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Some observations on vertical distribution and migration of the phototrophic ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) in a stratified brackish inlet

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ABSTRACT: The vertical distribution of the phototrophic ciliate *Mesodinium rubrum* (= *Myrionecta rubra*) was examined under relatively stable conditions in Inre Verkviken, a brackish inlet on the Åland Islands, Finland, in early summer 1991. Distribution was characterized by a population maximum situated persistently within the thermocline (8 to 11 m depth) just above the nitracline, and at an irradiance (~1 to 10 µmol photons m^{-2} s^{-1}) below the estimated irradiances required either for photosynthetic saturation ($I_k \approx 275$ µmol photons m^{-2} s^{-1}) or even compensation ($I_c \approx 15$ µmol photons m^{-2} s^{-1}). This population maximum often co-occurred with a second deeper maximum at around 14 to 16 m, with transient evidence of a third poorly defined peak within the upper 5 m. Maximum cell numbers reached over 200 cells ml^{-1} at 15 m, but were more typically observed at around 50 to 100 cells ml^{-1} within the 2 lower population maxima. Cells were usually present at all depths down to the anoxic boundary (15 to 16 m), but were occasionally almost absent from the surface few metres. Total depth integrated population (over 0 to 20 m) was of the order 550×10^6 to 900×10^6 cells m^{-2}, only a factor of about 2 lower than typical red-water integrated abundances. Despite the distinct vertical separation between irradiance and dissolved nutrients, no consistent diel pattern of vertical migration was discerned. Apparent movements of maxima were observed but were not associated with diel changes in the depth of either I_k or I_c. Given the exceptional swimming speed and photosynthetic efficiency of *M. rubrum*, and these complicated changes in distribution, a diel migration pattern may not be necessary, and we speculate that migration might occur on an 'individual needs' basis. However, this migration potential was a constant logistical complication hampering temporal and spatial sampling design, and artefactual changes in distribution cannot be ruled out. Improved future understanding of the migration of this species will only be realized with a much more dynamic approach to sampling in order to minimize the possibility that migration might be quicker than data collection.

KEY WORDS: *Mesodinium rubrum* · *Myrionecta rubra* · Planktonic ciliates · Vertical distribution · Vertical migration

INTRODUCTION

The photosynthetic planktonic ciliate *Mesodinium rubrum*[1] (Lohmann) Hamburger & Buddenbrock (= *Myrionecta rubra* Jankowski) has an exceptional swimming speed of some 5 to 8.5 mm s^{-1} (Lindholm 1985, Jonsson & Tiselius 1990), an order of magnitude quicker than most dinoflagellates. Surface, near-surface and deeper accumulations are characteristics of reports of *M. rubrum*, both in red water and non-bloom conditions (for reviews see Taylor et al. 1971, Lindholm 1985, Crawford

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[1]We retain the name *Mesodinium rubrum* over the more recently proposed *Myrionecta rubra* (see Small & Lynn 1985, Krainer & Foissner 1990). The life cycle of *M. rubrum* is unknown, the obligate nature of the symbiosis has never been confirmed beyond doubt, and profound variations in size and morphology occur in both red water and non-bloom populations (e.g. Taylor et al. 1971, Lindholm 1985, Crawford 1993). For these reasons we feel that changes in nomenclature are premature.

1989), and an improved understanding of vertical distribution and migration may give some clues as to the mechanisms involved in the appearance of red water.

Information on the vertical distribution of *Mesodinium rubrum* in stable water bodies is available for different seasons (Lindholm 1981, Dale 1987, Lindholm & Mörk 1990), but the dynamics of distribution and migration on smaller temporal and spatial scales, and in open water conditions, are clearly complex and not well understood (e.g. Lindholm & Mörk 1990, Crawford & Purdie 1992, Owen et al. 1992, Cloern et al. 1994, Crawford et al. 1997). Vertical migration is not limited by depth, at least down to 40 m (Smith & Barber 1979, Sorokin & Kogelschatz 1979), and gradients in temperature, salinity and dissolved oxygen seem to pose no barrier (Taylor et al. 1971, Lindholm 1985). The behaviour of *M. rubrum* has usually been assumed to consist of an upward phototaxis (Bary & Stuckey 1953, Smith & Barber 1979) followed by downward migration, or dispersal, at night (Soulsby et al. 1984). Passow (1991) suggested that the presumed light dependent migration by *M. rubrum* might be complicated by another unmeasured environmental parameter and indeed, more recently, Crawford & Purdie (1992) proposed that a direct motile response to turbulence could be a complicating factor.

