesses a red phycobiliprotein pigment, giving blooms their characteristic colour. Other than the cryptophyceae, this pigment is only found in the cyanophycean and rhodophycean classes of algae (White et al. 1977). Another pigment diagnostic of the cryptophyceae is alloxanthin, which has been detected by HPLC when *M. rubrum* is abundant in the North Sea (Gieskes & Kraay 1983).

Considerable success has been achieved in detecting blooms of *Mesodinium rubrum* in British Columbian coastal waters, using the Fluorescence Line Imager (Lin et al. 1984) and, with more limited success in Southampton Water, using the 'Daedalus' airborne thematic mapper (Purdie et al. 1988). The resolution obtained by Purdie et al. (1988) was limited by the sparsity of sea-truth measurements, which prohibited a statistically valid calibration of the spectral data set. However, more recent overflights using the same instrument (Purdie & Garcia 1988) have mapped, in detail, changes in the distribution of a bloom of *M. rubrum* over part of the tidal cycle in the Southampton Water estuary. A bloom of *M.*

rubrum in this estuary in July 1984 was also detected by satellite, through processing of Landsat TM data (Robinson & Holligan 1987).

Although these preliminary remote sensing studies appear promising, difficulties associated with the vertical migration of motile phytoplankton, and particularly *Mesodinium rubrum*, must be considered. Diurnal migrations of 30 to 40 m, such as those undertaken by *M. rubrum* in the ocean upwelling off Peru (Smith & Barber 1979, Sorokin 1979, Sorokin & Kogelschatz 1979, Barber & Smith 1981), pose problems for the remote sensing of ocean colour, since this principally involves detection of integrated near surface colour. Because the blooms are only present close to the surface between about 11.00 and 15.00 h, any remotely sensed data collected outside of this period may completely ignore a substantial proportion of the depth integrated chlorophyll. Although vertical migration of this species in coastal waters and estuaries is more limited (e.g. Soulsby et al. 1984, Dale 1987a), and may be complicated by tidal effects, the penetrating capabilities of detectors is also reduced in these more turbid environments, and difficulties resulting from migration may also be envisaged. Meaningful interpretation of remotely sensed images from areas susceptible to blooms of *M. rubrum* are limited without detailed knowledge of the local dynamics of migrations of this species.

ENUMERATION

Live counting

The technique of live counting is advocated by some (e.g. Sorokin 1981) to be the only reliable means of enumerating pelagic ciliates. However, movement itself can be a problem in the live observation of highly motile ciliates. *Mesodinium rubrum* is a particular problem since it alternates between periods of total motionlessness, and such explosive bursts of swimming activity that the direction of these is impossible to follow out of the field of view (Lindholm 1985). Various narcotizing agents have been successfully employed to immobilize *M. rubrum*, such as hydrogen peroxide (Bary & Stuckey 1950), MS222 (Sandoz, Basel) (Lindholm 1978, 1981), EDTA (ethylenediaminetetraacetate) and oxalic acid (Lindholm 1982) and droperidol (Tumantseva 1985). Zaika & Averina (1968) apparently used, to their advantage, the rheotactic swimming behaviour exhibited by *M. rubrum* and other ciliates, by adjusting the rate of gravitational flow of water through a capillary tube until just sufficient to counter the movement of the ciliates, which could then be enumerated.

An additional problem is that *Mesodinium rubrum* is

so delicate that it often explodes under the microscope, due to thermal effects and possibly physical damage (Taylor et al. 1971, Lindholm 1985). Dale & Burkill (1982) described an isothermal cell counting chamber in which ciliates can be enumerated in the live state and which overcomes the problem of thermal shock. With this technique they demonstrated an improvement of up to 20 % over counting of conventionally fixed pelagic ciliate species. However, numerical estimates of *Mesodinium* spp. were shown to be some 20 % lower than those from fixed samples. This they attributed either to the difficulty in observation of the very small forms of this genus when motionless, or to misidentification and overestimation of poorly fixed specimens of other genera in the fixed counts. Alternatively, it may simply be that *M. rubrum* and other *Mesodinium* spp., being so extremely delicate, are particularly sensitive to handling or containment of any description. Thus, live counting is arguably not the optimum method of enumeration for this species. Additionally, in any sampling program, the time constraints involved with live counting have to be 'weighed' against the convenience of fixing samples and the subsequent increase in resolution of sampling spatial and temporal distributions, which are of such critical importance in abundance estimates of *M. rubrum*.

