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New aspects of migratory behavior of phytoplankton in stratified waters: Effects of halocline strength and light on *Tetraselmis* sp. (Prasinophyceae) in an artificial water column

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Abstract

There is very little information in the literature about how phytoplankton flagellates respond to rapid changes in salinity (e.g., haloclines of different strength). Here we present such data obtained from experiments with *Tetraselmis* sp. (Prasinophyceae) in a specially designed artificial water column. The experiments were performed with surface salinities varying from 27.4 to 33.4‰, whereas bottom salinities were essentially constant (34.0–34.6‰). Cells were introduced near the bottom. The first stage of the ascent was an accumulation of cells in the lower part of the halocline. The second was a transit to the upper part of the halocline after a variable time lag, and the third stage was a further ascent to the surface layer, again after a variable time lag. Our results reveal a strong positive phototaxis of the swimming cells under continuous surface irradiances in the range 17–144 μmol quanta m^{-2} s^{-1}. Maximum swimming speeds were found to be 0.9 m h^{-1}. Increasing halocline strength (ΔS = 0.7, 3.0, and 6.6‰), resulted in reduced swimming activity, but the cells managed to pass through after an adaptation period. Under a 14 : 10 light : dark (LD) cycle, the cell concentrations of the bottom layer decreased gradually for each cycle, and cells accumulated in the surface layer during the light period. During the dark period, cell concentrations were also increasing in the halocline for each cycle. A downward migration started about 2 h before the light period ended and was slower than the ascent of cells from the halocline. It therefore seems that positive phototaxis was stronger than the positive geotaxis as a driving force of cell motility. We conclude that strong haloclines can prevent phytoplankton flagellates in the surface layer from reaching the nutrient-rich deeper layer during the night and therefore play an important regulating role in the bloom dynamics of phytoplankton.

Some stratification of the water column is usually a characteristic feature of most pelagic environments during the productive season. Water column stability plays an important role in relation to pelagic primary production and to the vertical structure of phytoplankton (Braarud et al. 1958*a*; Erga and Heimdal 1984; Bjørnsen and Nielsen 1991).

In fjords and coastal waters, salinity is the main governing factor with respect to the density of seawater because of the freshwater supply from land. Therefore, the halocline is the main contributor to the stratification of these waters. It is also evident that the strength and duration of stratification are of great importance for initiating and sustaining phytoplankton blooms (Cloern 1984; Frette et al. 2001). Stratified water masses often prevail during extended periods of calm weather, which is often the case during summer (Paasche and Erga 1988; Erga 1989*a*; Erga and Skjoldal 1990). This leads to a nutrient-depleted euphotic zone being isolated from the deeper and nutrient-rich water by a seasonal pycnocline. Such conditions are reported to be favorable for growth of phytoplankton flagellates (Smayda 1980; Cushing 1989). This is usually considered to be due to their ability to swim rapidly up and down during the day and night cycle to satisfy both their light and nutrient demand. The ecological consequences of prolonged stratification are, however, more than these two phenomena. This will be referred to in more detail.

According to the ‘‘critical depth’’ theory (Sverdrup 1953; Nelson and Smith 1991), stability of the upper layer of the water column prevents algal cells from being mixed below the critical depth by turbulence, which is the reason for the existence of net photosynthesis. The existence of a marked pycnocline has also been reported to play a key regulatory role for development of many toxic algal blooms. Holligan (1979) found that blooms of *Gyrodinium aureolum* (Dinophyceae) around the British Isles started at the depth of the pycnocline and that accumulation of cells in a restricted surface layer was the final stage. The unexpected bloom of *Chrysochromulina polylepis* (Prymnesiophyceae) in Scandinavian waters in May–June 1988 also developed close to the halocline (Kaas et al. 1991; Maestrini and Granéli 1991; Skjoldal and Dundas 1991). At the height of this bloom, maximum cell concentrations were encountered at the depth of the hal-

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ocline (Nielsen et al. 1990). Skjoldal and Dundas (1991) emphasize the importance of low wind activity and large freshwater runoff for the building up of the bloom. This also caused the summer blooms of *Prymnesium parvum, P. patelliferum,* or both Prymnesiophyceae being encountered several times since 1989 in the inner Ryfylkefjord system in Norway (Kaartvedt et al. 1991; Larsen et al. 1993). In recent investigations, it has been shown that peak concentrations of *Pseudo-nitzschia* spp. (Bacillariophyceae) were restricted to very thin layers (only a few centimeters thick) at the base of, or within, the pycnocline in the East Sound, Washington (Dekshenieks et al. 2001; Rines et al. 2002).

Vertical migration in general has been demonstrated for many phytoplankton flagellates both in situ (Hasle 1950; Blasco 1978; Park et al. 2001) and in experimental columns (Rasmussen and Richardson 1989; Olsson and Granéli 1991; MacIntyre et al. 1997). The algal mode of handling this seems to be that the cells migrate down to the nutrient-rich water during the dark period to take up nutrients and returning to the nutrient-depleted surface water during the light period, where they can utilize accumulated nutrients for photosynthesis (MacIntyre et al. 1997; Kamykowski et al. 1999; Kimura et al. 1999). It is generally accepted that taxis-directed orientation could be interpreted as being due to positive phototaxis in the light and positive geotaxis in the dark (Kamykowski and Yamazaki 1997).

Another important ecological aspect of vertical migration is that the algal species possessing this ability to adjust their vertical position especially fast might be trapped within horizontally advected water masses and thereby transported into new and growth-favorable areas. An example of this is subsurface transport of cells into fjords and bays below a less saline and outflowing surface layer (Braarud et al. 1958*b*; Tyler and Seliger 1978; Erga 1989*a*).

Even if haloclines are widespread and decisive for the development of algal blooms and for the primary production levels of coastal and fjord ecosystems (Erga and Heimdal 1984; Erga 1989*a,b*), little is known about how the vertically swimming microalgae behave in such an environment of abrupt changes in salinity. Characteristic for the few studies conducted in this field is the lack of information on the fine-scale swimming pattern in the vicinity of the halocline (Rasmussen and Richardson 1989; Olsson and Granéli 1991; Kamykowski 1995). An important regulating factor in this context is light, confirmed by the phototactic response shown by many species (Eggersdorfer and Häder 1991; Passow 1991; Kamykowski et al. 1999).

Because advective processes often influence vertical migration of phytoplankton in situ, the value of conducting fine-scale motility studies in a stratified artificial water column is not diminished. On the contrary, such studies might give detailed knowledge on how microalgae respond to haloclines of different strength, which would be difficult to show in situ.

The occurrence of phytoplankton flagellates during stratified water conditions is considered to be a result of their ability to conduct diurnal vertical migration down below the pycnocline to satisfy their nutrient demand. The important question is: Are they able to penetrate the haloclines? To find the answer to this, we must be able to reveal the migrational behavior of the algae under conditions as similar to the natural conditions as possible. This can only be achieved by tracking the movements of the algae without disturbing the fine vertical gradients in physical, chemical, and biological structures. For this purpose, we have developed an artificial water column equipped with an externally moving optical system—AWCEMOS—that measures the vertical distribution of cell concentration (Erga et al. 1999). Here, we present results from such experiments with the marine flagellate *Tetraselmis* sp. Special focus is put on the swimming behavior in the vicinity of the halocline and how it is influenced by the strength of the salinity gradient and light : dark shifts (LD). According to our knowledge, such data have not been obtained earlier.