As *Mesodinium rubrum* cannot yet be cultured, a stable 'mesocosm-like' environment probably provides the best source of further information, as both turbulence and advective horizontal displacement of the population are minimized. Here we present some observations on the vertical distribution and migration of *M. rubrum* in such an environment with the added advantage that the population was constrained to a vertical distance of only 20 m, allowing relatively close interval sampling through the whole population.

METHODS

The study was undertaken at Husö Biological Station (Åland Islands, Bothnian Sea, off southwestern Finland), and sampling conducted in Inre Verkviken, a 20 m deep fjord-like brackish inlet (for map, see Lindholm 1981, 1992, Lindholm & Mörk 1990) connected to the Bothnian Sea via a 200 m long, 1 m deep canal. Inre Verkviken is currently going through a meromictic phase (Lindholm 1996).

Sampling was conducted from a rowing boat approximately in the centre and deepest part of the lake. Profiles of physical parameters were taken at intervals of 1 m; temperature and salinity were recorded with a YSI probe and irradiance with a Li-Cor 188B radiometer. Water samples were taken with a Ruttner-type sampler, down to 18–20 m, at close intervals of either 0.5, 1.0 or 2.0 m in order to minimize underestimation of population maxima (e.g. Crawford 1989). Subsamples were removed for cell counts, oxygen concentration, chlorophyll *a* (chl *a*), and in some profiles total phosphorus and dissolved nitrate. Samples for enumeration of *Mesodinium rubrum* were dispensed directly from the sampler into glass bottles containing acid Lugol's iodine preservative, with a final concentration of 1% v/v (Throndsen 1978, Crawford 1989). On-site preservation minimized the possibility of lysis of cells during transport back to the laboratory since *M. rubrum* is particularly fragile (Lindholm 1985, Crawford 1989). *M. rubrum* was enumerated from 10 or 25 ml subsamples in Hydrobios sedimentation chambers using a Nikon inverted microscope. Cell number was calculated as the mean from 5 passes across the base of the sedimentation chamber, with a typical number per pass being around 50 (in a 10 ml chamber with cell number at 100 ml^{-1}).

Dissolved oxygen and nitrate, and chl *a* were determined according to Parsons et al. (1984), and total phosphorus (particulate plus dissolved) according to Grasshoff (1976).

RESULTS AND DISCUSSION

A single exploratory depth profile was taken on 27 May in order to demonstrate typical daytime conditions (Fig. 1) and shows a weak halocline and a reasonably strong thermocline. The bulk of the population of *Mesodinium rubrum* was residing at depth and was distributed as 2 maxima, perhaps with evidence of a poorly defined third maximum in the upper 5 m. Cells were present at all depths down to about 18 m, with maximum abundance at around 100 ml^{-1} within the population maxima. The central population maximum was located within the thermocline, as marked visually (Fig. 1) by the zone between the 5 and 10°C isotherms. Counting error is indicated and the mean coefficient of variation varied from about 3% (±5 cells ml^{-1}) at abundances of over 100 cells ml^{-1} to about 70% (±0.4 cells ml^{-1}) at abundances of less than 1 cell ml^{-1}. Sampling error was estimated from 4 replicate bottle samples taken from 10 m depth; mean count from the 4 replicate bottles was 99.0 cells ml^{-1} (±1.4 cells ml^{-1} standard error). Although a 1-way ANOVA gave no significant difference between the counts from the 4 replicates, it is unlikely whether such replication would have held under all circumstances, for example when a population maximum was migrating. The total integrated population of *M. rubrum* between 0 and 20 m was 761×10^6 cells m^{-2}.