Fixation and preservation

In common with the majority of naked ciliates (e.g. Sorokin 1981), the fixation and subsequent preservation of *Mesodinium rubrum* cells in a recognisable state is a major difficulty. This problem may be more serious for *M. rubrum* due to its structural weakness, probably resulting from the thin pellicle, reduced alveoli and high degree of internal vacuolation (Taylor et al. 1971, Hibberd 1977, Grain et al. 1982). *M. rubrum* has been noted not only to distort, as do other naked ciliates, but often to disintegrate or explode, both in commercial formalin (Taylor et al. 1971) and buffered formaldehyde (e.g. Ryther 1967, White et al. 1977, Sampayo & Cabecadas 1981). Although Fonds & Eisma (1967), Fenchel (1968), McAlice (1968) and Lindholm (1978) all found formaldehyde fixation adequate for counting cells during blooms, the relative fraction of cells that disintegrated is unknown. Moreover, positive identification of distorted cells under non-bloom conditions is much less certain. Thus the use of formaldehyde for routine microplankton counts must be considered questionable.

Several microplankton studies employing buffered formaldehyde as a fixative have noted numerous poorly fixed ciliate specimens, e.g. 'apparently not oligotrichs' (Beers & Stewart 1971) and 'predominantly

holotrichs' (Beers et al. 1975). Beers & Stewart (1971) suggested that in their category of 'other ciliates' (other, that is, than sheathed or unsheathed oligotrichs), which included the holotrichs *Mesodinium* sp. and *Didinium* sp., almost 40 % of specimens were of questionable identification due to poor fixation. Jimenez & Intriago (1987) have commented on the lack of records of *Mesodinium rubrum* in phytoplankton counts in the eastern Pacific, caused by the use of 'formalin solution' as a routine fixative. Several studies recording *M. rubrum* as common have used buffered formaldehyde as a fixative and may be regarded as potential underestimates (e.g. Reid et al. 1978, Cullen et al. 1982).

The use of formaldehyde in fixation and enumeration of *Mesodinium rubrum* can be improved to some extent by combination with epifluorescence microscopy, with which the characteristic orange-red autofluorescence of the phycoerythrin pigment is apparent. This was utilised effectively by McManus & Fuhrmann (1986), Sherr et al. (1986), and Stoecker et al. (1989), all of whom recorded *M. rubrum* as abundant.

Lugol's iodine appears to be a rather more reliable routine fixative for *Mesodinium rubrum* (Jimenez & Intriago 1987, Crawford pers. obs.), and has been experimentally established to preserve non-loricate ciliates better than buffered formaldehyde, which caused 30 to 70 % loss of these forms (Revelante & Gilmartin 1983). Taylor et al. (1971) also noted cells to remain intact in Lugol's iodine, though with a serious disorganisation of the cirri and ciliary belt. Several recent studies employing Lugol's iodine as a fixative have recorded *M. rubrum* as an important component of the plankton (e.g. Gieskes & Kraay 1983, Revelante & Gilmartin 1983, 1987, Andersen & Sørensen 1986, Kivi 1986, Leppänen & Bruun 1986). Some caution should be exercised in the use of Lugol's iodine however, since Crawford (unpubl.) has preliminary evidence of a sensitivity in the fixation of *M. rubrum* cells to the concentration of Lugol's adopted. The weakest solutions (e.g. Kimor 1976) result in up to 100 % cell lysis. This is unfortunate, since guidelines in the literature for the concentration and quantity of Lugol's iodine required are rather vague, and can vary by at least an order of magnitude (e.g. contrast recommendations by Kimor 1976 with those of Throndsen 1978a). At least until adequate comparisons have been undertaken, the stronger acid version (e.g. Throndsen 1978a) is recommended (100 g KI, 50 g iodine, 100 ml glacial acetic acid, 1 l distilled water), in a ratio of 100:1 (sample:fixative).