Materials and methods

Algae culture—We used cultures of the green flagellate *Tetraselmis* sp. isolated from a fjord system outside the city of Bergen. For these waters, salinity is normally between 26 and 34‰ (Erga and Heimdal 1984). Earlier studies in our laboratory on this species of *Tetraselmis* revealed that optimal growth was obtained within the salinity interval 28–35‰, temperature interval 23–25°C, and light intensity interval 250–350 μmol quanta m^{-2} s^{-1} (unpubl. data). It was also confirmed that cell volumes of *Tetraselmis* sp. remained constant when growing in water with salinity between 26 and 34‰ (unpubl. data). The cells were batch-cultured (nonaxenic) at 20°C in 350-ml conical-bottom tubes (3.5 cm internal diameter) containing 200 ml of 0.22-μm-filtered natural seawater supplemented with Conway nutrients (Walne 1966). The cultures were aerated with filtered air enriched with 2% carbon dioxide. Cell density and size were monitored using a Coulter Counter (Model ZM) coupled to a Channelyzer 256, and the electronic cell counts were verified against microscopic cell counts in Fuchs-Rosenthal counting chamber. The physiological condition of the cells was also judged from microscopy. The cultures were harvested at midexponential growth, consistent with a cell density of approximately 10^6 cells ml^{-1}. The diameter of the algae during the experiments was 7–10 μm. Growth rates (μ) given as divisions per day (div. d^{-1}) were calculated as follows.

$$\mu = [\ln(N_f/N_i)]/(\ln 2)t$$

N_f and N_i are the final and initial cell concentrations, respectively, and t is the time in days (24 h).

Seawater—The seawater used in the experiments was obtained from a deep-water intake at 100 m depth in the fjord just outside the city of Bergen. Typical for this water are relatively stable values of temperature (5–10°C), salinity (33–35‰), and nutrients (10–20 μmol L^{-1} nitrate, 10–15 μmol L^{-1} silicate, and 0.5–1.5 μmol L^{-1} phosphate) during the year. The seawater was stored in darkness at room temperature (20°C) for several weeks before being used, without lowering the oxygen content more than a few percent (94% saturation, equivalent to 5.0 ml L^{-1}). All experiments were run at room temperature. Just before the start of the experiments, the seawater was filtered through a net (ARL Filter

Table 1. Duration and range of conditions for the four water column experiments. The environmental parameters comprise surface light (photosynthetic available radiation, PAR), salinity (S), and temperature (T). The salinity gradient (halocline) is symbolized by ΔS, and the ratio of volumes of the upper less saline layer and the lower saline layer (upper/lower) are reported.

Exp. no.	Duration (d)	Light (PAR) Intensity (μmol m^{-2} s^{-1})	Light (PAR) LD (h)	T (°C)	ΔS (‰)	Volume, upper/lower (liters)
1	3.8	↓17, ↓50, ↓108, ↓144, ↑36	24 : 0	19.2	0.7	91.0/94.0
2	1.9	↓108	24 : 0	18.8	3.0	88.5/98.5
3	3.0	↓108	24 : 0	19.8	6.6	88.0/98.4
4	2.8	↓66	14 : 10	20.4	1.4	95.0/85.0

↓ Downward irradiance (top light source).
↑ Upward irradiance (bottom light source).

AB) with a mesh size of 1 μm. This treatment increased the oxygen saturation of the intake water to 100%.

Artificial water column—The experimental system for the study of fine-scale vertical displacement of microalgae consists of an artificial water column equipped with an externally moving optical system (AWCEMOS). The column, made of clear Plexiglas (also the bottom is clear) has a maximum volume of 212 liters (height 149.0 × width 52.0 × depth 27.4 cm). The experimental tank is filled with seawater through a bottom tap connected to an elevated container. Downward irradiance is provided by three 20-W fluorescent light tubes (2 Philips TLD/79, 1 Philips TLD/96) at the top of the water column. The optical detection system is mounted on a movable frame on the outside of the tank. It consists of a laser diode light source (with maximum output signal at 670 nm) at the front of the tank, a detector at the back of the tank, and a lens system in between. When operated, the attenuation of the light beam will vary in accordance with the cell concentrations within the light path. The correlation between these two parameters is found from calibration experiments (*see below*). For further information and details on AWCEMOS, see Erga et al. (1999). Salinity and temperature profiles of the water column were obtained by using a Conductivity Meter LF 538 coupled to a Tetracon 325 sensor system (both produced by Wissenschaftlich-Technische Werkstätten GmbH) in the beginning and in the end of the experiment. The initial measurements were conducted on the inflowing water, before entering the Plexiglas tank, to prevent any disturbances of the fine-salinity gradients being formed. The final salinity and temperature profile was obtained by carefully lowering the sensor downward in the water column.

Haloclines—Seawater with a desired salinity was obtained by diluting the natural seawater (33–35‰) with deionized water (Millipore Corp.; Milli-RO Plus Reverse Osmosis—and Milli-Q Plus Reagent Grade—Water Purification System). Fine-layered haloclines were established (Table 1) by carefully filling seawater with different salinities into the water column through the bottom tap. This was achieved with minimal turbulence (Erga et al. 1999). Thus, the bottom salinity was essentially constant (34.0–34.6‰) between experiments, while surface salinity was adjusted (27.4–33.4‰) to create the desired gradient.

Light conditions—Start cultures for the experiments were adapted to the conditions the cells would meet in the column, both under continuous illumination in the case of halocline experiments, and under a 14 : 10 LD cycle in the case of LD shift experiments (Table 1). The preconditioning light was provided by 40-W fluorescent light tubes, regulated to give an incident irradiance of about 150 μmol quanta m^{-2} s^{-1}. Full-surface irradiance of the experimental column varied between 66 and 108 μmol quanta m^{-2} s^{-1}. This level of surface irradiance was selected in order to match the lower part of the I_k (index of adaptation to low light) range found for this species of *Tetraselmis* during exponential growth (unpubl. data).

Calibration—All cultures being used in the experiments were preconditioned in the same way and harvested at exponential growth. The relationships between algal cell concentration and light attenuation were investigated just prior to the present four experiments. The most extensive of the calibrations had 72 data points and is here chosen to represent the relationship between algal cell concentration and light attenuation (Fig. 1). Note that the low-concentration relationship is inserted. The slope value of the functional regression line was found to be nearly the same for all the calibration experiments.

Results

Halocline longevity—The halocline was found to persist with only small changes in salinity during the experimental periods (2–3 d). An example of this can be seen in Fig. 2. Here, vertical profiles of salinity at the start and end of experiment 3 are shown. There was a small increase in salinity above the halocline (0.4–0.5‰) from evaporation. Below the halocline, only a slight decrease in salinity (0.1–0.2‰) appeared, probably from molecular diffusion. For the other experiments, the same pattern of small changes in salinity appeared. The temperature did not change appreciably during the experiments, except for a slight increase at the surface (0.1°C). For the rest of the water column, temperatures remained stable around room temperature.

Effects of halocline strength—Experiment 1 (ΔS = 0.7‰): The upper layer had 33.4‰ and the lower 34.1‰ salinity. During this experiment, both the light intensity and the po-

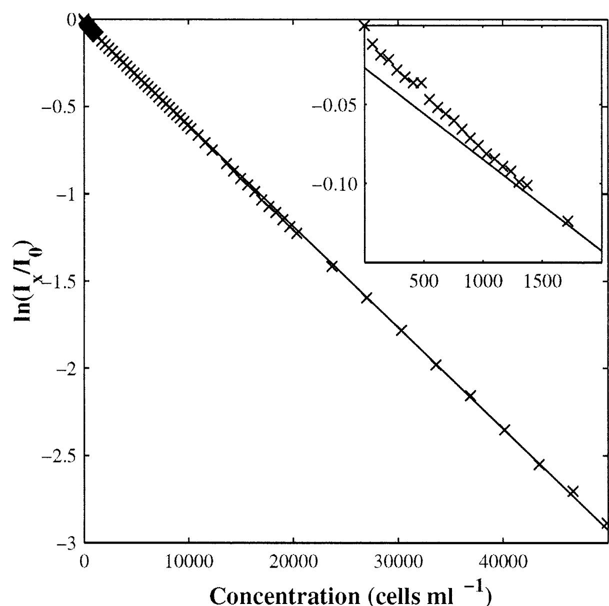

Fig. 1. Calibration curve for experiment 1. The natural logarithm of the radiant intensity ratio $I_x I_0^{-1}$ versus cell concentration N^* of *Tetraselmis* sp. (cells ml^{-1}). Crosses mark data points. I_x and I_0 are the transmitted and incident radiant intensity, respectively. Magnification of the relationship for low cell concentrations is inserted. The theoretical linear relationship is also shown (solid line). Linear regression analysis (n = 69) gives r^2 = 0.999 and a x regression coefficient of −17,142.8.