Chl *a* clearly showed a similar trend to cell numbers (Fig. 1) suggesting that *Mesodinium rubrum* was the

dominant chl *a* containing species. With cell numbers of 100 ml^{-1}, and assuming a mean cell diameter of 30 µm and chl *a* content of 2.4 fg $µm^{-3}$ (Stoecker et al. 1991), this gives a theoretical chl *a* concentration of around 4 µg l^{-1} for *M. rubrum* alone. Ambient concentrations of chl *a* in the population maxima were around 5 to 6 µg l^{-1}, suggesting that the contribution of *M. rubrum* was of the order of 70 to 80%.

Compensation irradiance (I_c) can be defined as irradiance (I) at which photosynthetic rate (P) just exceeds respiration rate (R). There are no published values of I_c for *Mesodinium rubrum*, but this was crudely calculated from R, and the assumption of a simplistic linear relationship between P and I up to saturation irradiance (I_k) at which P_{max} is achieved. I_k has been estimated at around 275 µmol m^{-2} s^{-1} when P_{max} is around 11 to 14% cell C h^{-1} (Stoecker et al. 1991), and R has been estimated at about 0.7% cell C h^{-1} from a careful review of published rates of O_2 consumption and CO_2 production from incubations of red water caused by *M. rubrum* (Crawford 1992a). Using these values, a value for I_c of 15 µmol photons m^{-2} s^{-1} was calculated (Fig. 1; see also Crawford et al. 1997). *In situ* I (4 to 13 µmol photons m^{-2} s^{-1}) was lower than I_c within the central population maximum (8 to 10 m) and barely detectable ($\ll$1 µmol photons m^{-2} s^{-1}) in the lower maximum (14 to 16 m). Within the upper 4 to 6 m, variation in *in situ* I was of the order 40 to 1200 µmol photons m^{-2} s^{-1}, although the shallow I_k depth suggested that only a small proportion of the population was subject to irradiance in excess of I_k at a given time.

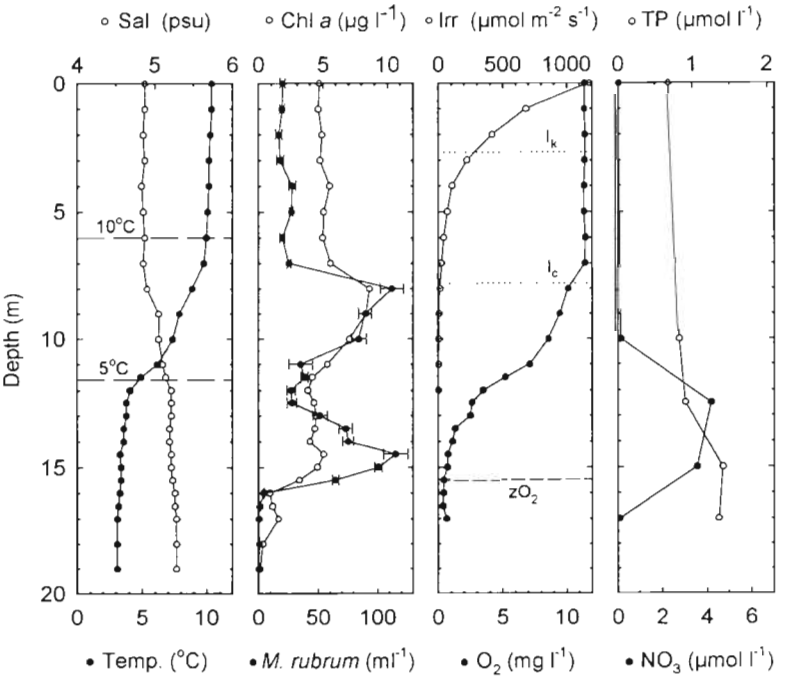

Fig. 1 Inre Verkviken, 15:00 h, 27 May 1991; depth profiles of temperature, salinity, abundance of *Mesodinium rubrum*, chl *a*, irradiance, dissolved oxygen, total phosphorus and dissolved nitrate. The upper and lower horizontal long-dashed lines indicate the depths at which temperature was 10°C and 5°C respectively. The upper and lower horizontal dotted lines indicate the respective depths of the estimated saturation irradiance (I_k) of 275 µmol photons m^{-2} s^{-1} and the estimated compensation irradiance (I_c) of 15 µmol photons m^{-2} s^{-1}. Horizontal short-dashed line indicates depth at which O_2 concentration was <0.5 mg l^{-1} (zO_2). See text for further details