A number of other fixatives have been utilized in cytological studies on *Mesodinium rubrum* such as Bouin's solution (Powers 1932, White et al. 1977), Schaudinn's fluid (Powers 1932, Bary & Stuckey 1950)

and, more commonly, buffered glutaraldehyde (Taylor et al. 1969, 1971, Hibberd 1977, Oakley & Taylor 1978, Grain et al. 1982, Lindholm et al. 1988). Sampayo & Cabecadas (1981) and Cabecadas et al. (1983) found glutaraldehyde better than either formaldehyde or Lugol's iodine for routine fixation of *M. rubrum*. White et al. (1977) tried a range of fixatives on samples from a bloom of *M. rubrum*; the best results were obtained using osmium tetroxide. However, none of these studies gave any indication of the fraction of disintegrated cells. Moreover, the use of these fixatives for routine counts is normally precluded by their cost, their toxicity, and their more complex method of application (Kimor 1976).

For preservation of the characteristic pattern of cilia and cirri of living *Mesodinium rubrum* cells, the only fixative successfully employed to date has been Parducz's fixative (Parducz 1966), which was utilized extensively for light microscopy in the comprehensive study by Taylor et al. (1971).

The simplest and most reliable fixative to date for *Mesodinium rubrum* appears to be Lugol's iodine, though this may cause problems in its acid form for other groups such as coccolithophorids (Kimor 1976, Thronsen 1978a) and loricate oligotrichs (Dale & Dahl 1987). Recent developments with protargol staining after Bouin's fixation (Montagnes & Lynn 1987) appears promising for the study of *M. rubrum* (Montagnes & Lynn 1989) and ciliates generally (Montagnes et al. 1988a).

Future perspectives

Any form of enumeration that necessitates removal of microplankton samples from their environment, must introduce at least some bias and probably damages the more delicate forms. Perhaps the most valuable means of sampling fragile microplankton would be an in situ, non-destructive, perhaps photographic, type of detector. The only development in this direction has been that of Beers et al. (1970), who described the use of holography for providing a permanent record of the contents of settling chambers for the inverted microscope. However, this system was restricted in resolution to the larger phytoplankton ($> 30 \mu\text{m}$), and worked only in 1 plane. Beers (1978c) suggested that future developments in laser holography could theoretically provide the potential for 3-dimensional permanent records of the total size spectrum of phytoplankton, avoiding both concentration and fixation of samples. Whether these developments could be incorporated into an in situ device seems a question unlikely to be resolved in the foreseeable future, since no known recent progress has continued in this field.

PHYSIOLOGICAL MEASUREMENTS

Sub-sampling

The behaviour and fragility of *Mesodinium rubrum* present experimental problems whenever this species is relatively abundant. Any subsampling for experimental purposes must take account of the extreme rapidity of aggregation, both in response to light and local currents (see Taylor et al. 1971, Lindholm 1985). This aggregation can be observed in bucket samples from dense blooms (Lindholm 1985, Crawford pers. obs.). Any sample to be divided which has stood for more than a few seconds, should be gently though thoroughly mixed, whilst avoiding severe agitation which may cause damage or lysis of cells. Ignorance of these procedures may lead to accumulation of cells in a sample being subsampled (Cabecadas et al. 1983), and poor replication of cell counts between subsamples (Crawford pers. obs.).

Productivity

The few studies to date which have examined the photosynthetic rate of *Mesodinium rubrum*, suggest this species to be exceptionally productive (Packard et al. 1978, Smith & Barber 1979, Cabecadas et al. 1983). Not only is the assimilation number (P_m^B) high and photo-inhibition (β) apparently minimal (Smith & Barber 1979, Harrison et al. 1981, Platt et al. 1980), but the initial slope of the photosynthesis/irradiance (P/I) curve (α), a measure of photosynthetic efficiency at low light levels, appears comparable at least during blooms to that of the diatoms (Platt et al. 1980, Harrison et al. 1981).