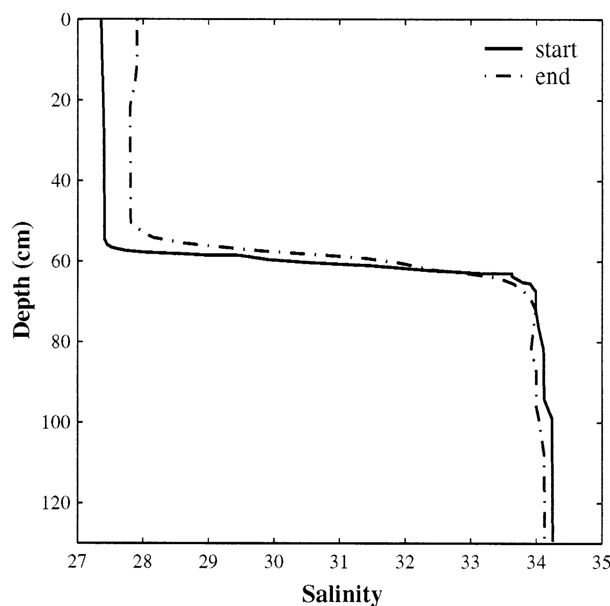

Fig. 2. Depth profile of salinity at the start and after 95 h of experiment 3. The halocline is situated at 55–65 cm.

sition of the light source (top/bottom) were changed during the experiment in order to test the degree of positive phototaxis (Table 1). After inoculation, the layer of algae extended upward to 30 cm above the bottom (Fig. 3). From the vertical profiles, it emerged that the "fastest swimmers" of *Tetraselmis* sp. approached the lower halocline already after 20 min. This meant that even a surface irradiance of 17 μmol m^{-2} s^{-1} was sufficient to initiate an upward migration (i.e., positive phototaxis). It appeared that most of the cells stopped their upward migration when they approached the lower part of the halocline. After 1 h 2 min, the upward-migrating cells started to accumulate in the upper part of the halocline. After 2 h 19 min, there were more cells at the upper part of the halocline than at the lower part. Further on, the cells left the upper halocline and started to accumulate at the surface. After 2 h 47 min, cells were detected in the surface layer. This pattern prevailed during the next hours.

It should also be noted that the increase in cell concentrations in the upper layer during the first 7 h was higher than can be explained from the number of cells ascending from below. This is from growth by some fraction of the population. After about 11 h, the algal concentrations were about the same above the halocline as below, but still the tendency of accumulation of cells in the upper part of the halocline remained. The pattern of upward migration was reinforced when the surface irradiance was increased from 17 to 50 μmol m^{-2} s^{-1} after 22 h 18 min. During the following 2 h, it led to higher concentrations of cells from the lower part of the halocline upward, while cell concentrations slowly decreased below the halocline. The changes in vertical distribution were, however, relatively small until 31 h 19 min. After this "resting" period, the number of ascending cells again increased strongly. This trend was strengthened when the surface irradiance was increased to 108 μmol m^{-2} s^{-1} after 41 h 15 min (i.e., increased positive phototaxis). It should also be noted that the peak value in cell concentrations in the upper part of the halocline remained stable until this point. From then on, the main increase in cell numbers appeared above the halocline, especially toward the surface, apparently mostly from cell division since the concentrations below the halocline did not change. At 47 h 18 min, the main light source at the top of the tank was switched off and a 36 μmol m^{-2} s^{-1} light source (one 20-W fluorescent light tube) placed below the tank was turned on. This resulted in an immediate descent from the surface layer, and an increase in cell number was observed close to the halocline only after 1 h. For the fastest swimming cells, this meant a distance covered of 0.6 m in 1 h.

During the next 16 h, the downward migration (e.g., positive phototaxis) continued, and the cells descended down toward the bottom. At 64 h 18 min, the bottom light was switched off and the surface light switched on (108 μmol m^{-2} s^{-1}). The first response was upward migration of cells from the bottom layer, resulting in surface accumulation of cells at 69 h 39 min. At 76 h 21 min, a peak in cell concentration was seen at 105 cm. After the surface irradiance was increased to 144 μmol m^{-2} s^{-1} at 76 h 21 min, the main response was increased cell concentrations close to the surface and below the halocline at 88 h 11 min. In accordance with such a pattern, the increased surface irradiance toward the end of this experiment seemed to have a stimulating effect both on cell division and positive phototaxis.

Experiment 2 (ΔS = 3.0‰): The upper layer now had 31.6 and the lower 34.6‰ salinity. The surface irradiance was kept at a constant value of 108 μmol m^{-2} s^{-1} during

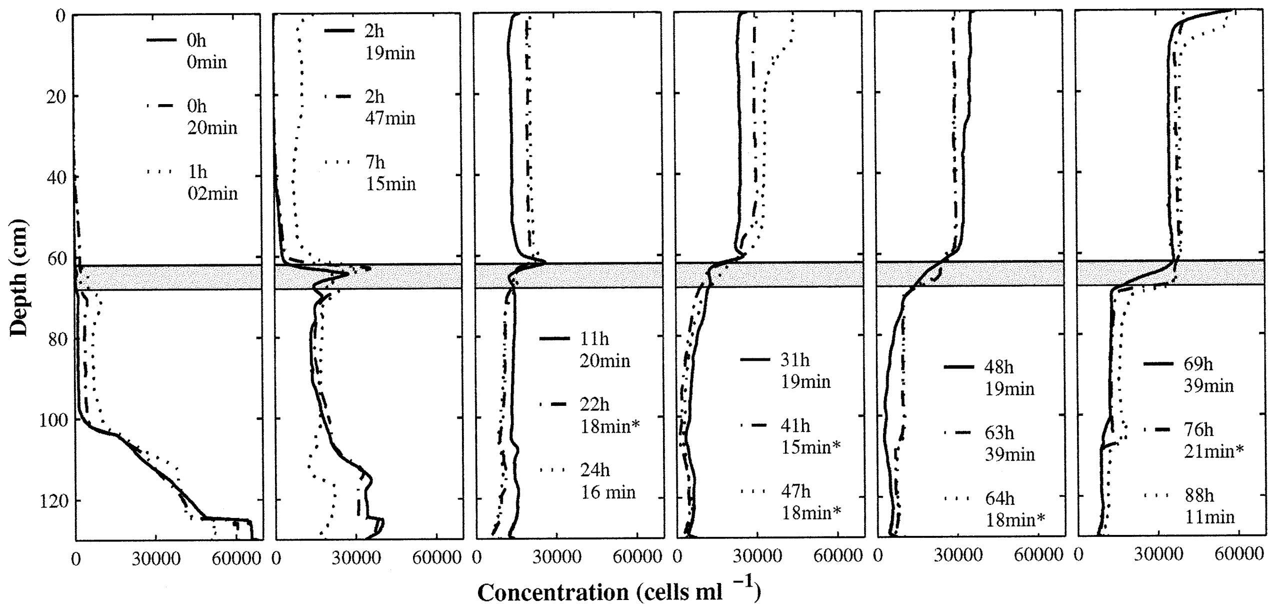

Fig. 3. The influence of halocline strength on the upward migration of *Tetraselmis* sp. Selected fine-scale profiles at various times during experiment 1 are shown. The initial population was situated in the bottom layer. The position of the halocline ($\Delta S = 0.7‰$) is indicated by a horizontally shaded bar. Light intensities are according to Table 1. Times for altering light intensity during experiment 1 are marked by asterisks. Note that for the 47 h 18 min, 48 h 19 min, and 63 h 39 min profiles, light was from below. For the other profiles, light was from above. Water temperature was kept at room temperature.