Dissolved oxygen exceeded saturation near the surface and remained constant down to a depth of about 7 to 8 m, below which concentration declined sharply with depth (Fig. 1). The depth of this decline coincided almost exactly with the depth of estimated I_c, consistent with I_c representing a realistic *in situ* compensation intensity when *Mesodinium rubrum* was dominant. At about 16 m the water became almost anoxic; oxygen concentration did not quite reach zero values (0.1 to 0.3 mg O_2 l^{-1}), perhaps, for example, due to small amounts of oxygen introduced with Winkler reagents. However, an odour of H_2S from samples below 16 to 17 m suggests that this water probably was anoxic. A value of 0.5 mg O_2 l^{-1} (about 5% saturation) was arbitrarily defined as the 'anoxic' boundary for graphical purposes (zO_2; Fig. 1). The deeper abundance maximum of *M. rubrum* seemed to be constrained by this boundary as a lower limit, although a few individuals were observed even below this down to 19 m (see also Lindholm & Mörk 1990).

Surface nutrients were low (Fig. 1) and the central population maximum resided just above the nitracline. Nitrate was between 0.1 and 0.5 µmol l^{-1} in the surface 10 m, but increased sharply below this depth to maximum values of over 4 µmol l^{-1} in the deeper less oxygenated water. In the 'anoxic' water below 16 m, nitrate declined sharply, perhaps due to anaerobic denitrification processes in the reducing environment. Phosphorus concentrations increased with nitrate in the 10 to 15 m depth range, but phosphorus was present in concentrations of 0.5 to 1.5 µmol l^{-1} throughout the water column, suggesting that nitrogen was the limiting nutrient. Unfortunately, only total phosphorus was determined, but crude estimation from Redfield ratios and chlorophyll or cell carbon (i.e. from abundance of *Mesodinium rubrum*) gave a maximum particulate phosphorus of only about 0.1 µmol l^{-1}, suggesting that the greatest proportion of the total phosphorus was in the dissolved form.

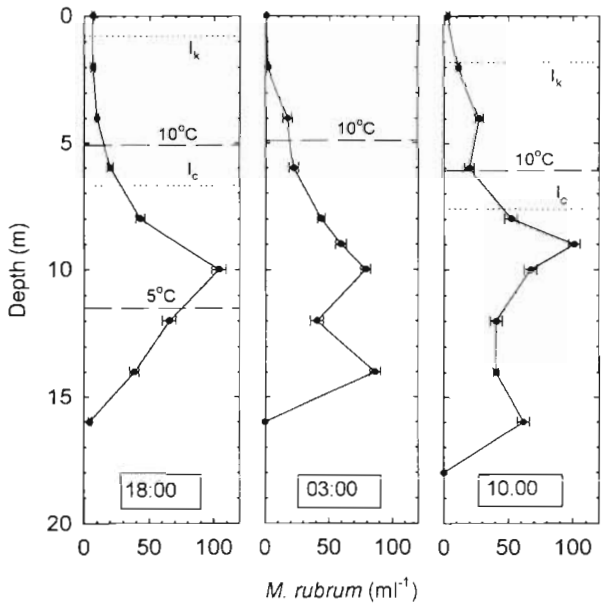

Fig. 2. *Mesodinium rubrum*. Inre Verkviken, 28 and 29 May 1991; sequence of profiles of abundance taken at 18:00, 03:00 and 10:00 h. Horizontal long-dashed lines, dotted lines and labels as in Fig. 1. Surface irradiance at 03:00 h was below detection limit. O_2 profiles not taken, temperature profiles incomplete at 03:00 and 10:00 h

An important consideration relating to this first exploratory profile (Fig. 1) was the time required to sample all of the relevant parameters. Using a single water bottle, and 2 additional separate rigs for temperature and salinity, and for irradiance, this profile required well over 2 h to complete. This became a critical logistical consideration, given the migration potential of *Mesodinium rubrum*; if sampling time for one particular profile became 'temporally stretched', then the vertical position of the population could conceivably have changed during the course of sampling. This placed constraints on how many parameters could be sampled and explains why some are missing from subsequent profiles.