This remarkable photosynthetic capacity, coupled with the elevated biomass levels encountered during blooms (see Lindholm 1985), is not without its drawbacks. For instance, Packard et al. (1978) and Smith & Barber (1979) have shown depressed photosynthesis in longer incubations of *Mesodinium rubrum* samples from blooms, compared to shorter ones, resulting either from lysis of cells or nutrient exhaustion. Smith & Barber (1979) estimated that incubations of these samples for more than 1 h, would result in nutrient exhaustion, since the level of inorganic nitrogen was $12.1 \mu\text{g-at. N l}^{-1}$ at the start of the incubation, whilst the calculated nitrogen demand of the samples was $15.5 \mu\text{g-at. N l}^{-1} \text{ h}^{-1}$. Dugdale et al. (1987) actually measured a nitrate uptake rate of $5 \mu\text{g-at. N l}^{-1} \text{ h}^{-1}$ in samples from blooms of *M. rubrum*, thus supporting the contention that nutrients may be limiting during longer incubations.

Lysis of cells during containment, mentioned by Smith & Barber (1979), may be a general problem in physiological studies of microplankton (e.g. Venrick et

al. 1977), though *Mesodinium rubrum* is probably particularly susceptible. Rupture of cells upon filtration is a further difficulty particularly for ^{14}C estimates of productivity. After gentle filtration, Smith & Barber (1979) were able to reject filters on the basis of red/pink pigment colouration to the edges, as an indication of mass lysis of cells. However, lysis on a smaller scale or rupture of cells during incubations at lower cell densities would be undetectable. Considerable distortion of physiological parameters could result when *M. rubrum* is abundant. In particular, this may cause underestimation of particulate production and consequential overestimation of dissolved excretion products in ^{14}C incubations. The red colouration to filters and elevation of extracellular excretion products has been noted by Sellner (1981) in blooms of *M. rubrum* off the coast of Peru. Thronsen (1978b) observed mass rupture of *M. rubrum* upon addition of slightly hypotonic rinsing water to fractionation screens. This resulted in overestimation of the ^{14}C productivity estimate for the $<5\ \mu\text{m}$ fraction, caused by symbionts of *M. rubrum* (accounting for 54 % of productivity) passing through this screen.

A major limitation in the physiological studies on *Mesodinium rubrum* to date, has been the presence of other phytoplankton taxa and micro-organisms, even during major blooms. Single species techniques or pure cultures are now required to determine physiological properties of *M. rubrum* under controlled conditions. Stoecker et al. (1989) have provided the first such data through isolation of cells of *M. rubrum*. Using the ^{14}C technique, Stoecker et al. (1989) established a photosynthetic rate of $85\ \text{pg C cell}^{-1}\ \text{h}^{-1}$ for *M. rubrum*, at an irradiance of $100\ \mu\text{E m}^{-2}\ \text{s}^{-1}$. The prospects for establishment of pure cultures is remote however, since no known author has maintained cells of *M. rubrum* in the laboratory for an extended period (Taylor et al. 1971, Lindholm 1985).

Respiration

The respiration rate of *Mesodinium rubrum* is of particular interest in view of its motile capabilities, but has received little detailed attention. Although Margalef et al. (1979) speculated that *M. rubrum* probably allocates more energy to swimming than to reproduction, the studies to date (Packard et al. 1978, Setchel et al. 1978, Smith & Barber 1979) suggest the respiration rate to be rather low and within the range of conventional phytoplankton. This is perhaps not surprising in view of the claim by Fenchel & Finlay (1983) that motility in protozoa accounts for an insignificant fraction of the respiration rate. However, it should be noted that *M. rubrum* can swim at over $5\ \text{mm s}^{-1}$ (Lindholm 1985), an order of magnitude faster than the majority of