the whole experiment (Table 1). The inoculation layer extended about 15–20 cm above bottom (Fig. 4). During the first 10 h, most of the changes in vertical distribution were from upward vertical migration. During the first hour, as in the first experiment, some of the algae migrated upward to the lower part of the halocline where they stopped before swimming through. The first cells reached the surface after 1 h 21 min. This is faster than for the preceding experiment. It therefore seemed that the higher surface light intensity in the beginning of this experiment led to an increased upward swimming response, even if the halocline was stronger. After 4–6 h, the surface cell concentrations had increased strongly. During the following hours, this tendency continued, but was now accompanied by decreasing cell concentrations in the bottom layer. This ascending pattern was, however, not enough to explain the increased cell concentrations being

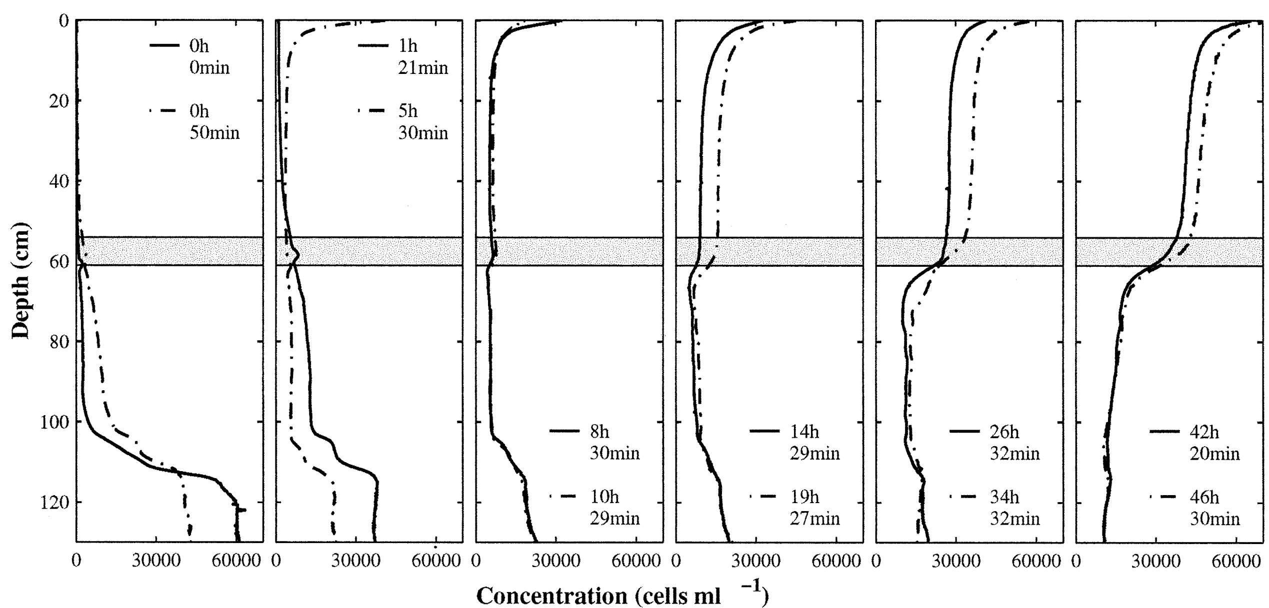

Fig. 4. The influence of halocline strength on the upward migration of *Tetraselmis* sp. Selected fine-scale profiles at various times during experiment 2 are shown. The initial population was situated in the bottom layer. The position of the halocline ($\Delta S = 3.0‰$) is indicated by a horizontally shaded bar. Surface light intensity was 108 μmol m^{-2} s^{-1}. Water temperature was kept at room temperature.

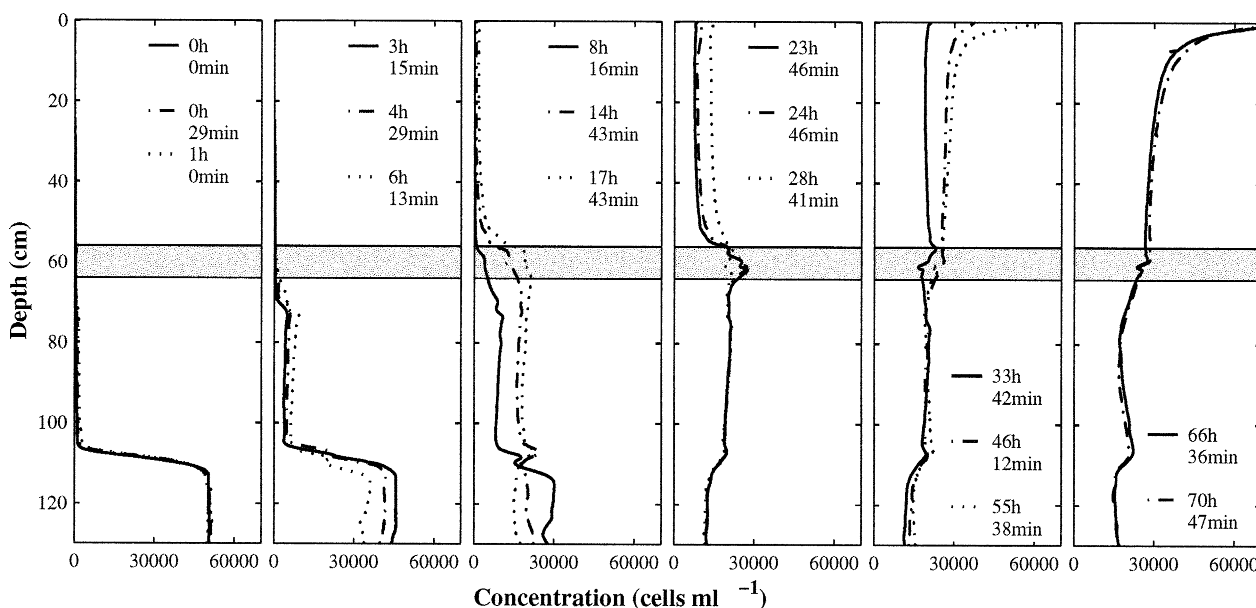

Fig. 5. The influence of halocline strength on the upward migration of *Tetraselmis* sp. Selected fine-scale profiles at various times during experiment 3 are shown. The initial population was situated in the bottom layer. The position of the halocline ($\Delta S = 6.6‰$) is indicated by a horizontally shaded bar. Surface light intensity was 108 μmol m^{-2} s^{-1}. Water temperature was kept at room temperature.

observed in the upper part of the water column during the period 8 h 30 min to 26 h 32 min. This discrepancy is accounted for by cell division. Around 14 h, the total cell concentrations above the halocline were about the same as below. This event thus happened about 3 h later in this experiment than in the preceding experiment, probably because the majority of cells remained for a longer time below the halocline. Between 34 h 32 min and 42 h 20 min, there was a marked decrease in cell concentrations close to the bottom (0–20 cm above). It was accompanied by a corresponding increase in cell concentrations for the rest of the water column because of upward migration of cells. The increase in cell concentrations above the halocline continued until the end of the experiment (46 h 30 min). During the last 4 h of the experimental period, the cell distribution below the halocline did not change much. At the same time, however, there was a marked increase in cell concentrations in the upper layer, caused by cell division. It should be noted that even after almost 2 d, it was still possible to see a peak in cell concentration at the top of the inoculation layer (20 cm above bottom) in this experiment.