In order to highlight potential differences between daytime and night-time distribution, a sequence of lower resolution depth profiles was taken between the evening of 28 and morning of 29 May (Fig. 2). At 18:00 h the distribution was in the form of a single, though 'smeared' maximum centred at around 10 m, but with cells observed at all depths down to 16 m. At 03:00 h, this distribution had split into 2 lower maxima, with evidence perhaps of the formation of an upper one at around 4 to 5 m. By 10:00 h, these maxima persisted with the upper one slightly more pronounced, and the lower 2 further apart. Significant numbers of cells (>20 ml^{-1}) occurred at all depths down to the 'anoxic' boundary. The total integrated populations over 0 to 20 m were 598×10^6, 601×10^6 and 699×10^6 cells m^{-2} at 18:00, 03:00 and 10:00 h respectively. In terms of the population potentially residing at a preferential isolume, there was no evidence that changes in depths of either I_c or I_k influenced the vertical distribution of the population. Again, the central population maximum seemed to maintain itself in the thermocline zone, although there was evidence of limited movement of the upper and lower maxima into zones respectively replete in irradiance and nutrients. For the profiles above, sampling intervals were reduced to a few hours, and so *Mesodinium rubrum* could theoretically have made several surface-bottom migrations in between profiles. It was clear from these initial exploratory surveys that conflicting spatial and temporal logistics dictated that sampling for all parameters at 1 or even 2 h intervals was impossible. A 24 h survey could only be achieved by reducing the sampling frequency to every 4 h or so, in which case, the population distribution could conceivably change both within and between profiles.

A further sequence of profiles was taken on the morning of 4 June 1991 (Fig. 3) in which it was attempted to extract as much information as possible from a 2-hourly sampling framework. At 06:00 h, 2 abundance maxima

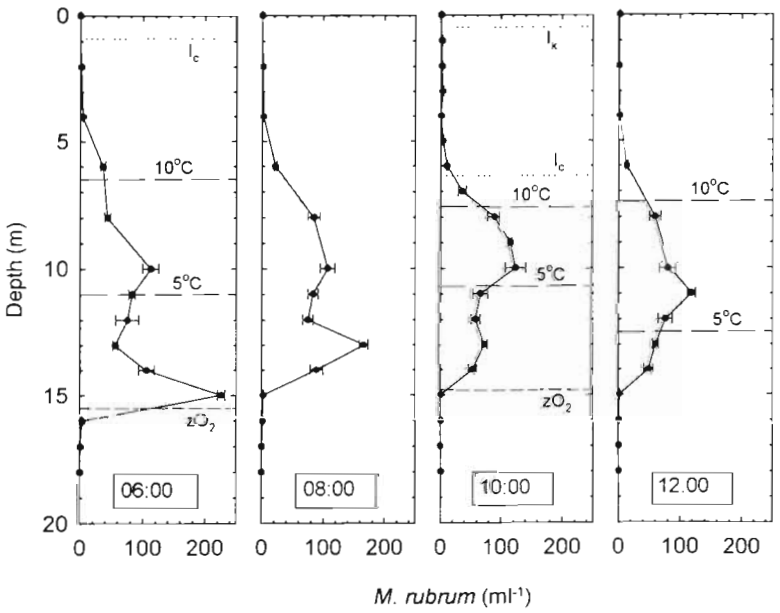

Fig. 3. *Mesodinium rubrum*. Inre Verkviken, 4 June 1991; sequence of profiles of abundance taken at 06:00, 08:00, 10:00 and 12:00 h. Horizontal long-dashed lines, short-dashed lines, dotted lines, and labels as in Fig. 1. Irradiance and O_2 profiles not taken at 08:00 and 12:00 h; temperature not taken at 08:00 h