dinoflagellates (Smith & Barber 1979), and some 5 times quicker than most ciliates. Therefore, a more significant fraction could be anticipated for this species which, one could speculate, may not necessarily be swimming in incubation bottles. Should motility account for a significant proportion of the metabolic rate in *M. rubrum*, this may have important implications, not only for measurements of respiration rate, but also for determinations of photosynthetic rate. Smith & Barber (1979) noted cessation of swimming activity by *M. rubrum* at optimum light levels, thus distortions of P/I curves may result, since conventional techniques of photosynthesis determination assume a constant respiration rate. Clearly, the respiration rate of *M. rubrum* has aroused considerable speculation both in this paper and elsewhere, and deserves more detailed examination using single species techniques or pure cultures.

RECENT ESTIMATES OF ABUNDANCE

Although Taylor et al. (1971) commented upon the extremely widespread geographical distribution of *Mesodinium rubrum*, it has only recently become apparent how abundant this species may be. A preoccupation with bloom studies, in addition to the difficulties described in this paper, may have diverted attention from the potential role of *M. rubrum* as a regular component of the phytoplankton.

Mesodinium rubrum has often been noted to be the dominant member of the protozoan plankton during certain periods of the year (e.g. Michanek 1965, Eriksson et al. 1977, Takahashi & Hoskins 1978, Revelante & Gilmartin 1983, Mamaeva 1985, Andersen & Sørensen 1986, Leppänen & Bruun 1986). Ironically though, only a few recent studies minimizing some of the problems involved, have conceded its potential contribution to primary productivity (Reid et al. 1978, Grice et al. 1980, Revelante & Gilmartin 1983, 1987, Leppänen & Bruun 1986, Mackenzie & Gillespie 1986, Mackenzie et al. 1986, Stoecker et al. 1989).

Table 1 summarizes some recent studies which have attempted to quantify the contribution of *Mesodinium rubrum* to microplankton biomass or productivity.

In British Columbian waters near Vancouver, *Mesodinium rubrum* is often recorded during blooms (Taylor et al. 1969, 1971, Oakley & Taylor 1978) and was commonly encountered during many of the 'CEPEX' enclosure studies (Takahashi et al. 1975, Beers et al. 1977a,b, Parsons et al. 1977, Grice et al. 1980). The significance of *M. rubrum* in this area was further emphasised by Takahashi & Hoskins (1978), who, during winter months, demonstrated *M. rubrum* to represent 43 to 85 % of the microzooplankton carbon biomass, an order of magnitude greater abundance than

Table 1 *Mesodinium rubrum*. Some recent estimates of its contribution to microplankton biomass or productivity in marine ecosystems

Location	Period	Contribution of <i>M. rubrum</i>	Source
Saanich Inlet, British Columbia	Dec 1975–Feb 1976	43–85 % protozoan carbon biomass, an order of magnitude greater than other species. Averaged about 8 % phytoplankton biomass between 0 and 10 m	Takahashi & Hoskins (1978)
Saanich Inlet, British Columbia (CEPEX unmixed enclosure)	Summer 1978	Biomass peaked at 15 $\mu\text{g C l}^{-1}$ throughout water column; 13 % average phytoplankton carbon; 205 % average heterotrophic ciliate carbon. Significantly less in mixed enclosure	Grice et al. (1980)
Adriatic Sea	Summer and Winter 1978–1982	Averaged 173 % total microzooplankton numerically, and 40 % biomass throughout water column, under stratified conditions. Not present under well-mixed conditions	Revelante & Gilmartin (1983)
Baltic Sea	Mar–Jun 1982	Ca 10 % total phytoplankton production, and 2 % biomass	Leppänen & Bruun (1986)
Damariscotta Estuary, Gulf of Maine	Mar 1981–Jun 1982	Within order of 100 % (from their Figs. 3 and 8) of total microzooplankton biomass between Dec and Apr. Sporadic occurrence during the rest of the year	Revelante & Gilmartin (1987)
Georges Bank, Gulf of Maine	Summer 1987	<i>M. rubrum</i> & <i>Laboea strobila</i> (approx. equal) contributed 1 to 7 % total phytoplankton carbon fixed, and 14 to 90 % microplankton carbon fixed. <i>M. rubrum</i> numerically 30 % of total ciliates at shallower stations, and 3 % at deeper stations off the bank	Stoecker et al. (1989)
Isles of Shoals, Gulf of Maine	May 1985–Aug 1986	Ca 0.3 % annual phytoplankton production	Montagnes & Lynn (1989)