Experiment 3 ($\Delta S = 6.6‰$): Salinity of the upper brackish layer was now reduced to 27.4‰, and the layer below had a salinity of 34.0‰ (Table 1). The relatively strong halocline was chosen for its relevance to the spring/summer hydrographical conditions of the fjords of Western Norway (Erga and Heimdal 1984; Erga 1989*a;* Erga and Skjoldal 1990). The surface irradiance during this experiment was 108 μmol m^{-2} s^{-1}. The inoculation layer extended about 20 cm above bottom (Fig. 5). The ascent of cells toward the halocline started already during the first hour. Unlike the pattern described for the two preceding experiments, the majority of ascending cells stopped about 60 cm above the bottom (*see* the 3 h 15 min profile). At 4 h 29 min, another peak emerged at the upper part of the inoculation layer at about 108 cm depth. At the same time, the first cells had reached the lower halocline. Here, cells stopped their upward migration and an accumulation was seen during the next couple of hours. Around 6 h 13 min, the first cells started to move upward toward the upper halocline. Here, the cells accumulated before breaking into the upper brackish layer at 8 h 16 min.

A crucial point of time during this experiment was after about 15 h. At this time, two main events occurred. First, the fastest swimmers reached the surface, which is about 13 h later than for the two preceding experiments. Second, the cells were now evenly distributed in the whole haline lower layer, except for the peak at 108 cm depth. In agreement with the upward movement of cells, the cell concentrations had decreased in the bottom layer. This trend continued until 17 h 43 min. From now on, the main developmental pattern was a general increase in cell concentrations in the upper part of the water column because of division, since cell concentrations below the halocline did not change much during the same period. Within the halocline layer itself, however, cells divided only until 23 h 46 min. For the period 24 h 46 min to 33 h 42 min, the cells migrated from the lower halocline to the upper halocline. Consistent with these findings, cell concentrations in the upper and lower part of the halocline were equal at 28 h 41 min, and at 33 h 42 min they were higher in the upper part. It is also interesting to note that at 33 h 42 min, the cell concentrations were about the same above and below the halocline. After this, the main changes appeared in the upper brackish layer, where cell concentrations increased gradually until the end of the experiment (70 h 47 min). The cell concentrations, however, increased faster in the surface layer than for the rest of the brackish layer. It also appears that during the last period of the experiment (55 h 38 min to 70 h 47 min), there was again some upward migration of cells from below the hal-

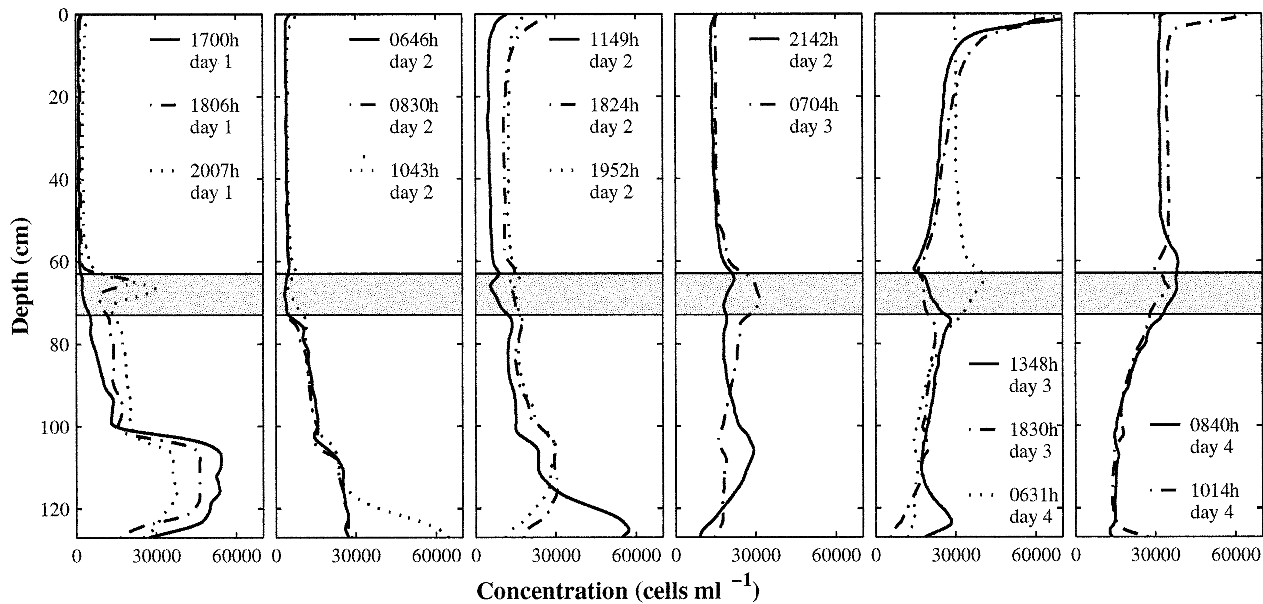

Fig. 6. Selected profiles from the diel variations in vertical distribution of *Tetraselmis* sp. during experiment 4 with a 14 : 10 LD cycle. The position of the halocline (ΔS = 1.4‰) is indicated by a horizontally shaded bar. Surface light intensity was 66 μmol m^{-2} s^{-1} and temperature 20.4°C. The initial population was situated in the bottom layer.

ocline and into the upper layer, as revealed by decreasing cell concentrations in the depth interval 75–95 cm.

These ascending cells cannot alone, however, account for the steep increase in cell concentrations in the upper part of the brackish layer. Therefore, it must be because of a combination of upward-migrating cells and cell division of the cells that had already reached this layer. Three peaks in cell concentrations can be seen at 66 h 36 min: one in the surface layer, one in the upper halocline, and one in the upper part of the original inoculation layer. For ascending cells of *Tetraselmis* sp., it therefore seems that the halocline strength of this experiment was a stronger obstacle for upward migration than for the preceding experiments with weaker haloclines. It is also obvious that some part of the population did not leave the bottom layer during the whole experiment. Taking into account that initial concentrations were higher in experiment 2 than in this experiment, it is interesting to note that the concentrations of cells remaining below the halocline now were in the range 15,000–20,000 cells ml^{-1} after 46 h 12 min, which is higher than the concentrations found in the end (after 46 h 30 min) of experiment 2 (Fig. 4).

Effect of diel LD shifts—Experiment 4 (ΔS = 1.4‰, 14 : 10 LD): The major task of this experiment was to monitor the fine-scale vertical displacements of *Tetraselmis* sp. in and around the halocline during three consecutive LD shifts. Based on the experience from the preceding experiments, we decided to use both a modest halocline strength and light intensity. Salinity of the upper layer was now 33.1‰, and the lower layer had a salinity of 34.5‰ (Table 1). The surface irradiance during the light period was set to 66 μmol m^{-2} s^{-1}. The light period lasted from 0800 until 2200 h and the dark period from 2200 until 0800 h. In this experiment, the inoculation layer extended 23 cm above the bottom (Fig. 6). The first upward-migrating cells were seen in the lower halocline shortly after start of the experiment (1700 h, day 1). During the next couple of hours, the cells approached the upper part of the halocline. Thus, a maximum concentration of 30,000 cells ml^{-1} at 65 cm depth was achieved at 2007 h on day 1. Some cells also penetrated the halocline and migrated up to the surface within the first hour. A more thorough analysis of the data, however, reveals that about 2 h before the dark period began (i.e., 2007 h, day 1), the fraction of cells that had migrated upward to the halocline and to the upper layer started the descent from these sites (Fig. 7). This can indicate that the algae have a more complex behavior than expected. The downward migration continued throughout most of the dark period and thus led to a markedly lower cell concentration around the halocline, while most of the cells accumulated at the bottom (Fig. 6).