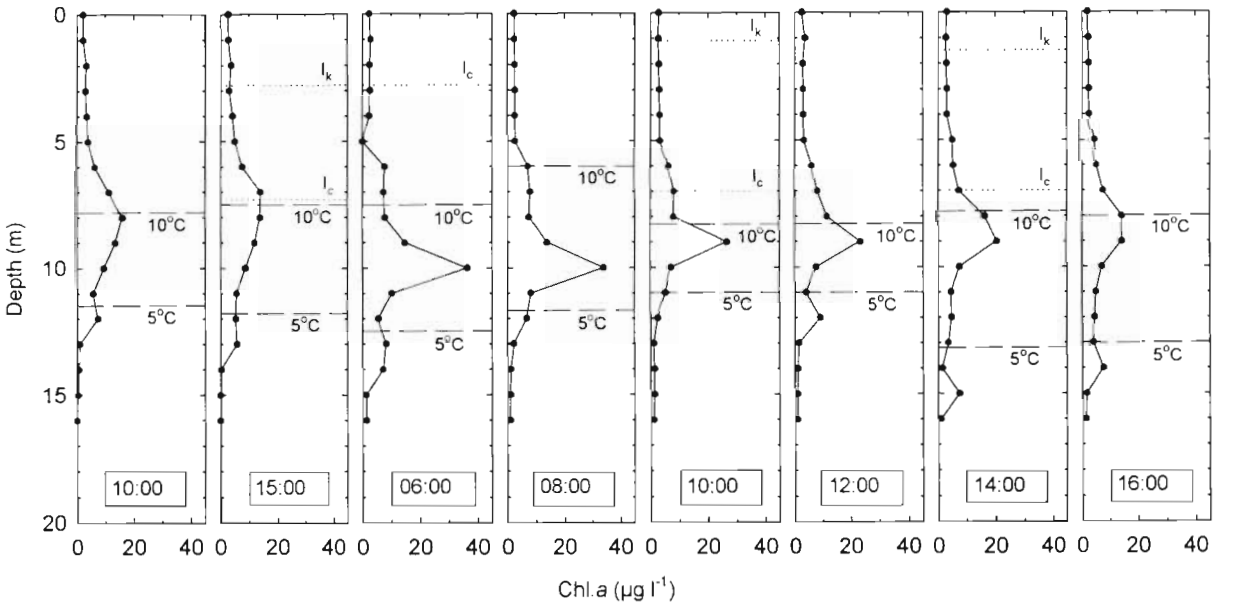

Fig. 4. Inre Verkviken, 10 and 11 June 1991; sequence of profiles of chl *a* over a period of 30 h. Horizontal long-dashed lines, dotted lines, and labels as in Fig. 1. Irradiance profiles not taken at 10:00 h on 10 June, or at 08:00, 12:00 and 16:00 h on 11 June

were apparent, with evidence of an additional poorly defined upper maximum; cells were present throughout the water column but in very low numbers in the surface 5 m. A marked lower maximum (>200 cells ml^{-1}), constrained by the 'anoxic' water below, appeared to migrate upwards throughout the morning. By 12:00 h the population was distributed as 1 single maximum with its peak at around 10 to 11 m, and few cells in the upper 6 m. The apparent 'mobility' of the 'anoxic' boundary during this period could possibly reflect significant consumption of oxygen during the migration of a large number of cells. Changes in I_c and I_k depths had little impact upon the distribution of the population, and the central population maximum was again largely constrained to the thermocline zone. Total integrated populations from 0 to 20 m were 833×10^6, 746×10^6, 637×10^6 and 548×10^6 cells m^{-2} at 06:00, 08:00, 10:00 and 12:00 h respectively.

A more extensive series of vertical profiles is presented from 10 and 11 June (Fig. 4), although using chl *a* concentration as an index of biomass and with temporal spacing between profiles at times rather lengthy. Maximum values of chl *a* approached 40 µg l^{-1}. Although *Mesodinium rubrum* was dominant, other species clearly made a contribution and so chl *a* distributions probably did not reflect those of *M. rubrum* in such a clear-cut manner as in Fig. 1. However, as observed with cell abundance, the population was typically distributed as 1 (8 to 10 m) or 2 (lower one 14 to 16 m) maxima with a 'smeared' distribution in the upper 6 to 7 m. The central maximum changed position by only about 2 m throughout the entire sampling period and was again generally constrained to the thermocline. As observed in earlier profiles, there was evidence that, when present, the lower maximum occasionally 'dipped' down to the approximate depth of the 'anoxic' boundary (although oxygen data not collected here). Even over a period of some 30 h there was no evidence that the depth of either I_k or I_c (when measured) had any significant impact upon the vertical distribution of the population. Total integrated chl *a* over 0 to 20 m varied between 87 to 120 mg chl *a* m^{-2} over the sampling period. Using the regression of chl *a*:cell number presented by Crawford et al. (1997) and assuming *M. rubrum* represented 75% of chl *a* (see Fig. 1), these integrated chl *a* values represent integrated populations of *M. rubrum* of the order of 650×10^6 to 900×10^6 cells m^{-2}.