any other species, and around 8 % phytoplankton biomass (between 0 and 10 m). In a 'CEPEX' enclosure study in the same area in summer, Grice et al. (1980) suggested that it constituted, at its peak abundance, about 13 % of the phytoplankton carbon in an unmixed enclosure.

Revelante & Gilmartin (1983) have shown that the numerical abundance of *Mesodinium rubrum* exceeded that of all the microzooplankton, under stratified conditions in the Adriatic Sea, and commented upon its potential importance as a primary producer.

Reports from the Baltic Sea have suggested *Mesodinium rubrum* to be a very significant species (e.g. Michanek 1965, Eriksson et al. 1977, Lindholm 1981, Smetacek 1981, Mamaeva 1985, Kivi 1986). During spring in the open northern Baltic, Leppänen & Bruun (1986) have estimated the contribution of *M. rubrum*, the dominant ciliate species, to be 10 % of the total primary productivity, and suggest this value may be even greater closer to the coast. However, this estimate was determined indirectly from production

equations derived for other species and may, or may not, be appropriate for *M. rubrum*.

There are few records of *Mesodinium rubrum* from the North Sea other than the report of a bloom by Fonds & Eisma (1967). However, observations in some areas suggest it is sufficiently abundant, at least during May, to dominate surface chlorophyll (Gieskes & Kraay 1983, Baars & Franz 1984, Crawford pers. obs.).

In upwelling areas where *Mesodinium rubrum* forms massive blooms (Ryther 1967, Barber et al. 1969, Packard et al. 1978, Smith & Barber 1979, Sorokin 1979, Sorokin & Kogelschatz 1979), little is known of its occurrence at other times, other than brief mentions in a few studies (e.g. Beers et al. 1971, Blasco et al. 1980, 1981). However, Jimenez & Intriago (1987) have recently discussed the potential role of both bloom and pre-bloom levels of *M. rubrum* in the upwelling off Ecuador

Several recent studies have examined the role of *Mesodinium rubrum* in different locations within the Gulf of Maine, USA. Revelante & Gilmartin (1987) found it to be a dominant ciliate in winter in the

Damariscotta Estuary, Gulf of Maine, and thus a potentially important phototroph. Montagnes & Lynn (1989) provided the first assessment of the annual contribution to productivity made by *M. rubrum*, in a study off the Isles of Shoals, Maine. The annual contribution was suggested to be only 0.3 % of phytoplankton production. However, as in the study by Leppänen & Bruun (1986), this was based on a rather indirect method of estimating production for heterotrophic ciliates, and may be inappropriate for *M. rubrum*. The study by Stoecker et al. (1989), during summer on the Georges Bank, Gulf of Maine, adopted the more objective method of comparing ^{14}C production estimates of isolated *M. rubrum* cells with those of intact water samples. They suggested that the photosynthetic ciliates *M. rubrum* and *Laboea strobila*, together contributed (approximately equal) 1 to 7 % total phytoplankton carbon fixed at stations on the bank.

Clearly, the quantity of useful non-bloom data presented to date is insufficient to determine the true role of *Mesodinium rubrum* in marine ecosystems, and precludes an assessment of whether its abundance has increased in recent years in response to coastal eutrophication. However, many reports do suggest it to be an important member of the phytoplankton, at least during certain periods of the year. In view of its potential contribution, considerably more research effort should be devoted to assessing its abundance and investigating its physiology, ecology, and taxonomy. Moreover, it must still be concluded, in agreement with Smith & Barber (1979), that the contribution of this enigmatic phototroph to the productivity of coastal, estuarine, and upwelling ecosystems has been seriously underestimated.

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