The first event in the early phase of the second light period was a new immediate massive upward migration of cells (Fig. 7). This could be seen from an initial increase of cells about 10 cm above the bottom (from 0830 h, day 2, until 1043 h, day 2) before ascending, first toward the halocline and later into the upper layer, finally reaching the surface (1149–1824 h, day 2) (Fig. 6). A couple of hours before the end of the second light period (1952–2142 h, day 2), the cells again started their downward migration (Figs. 6, 7). A massive and almost continuous descent of cells from the entire water column took place during the second dark period (Fig. 7). Fewer cells, compared with the preceding dark period, however, reached the bottom layer, as seen from the markedly lower concentration of ascending cells from the bottom layer occurring during the first part of the third light period (Figs. 6, 7). Accompanying the gradually decreasing cell concentrations of the lower layer were the increasing concentrations of the upper layer during the third light period until 1830 h, day 3 (Fig. 6). This was due to the continuous replacement of cells from below by upward-swimming cells.

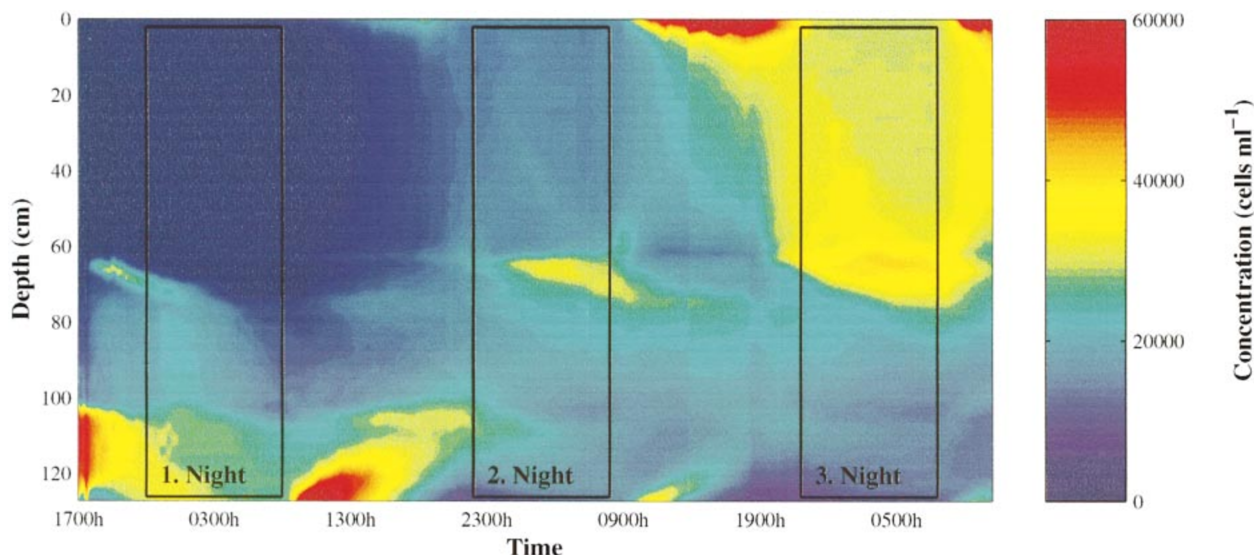

Fig. 7. High-resolution pseudocolor plot showing spatial and temporal displacements of *Tetraselmis* sp. cells during experiment 4. The halocline was positioned between 63 and 73 cm.

Now, more than 60,000 cells ml^{-1} were found in the surface layer, and very few cells were left at the bottom (Fig. 6). The pattern of cells starting their descent about 2 h before the end of the light period was now repeated for the third time (Fig. 7). During the third dark period, most of the cells left the upper surface layer and migrated down to the halocline (e.g., 0631 h, day 4), where concentrations increased to more than 40,000 cells ml^{-1} (Figs. 6, 7). Even if the cells of the lower layer also were descending to the bottom during the third dark period, fewer and fewer cells were found in the bottom layer (Figs. 6, 7). This trend was again confirmed during the first hours of the fourth light period. The majority of upward-migrating cells were now encountered from the depth of the halocline up to the surface layer. From 0840–1014 h, day 4, the cell concentrations of the surface layer had increased from 30,000 to 65,000 cells ml^{-1} (Fig. 6).

Discussion

Vertical migration versus cell division—The mean swimming speeds of *Tetraselmis* sp. emerging from the present experiments are calculated from time registrations of cell movements upward from the bottom to the surface (i.e., including passage of the halocline) (Table 2). The other swimming speeds given in Table 2 are representative for the three layers constituting the experimental water column. It could be speculated that the forces (e.g., double diffusion/thermohaline circulation) released by a 0.1‰ increase in salinity per day for the upper layer in our experiments (*see Results*), could have an effect on the vertical displacement of *Tetraselmis* sp. Based on the results from other experiments, however, it can be concluded that the circulation rates generated by these forces are insignificant compared with swimming speed of *Tetraselmis* sp. (unpubl. data). According to our experience with the swimming behavior of *Tetraselmis* sp. in AWCEMOS with the light source at the top, the swimming orientation is vertically toward the light source because of a strong positive phototactic response. Therefore, horizontal swimming orientation is not significant under these conditions.

In the case of a relatively strong halocline (i.e., experiment 3), the mean swimming speed is strongly reduced (Table 2) because of the longer time spent crossing the halocline. From the comprehensive literature on algal cell motility, Goldstein (1992) concluded that swimming speeds of 0.7 m h^{-1} are typical for flagellated microalgae, but that some dinoflagellates, which belong to the fastest algal swimmers, can have swimming speeds as high as 1.8 m h^{-1}. These values are in good agreement with our results (Table 2). It should be noted, however, that in most cases, the literature values cited above by Goldstein (1992) are based on microscale observation of single cell movements. Therefore, they should be considered extreme values and thus will not necessarily apply to stratified macroscale water columns. In our experiments, such conditions are basic because of their relevance to natural coast and fjord water. It is interesting to note that experiments conducted with the *Chatonella antiqua* (Raphidophyceae) in a large culture tank under moderate stratifi-

Table 2. Growth rates and swimming speeds of *Tetraselmis* sp. calculated for each experiment in AWCEMOS. Note that in experiment 4, light was periodic with a 14:10 LD cycle, whereas in experiment 1, 2, and 3, light was continuous.

	Swimming speed* ($m\ h^{-1}$)				
Exp. no.	A	B	C	D	Growth rate (div. d^{-1})
1	0.90	0.08	0.40	0.37	0.44
2	0.93	0.11	0.80	0.60	0.70
3	0.10	0.03	0.12	0.07	0.58
4	0.90	0.06	0.30	0.70	0.23

* A, from the top of the inoculation layer to the base of the halocline; B, through the halocline; C, from the top of the halocline to the surface; D, mean swimming speed from the top of the inoculation layer to the surface.