The most persistent feature of the study (Figs. 1–4) was the position of the central population maximum within the thermocline between the I_c depth and the nitracline. This observation is consistent with the notion that, like dinoflagellates, the vertical distribution of the population of *Mesodinium rubrum* may become a compromise between nutrient limitation in surface waters, and light limitation below around 6 to 8 m depth. This is supported by the observation that when incubated at the surface, samples of nutrient rich deeper water from this inlet were highly productive (Lindholm & Mörk 1990). Despite reasonable evidence of changes in vertical distribution with time, there was no clear diel pattern of population movements, supporting the preliminary contentions of Lindholm & Mörk (1990) from autumn profiles of *M. rubrum* in this inlet. Vertical

distribution generally suggested light limitation for much of the population, but there was no evidence that limited bulk migrations were associated with phototaxis alone. Moreover, it is clear from the extremely shallow I_k depths that distribution patterns did not result from avoidance of excessive irradiance in surface water, and so it is unlikely that photoinhibition plays any significant role in vertical distribution. In any case, evidence to date suggests that *M. rubrum* exhibits minimal photoinhibition even at high irradiance (Smith & Barber 1979, Platt et al. 1980, Stoecker et al. 1991).

Although *Mesodinium rubrum* in Inre Verkviken appears to be compromised between irradiance and nutrients, changes in vertical distribution observed here contrast with certain dinoflagellates which have been reported to migrate with diel periodicity in order to maximize growth in stratified environments (Eppley et al. 1968, Heaney & Eppley 1981, Cullen 1985, Kamykowski & McCollum 1986). Given the swimming speed of *M. rubrum*, it is however conceivable that migrations need not be performed with diel periodicity, and observed changes in distribution may represent the 'dynamic summation' of a population in which cells migrate according to the need for balancing individual requirements for carbon and nitrogen. With such a high photosynthetic efficiency (e.g. Smith & Barber 1979, Platt et al. 1980, Stoecker et al. 1991) cells would theoretically need to spend only about 1.3 h each day above the I_k depth in order to satisfy diel respiratory demands (assuming $R = 0.7\%$ cell C h^{-1} and $P_{max} = 12.5\%$ cell C h^{-1} as discussed earlier). This, of course, ignores the costs of locomotion itself which are unknown but potentially significant (Crawford 1992b). Cells maintained in darkness for several days show reduction in chlorophyll content and chloroplast number (Lindholm 1985, Crawford pers. obs.), whereas cells sampled from these deep maxima, at almost zero irradiance, are rich in chlorophyll and appear to photosynthesize normally (Lindholm & Mörk 1990). This suggests that individuals visit the surface at fairly regular intervals.

This study does not clearly illuminate the principal factor regulating vertical distribution and migration, but it is likely that a combination of factors are involved, and, indeed, a number of potential factors were unavoidably omitted. For example, the potential role of predators either directly through feeding or indirectly through provocation of avoidance reactions (e.g. see Jonsson & Tiselius 1990) was not evaluated. Similarly, the role of excretion or upward diffusion of reduced forms of nitrogen was not considered. However, the necessities of sampling design imposed by the peculiarities of *Mesodinium rubrum* itself (as discussed earlier) dictated that consideration of all possible factors was not feasible. Moreover, artefactual changes in vertical distribution cannot be ruled out because migration potential was a constant logistical complication hampering temporal and spatial sampling design. Improved future understanding of the migration of this species will only be realized with a much more dynamic approach to sampling in order to minimize the possibility that migration might be quicker than data collection.

This study does however present convincing new evidence that essentially discounts either positive or negative reactions to irradiance as a simple factor driving diel migrations. Earlier studies which suggested phototaxis as a major factor driving migrations (e.g. Bary & Stuckey 1953, Smith & Barber 1979) have been much cited, although these were in fact based upon few data in the original publications. *Mesodinium rubrum* does respond to light (e.g. Lindholm 1981), and it is likely that phototaxis is involved under certain circumstances, but probably mediated by additional factors. It seems that these factors do not drive simple bulk reactions since the population clearly does not respond in a uniform manner (Figs. 2 & 3; see also Lindholm & Mörk 1990).

The major population maximum usually coincided with the thermocline, approximately marked by the 5 and 10°C isotherms (Figs. 1–4). There is little evidence that distribution of *Mesodinium rubrum* is directly limited by temperature (e.g. see Lindholm & Mörk 1990), but with little density gradient afforded by only a slight halocline, temperature was probably the main influence on the stability of the water column. Crawford & Purdie (1992) presented evidence from a dynamic estuary that *M. rubrum* avoided near-surface turbulence and aggregated in relatively stable zones. Further evidence is emerging of the potential role of water column stability in development (Crawford et al. 1997) and dynamics (Cloern et al. 1994) of red tides caused by this species. It is possible that a proportion of the population of *M. rubrum* aggregated in the thermocline as the zone of greatest stability in Inre Verkviken, however, this cannot be confirmed as measurements of dynamic stability of the water column were not taken and indeed are not routine measurements in biological studies (e.g. see Crawford & Purdie 1992). Inre Verkviken was chosen as a relatively stable environment, but avoidance of wind-induced near-surface turbulence might explain, to some extent, the varying degrees of surface avoidance observed. It has been observed that surface accumulations of *M. rubrum* are more prevalent on calm days than windy ones (Lindholm 1981), but surface accumulations are also common in autumn, even with a very weak thermocline. Clearly the issue of the role of water column stability requires further clarification and dynamic stability should become a routine measurement.

Despite the choice of Inre Verkviken as a site with minimal advective influences (see 'Introduction'), changes in total integrated populations were observed to occur during individual sequences of profiles. However, it is unclear whether these changes represent real changes due to the influence of advection, cell division and grazing, or whether they represent artefactual variation due to the aggregation of this species. The degree to which sampling interval coincides with population maxima, together with the magnitude of maxima, will determine how well the real integrated population is estimated. The error associated with estimates of total integrated population is impossible to determine as this would require a stable population of known abundance.

Highest accumulations of *Mesodinium rubrum* in Inre Verkviken have occurred in autumn (Lindholm 1981, Lindholm & Mörk 1990) and seem to be associated with events which increase nutrient concentration close to the surface; for example winds, erosion of the thermocline or rainfall. This poses the question what limits *M. rubrum* here in summer? The absence of red water when irradiance and nutrients are vertically separated but 'within reach' (in less than 1 h) suggests that there could indeed be a significant metabolic cost involved in exploitation of the water column (see Crawford 1992b). However, caution in the interpretation of 'red water' is required; the working definition of visible red water for *M. rubrum* is often given as abundances of over 200 cells ml^{-1} (McAlice 1968), with abundances typically of around 1000 to 2000 cells ml^{-1} in dense red water (Crawford et al. 1997). Abundances in Inre Verkviken reached 200 cells ml^{-1} on one occasion (Fig. 3), but were more typically of the order 10 to 100 cells ml^{-1} as a mean abundance through the water column (Figs. 1–3); at least an order of magnitude lower than in dense red water. However, if all cells had concentrated near the surface, the abundances observed in Inre Verkviken could have been categorized as red water. A more workable definition of red water in terms of integrated water column abundance (cells m^{-2} water surface) could be more useful; for example red tides in the Southampton Water estuary (UK) are characterized by integrated abundance of *M. rubrum* of the order of 1000×10^6 to 2000×10^6 cells m^{-2} (Crawford et al. 1997). Placed in this context, the abundances in Inre Verkviken (Figs. 1–3) were relatively stable over the study period, of the order 550×10^6 to 900×10^6 m^{-2} and in fact only a factor of 2 lower than dense red water values. Whilst it is not suggested that red water is always formed just by simple accumulation of cells, it is clear that in summer and autumn in Inre Verkviken, factors promoting development of 'visible red water' could have more to do with factors regulating vertical distribution than previously anticipated.

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