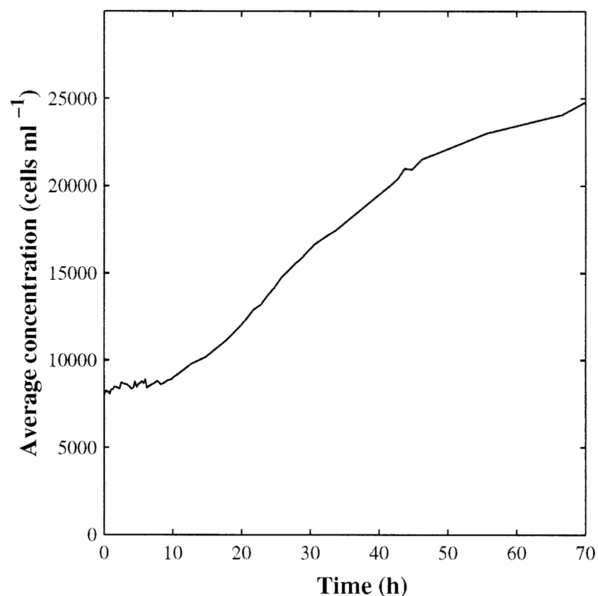

Fig. 8. Average concentrations of *Tetraselmis* sp. cells of the water column versus time in experiment 3 from data registered by our optical detection system AWCEMOS.

cation revealed swimming speeds of 0.6–1.0 m h^{-1} (Watanabe et al. 1991). Our results indicate that there are speed differences among the swimming cells. Apparently, some cells are ''fast'' swimmers and some are ''slow'' swimmers. This was clearly demonstrated in experiment 3, where most of the cells were slow swimmers (Table 2) but a small fraction of the cells (<1,000 cells ml^{-1}) achieved maximum swimming speeds of 0.90 m h^{-1} between the top of the inoculation layer and the bottom of the halocline. Such a differentiation in swimming speed has earlier been confirmed in our laboratory for synchronous cultures of *Clamydomonas reinhardti* (Chlorophyceae) (G. Knutsen pers. comm.). These variations in individual swimming speeds probably are due to genetic differences.

A further analysis of the observed changes in vertical distribution of cells shows that they are not always due to vertical migration alone, but to cell division as well. This is to be expected because a population of *Tetraselmis* sp. consists of swimming cells and nonmotile sporulation stages. These different stages of the life cycle were easily detected during our experiments. Thus ongoing cell division is revealed when increased cell densities are found within a certain depth interval without an accompanying decrease of cells in the layer below (experiments 1, 2, and 3) or above (experiment 4). Mean growth rates (div. d^{-1}) of our *Tetraselmis* sp. for the experimental periods are calculated from total cell counts of the inoculum and after complete mixing of the water column at the end of the experiment (Table 2). These values seem to be in good accordance with calculations based on the data registered by AWCEMOS.

Taking experiment 3 as an example (Fig. 8), a total growth rate of 0.55 div. d^{-1} was found for the experimental period. Another noteworthy point emerging from our experiments with constant and continuous surface light is that cell division occurred simultaneously over extended parts of the water column. Such a development was periodically encountered over the whole brackish layer in these cases (Figs. 4, 5), indicating that in this part of the water column, *Tetraselmis* sp. cells are growing synchronously. When introducing LD shifts (14 : 10), however, another growth pattern was seen (Figs. 6, 7). In this case, the growth rate was reduced to less than half compared with the preceding two experiments (Table 2). This could also be seen in connection with the 39% lower surface irradiance. From analysis of the vertical profiles, it seems that no cell division had taken place in the water column between the surface and bottom layer either during the light period or during the dark period. Instead, cell division was now restricted to the near-bottom layer, and it was mainly encountered during the dark period, as could be seen during the first hours of the new light period, when cell concentrations of the bottom layer increased to higher levels than during the last hours before the foregoing dark period. From experiments in an artificial water column, Olsson and Granéli (1991) found that the cell division frequency of *Prorocentrum minimum, P. micans,* and *Ceratium furca* (Dinophyceae) was highest at the bottom toward the end of the dark period. The same pattern has been confirmed in situ for *Cochlodinium polykrikoides* (Dinophyceae) (Park et al. 2001).

It should be remembered that the environmental conditions (light, salinity, temperature, and nutrients) selected for our experiments were not meant to be optimal for growth, but rather to be more like the conditions encountered in the stratified part of the water column during summer in Norwegian fjords and coastal waters (Erga and Heimdal 1984; Erga 1989*a*; Erga and Skjoldal 1990). It is therefore to be expected that the present growth rates are lower than the maximum values (2.0 div. d^{-1}) found for our strain of *Tetraselmis* sp. (unpubl. data). According to our data on light, nutrient, temperature, and salinity requirements of *Tetraselmis* sp., neither light nor nutrient and temperature conditions were optimal for growth during our experiments (unpubl. data). Salinity was obviously not limiting, since our experiments were conducted within the optimal salinity range of the species (28–35‰). Our temperature range, 19–20°C (Table 1) was not far from the optimal interval (23–25°C). When the experiments were terminated, the nutrients were still not exhausted. Consistent with this, microscopy of samples from different depths of the water column at the end of experiments revealed viable cells in all cases and no bacterial growth. It can therefore be inferred that the environmental conditions during the present experiments were sufficient to support growth only to a certain level. Our surface irradiances of 66–108 μmol quanta m^{-2} s^{-1} (Table 1) coincide well with typical daily maximum levels encountered at 10–15 m depth during sunny summer days. In many cases, this is also consistent with the lower part of the fjord halocline (Erga and Heimdal 1984; Erga 1989*a*; Erga and Skjoldal 1990). Because optimal light intensity for growth of our strain of *Tetraselmis* sp. is 250–350 μmol quanta m^{-2} s^{-1}, light is probably the main growth-limiting factor during our experiments.

Migratory patterns—From the present results, it seems that, in the case of the continuous surface light experiments,

a common vertical migration pattern across the halocline can be revealed. It can be separated into three stages: (1) an upward migration from the bottom layer and subsequent accumulation in the lower part of the halocline, (2) a transit to the upper part of the halocline after a variable lag time, before (3) further ascent to the upper layer and subsequent accumulation of cells, with maximum accumulations appearing at the surface. Concerning the importance of light intensity for the direction of the phototactic response, high surface irradiances (>350–550 μmol quanta m^{-2} s^{-1}) have been put forward to explain negative phototaxis, and low irradiances (<63–100 μmol quanta m^{-2} s^{-1}) positive phototaxis, among two species of autotrophic dinoflagellates (Eggersdorfer and Häder 1991; Passow 1991). Our results confirm that surface irradiances of 17–144 μmol quanta m^{-2} s^{-1} all gave positive phototaxis for *Tetraselmis* sp. and that the threshold value for negative phototaxis therefore must be >144 μmol quanta m^{-2} s^{-1}. The positive phototaxis response for cells situated below the halocline is probably triggered by lower surface light intensities than 17 μmol m^{-2} s^{-1} (our minimum value), which was also proven to be sufficient to provide maximal swimming speeds among the "fast swimmers" of *Tetraselmis* sp.

From the experiments with continuous top illumination (Figs. 4, 5), we found two migratory population types. Characteristic for the first type was that most of the cells swam to the surface where they accumulated, whereas the second consisted of the remaining fraction of cells that did not leave the bottom at all during the experiments. These bottom-dwelling cells probably were among those situated closest to the bottom in the beginning of the experiments. Most likely, some part of this bottom population of cells had entered the replication phase of the cell cycle at an early stage of the experiments and were not able to enter the sporulation phase because of light limitation caused by accumulation of cells in the layers above. In nature, such "leftover" populations might act as "seeding stocks" of a blooming species when light conditions become favorable again.

Our findings also show that increasing halocline strengths seem to increase the transit time of *Tetraselmis* sp. cells. This is clearly seen from the time needed to achieve equal cell concentrations in the lower and upper part of the halocline. For salinity gradients of 0.7, 3.0, and 6.6‰, this was accomplished within 1 h 49 min, 8 h 29 min, and 28 h 41 min, respectively (unpubl. data). In situ studies by Tyler and Seliger (1981) of how swimming speeds of *Prorocentrum mariae-lebouriae* (Dinophyceae) were altered by rapid changes in salinity revealed that even a decrease of 1.5‰ resulted in immediate reduction of the swimming rate and that haloclines of more than ΔS = 5‰ resulted in immotility. This observation supports our conclusion that increasing halocline strength seems to exert a gradually increasing inhibition on positive phototaxis. In addition, our results clearly show that even if a strong salinity gradient acts as a physiological obstacle to positive phototaxis among phytoplankton flagellates, the cells manage to pass through after a necessary adaptation time. Most probably this can be attributed to osmotic adjustment of the cellular ion concentrations, since the cells here meet a less haline environment. Such regulations are controlled both by passive and active transport processes. Another explanation could be that the flagellar beating was retarded when the cells entered the less haline water. It is also possible that the cells are accumulating in the halocline to adjust their buoyancy before entering the lighter upper layer of the water column. Among cyanobacteria and diatoms, this is accomplished by changes in cellular carbohydrate content (Oliver 1994; Moore and Villareal 1996). It is in this context interesting to note that Watanabe et al. (1991) found that cells of *Chatonella antiqua* were able to pass through haloclines of ΔS = 2.8‰, but not stronger. Another investigation conducted with *Gonyaulax tamarensis* (Dinophyceae) under light conditions similar to ours showed that cells seemed to interrupt their upward phototaxis and accumulate at the halocline when it was stronger than ΔS = 7‰ (Rasmussen and Richardson 1989). Also, from in situ experiments in Ria de Vigo (northwest Spain), Figueroa et al. (1998) showed that some phytoplankton flagellates are able to migrate through haloclines, whereas others are not able to do so. It could in this context be interesting to draw a parallel to the literature on zooplankton. Thus, Mann et al. (1991) concluded that swimming veliger larvae of mactrid bivalves tended to concentrate in the region of the halocline and that larvae adapted to 25‰ salinity crossed haloclines of ΔS = 5‰, but not of 10 or 15‰. There therefore seem to be considerable differences between species concerning their ability to pass through strong haloclines. This might have ecological implications not only for the vertical distribution of phytoplankton and the total primary production of the water column, but also for the interaction between grazers and phytoplankton in the region of the halocline.

In the case of the fourth experiment with a 14 : 10 LD cycle, a conspicuous migratory pattern was discovered. Here the total cell concentrations of the bottom layer decreased gradually for each LD cycle, and more and more cells accumulated in the surface layer during the light period because of positive phototaxis, whereas cell concentrations increased in the halocline during the dark period because of positive geotaxis. These descending cells did not, however, move through the halocline. Apparently, once the upward-migrating cells had managed to pass the halocline, they did not return to the layer below during the dark period. This could reflect a tendency of the downward-migrating cells to avoid spending energy on the physiological adaptation processes that are necessary if they are moving across the steep gradient in salinity. Besides, in view of the environmental conditions throughout the water column, the cells already situated in the upper part of the water column would probably derive minimal advantage in swimming down below the halocline.

A main developmental pattern emerging is therefore that more and more of the vertical migrations during time were restricted to the part of the water column extending from the halocline to the surface (i.e., the upper layer). This probably has to do with sufficient surface light intensity (66 μmol m^{-2} s^{-1}) for positive phototaxis to take place over the whole upper layer. In addition, this response seems to be gradually stronger toward the surface. The decrease with time in cell concentrations below the halocline (Fig. 7) is indicative of a temporal weakening of positive geotaxis for the lower part of the water column. It also seems that cell division at the bottom during the dark period decreased with time and could not keep up with positive phototaxis exhibited by the cells

in the water column below the halocline during the light period.

Compared with the experiments conducted under continuous surface light, the light conditions during the LD experiment were more variable because they depended on the diel changes in cell distribution. The implication for the migratory pattern is that the light intensities at the bottom were high enough in the beginning of the light period to trigger positive phototaxis the last day of the experiment (Fig. 7) as well. This could mean that the minimum light intensity necessary to trigger positive phototaxis (<17 μmol m^{-2} s^{-1}) is lower than the minimum intensity needed to sustain cell division. In an investigation with *Gymnodinium breve* and *Heterocapsa illdefina* (Dinophyceae) concerning diel vertical migration patterns in a nonstratified water column, Kamykowski et al. (1998, 1999) found that the cells that aggregated at the surface during the light period exhibited weakened positive geotaxis and strengthened positive phototaxis. They explained this by cellular biochemical changes, with special emphasis on lipid and free amino acid content, which was found to be very low in cells that had migrated to the surface. These alterations took place even if nutrients were replete during the course of their experiments. In our experiments, the duration was probably not long enough to cause nutrient limitation of the upper layer, hence indicating that the vertical migration of *Tetraselmis* sp. in our experiment was more dependent on light than on nutrients.

As opposed to our results, Rasmussen and Richardson (1989) found that the diel vertical migration of *Gonyaulax tamarensis* in tank experiments was characterized by an accumulation both at the surface and halocline during light, whereas the cells were more homogeneously distributed beneath the halocline during dark. It should be noted, however, that the duration of their experiments was only 24 h and that in our experiment, the cells of *Tetraselmis* sp. were more evenly distributed below the halocline during the first night (Fig. 7). Another noteworthy aspect of the migratory pattern of *Tetraselmis* sp. is that the downward migration started about 2 h before the end of the light period, indicating an internal control of the downward swimming response. A similar pattern has been found for many dinoflagellates species in artificial water columns (Eppley et al. 1968; Cullen and Horrigan 1981; Olsson and Granéli 1991). The upward swimming of *Tetraselmis* sp., on the other hand, started after the onset of the light period, a phenomenon that we at the moment cannot explain. Another vertical migration pattern being recognized is a slower descent of cells from the surface than the ascent of cells from the halocline (Fig. 7). This could be attributed to positive phototaxis being a stronger driving force than positive geotaxis for *Tetraselmis* sp.

Our high-resolution profiles of the vertical distribution of *Tetraselmis* sp. cells have provided insight both on how migrating cells act in relation to the halocline and how they pass through it. Obviously, the migrating cells are able to perceive small changes in salinity. This results in very sharp accumulation peaks of migrating cells in the halocline area. Increasing strength of the halocline leads to increasing passage times. Therefore, an important ecological aspect of our results is that if the vertical migrations conducted by many microalgal flagellates in natural water columns are to include passage through strong haloclines, their vertical migration rate will be strongly reduced. It is to be expected, however, that for many species, the cells will manage to pass through after a sufficient adaptation time, which in extreme cases can extend to more than 12 h. The effect of LD shifts is that if cells are being introduced below the halocline, they will accumulate with time in the upper layer above the halocline, where they migrate toward the surface during the light period and down to the halocline during the dark period. All together, our results therefore indicate that in strongly stratified waters, flagellates like *Tetraselmis* sp. could have problems by swimming down below the halocline during the night to satisfy their nutrient demand. To find out more about the migratory pattern of phytoplankton flagellates under different environmental conditions, we recommend that future investigations should be undertaken on a high-resolution scale, both temporally and spatially. Information from such studies is crucial for a better understanding of the basic processes driving the dynamics of planktonic populations of coastal and fjord ecosystems. Because inadequate data sets are a major limitation for the development of most ecosystem models, our results might contribute to an improved sensitivity of such models.

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