

# Nutrient fluxes and growth of *Cladophora sericea* in a shallow Danish bay

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**ABSTRACT:** *Cladophora* spp. form stable floating algal mats in the archipelago of southern Fyn, Denmark (2 m water) in the spring and summer months. There was a significant diel variation in the concentration of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{O}_2$  and in pH and temperature in the mats. These changes were observed in either a closed chamber positioned in the sediment or by *in situ* manifold sampling. Changes, particularly in  $\text{NH}_4^+$ , were used to estimate net mat nitrogen uptake rates. Much recycling of nitrogen occurred in the mat and there was evidence of  $\text{NH}_4^+$  concentration peaks, even during the day. Phosphate had a similar pattern. The highest  $\text{NH}_4^+$  uptake rates were in the bottom of the mat, probably due to nutrient supply from the sediment. A large release of  $\text{NH}_4^+$  at the onset of dark, followed by low uptake rates in the dark, was evidence for the release of loosely bound, rather than intracellular  $\text{NH}_4^+$ . Diel and monthly uptake rates ( $\Delta\text{NH}_4^+ \text{ h}^{-1}$ ) showed that growth may have been light-limited in the spring and N-limited in the summer. High algal C:N ratios in the summer were consistent with this hypothesis. A budget for June showed the importance of recycling of N within the mat ( $2.57 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) compared with  $\text{NH}_4^+$  input from the sediment ( $0.83 \text{ mmol m}^{-2} \text{ d}^{-1}$ ), lateral water transport ( $0.31 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) and the deposition from the atmosphere ( $0.40 \text{ mmol m}^{-2} \text{ d}^{-1}$ ). *C. sericea* out-competes phytoplankton, resulting in clear water. Growth of *C. sericea* resulted in  $\text{O}_2$  deficit under the mat due to respiration of the mat and sediment. Sinking and export of the mat at the end of July could cause local problems.

## INTRODUCTION

In recent years there has been an increased production of filamentous algae in coastal waters, e.g. in Bermuda (Bach & Josselyn 1978), Australia (Gordon et al. 1981, Lavery et al. 1991) and Scotland (Hull 1987). Blooms of filamentous algae are associated with nutrient availability, although other factors, such as light and temperature, have an effect (Norin & Wærn 1973, Bach & Josselyn 1978, Gordon et al. 1981, Lowthion et al. 1985, Tewari & Joshi 1988, Cambridge et al. 1990a, b).

There have been changes in the vegetation in Danish coastal waters (0 to 10 m) in the last decades (Fyns Amt 1990, H. Mathiesen & L. Mathiesen pers. comm.), with the appearance of filamentous algal mats and a substantial decrease in the abundance of eelgrass *Zostera marina*. A marked increase in algal mats has been observed during the last decade in the archipelago of southern Fyn, Denmark. In the early spring, large masses of filamentous algae cover the sediment.

Algal growth and trapped gases create floating algal mats covering large areas of the shallow coastal waters in May–June. In addition to the adverse aesthetic effects on marine environments, the algal mats cause economic losses related to fishing.

Despite the availability of nutrients in the spring, the water apart from the mat was not turbid. This observation led us to the hypothesis that the filamentous algae assimilate most of the available N and P. The purpose of the present study was to determine *in situ* profiles, diel and seasonal variations in nutrient fluxes, and growth of the mat. The methods are simple and suitable for monitoring the environmental effects of algal mats, e.g. by biologists employed by government environmental agencies. Because of the simplicity of the methods, the resulting nitrogen budget for the system is based on net changes in the various nitrogen compartments. Two new devices were developed: a macrophyte incubation chamber located on the sediment and an *in situ* water sampler.

## MATERIALS AND METHODS

The archipelago of southern Fyn, Denmark is a 415 km<sup>2</sup> shallow water area (Fig. 1). In one-third of the area, the water depth is < 2 m. The Lunkebugten Bay (54° 59' N, 10° 39' E) was chosen as a representative shallow water area for the *in situ* measurements. The abundance of the different macroalgal species was determined by harvesting five 0.25 m<sup>2</sup> areas in randomly selected localities. The filamentous green alga *Cladophora sericea* was the most abundant species in May–June in shallow waters (0 to 4 m), whereas *Ectocarpus siliculosus* dominated the deeper waters (4 to 6 m). *Pilayella* spp. were dominant in early spring; in late summer *Chaetomorpha linum* replaced *Cladophora* spp. (Rasmussen et al. 1993). The term 'mat' is used to refer to *Cladophora sericea* algal mats in the present study. All samples were water samples. When presenting data for the mat, the values were from the seawater of the mat-seawater complex.

**Sampling methods.** The aim was to sample from vertical columns with as little disturbance of the profile as possible.

**Incubation chamber:** An incubation chamber was constructed for measuring nutrient fluxes in a vertical

column containing a mat (Fig. 2). The chamber was a cylinder made of transparent Plexiglass with a height of 40 cm and an interior diameter of 19.1 cm. The chamber had a vertical column of silicone-filled holes at 1 or 2 cm intervals. The top of the chamber was covered with a thin layer of plastic which transferred external water movements to the water in the chamber. At the top of the chamber a Plexiglass collar was used to fasten the plastic cover. The chamber was gently pressed into the sediment to a depth of 8 cm and fixed with 3 pegs. The open bottom allowed interactions between the water and the sediment. In the middle of the chamber, a permanent fine net was fixed. The chamber was placed in a locality with a water depth of 0.8 to 1.2 m. A mat was put on the net at the same level and in the same concentration as that of the surrounding water. A coarse net was then fixed 6 cm above the fine net to retain the algae. Water samples were collected by a SCUBA diver using a syringe with a 50 × 3 mm cannula with a side hole principal, inserted through the silicone holes. Along the cannula, 15 holes were drilled to prevent algal plugging. To describe the vertical profiles, 12 samples at different heights in the chamber were collected. A control chamber was incubated without a

mat. In addition, chambers made of opaque green PVC and covered with black plastic were used for dark incubation measurements. The first samples were taken after 1 h of incubation.

**Water sampling manifold:** The water sampling manifold was a 1.5 m long wooden rod with a sharp end for locating in the sediment (Fig. 3). Cannulae were fixed to the rod at suitable heights. At the top of the rod, 6 rubber tubes were attached to a horizontal board. The other end of the rubber tubes were connected to the perforated 50 × 3 mm cannula. The sampler was placed in a mat and fixed in the sediment at a water depth of 0.8 to 1.2 m. The tubes and cannulae were fixed to the sampler at levels below, inside, and above the mat. Using a 10 ml syringe at the horizontal board, the tubes were filled with seawater and closed with clamps. The dead space of the tubes was 6 to 7 ml. The first 8 to 9 ml representing the dead space were discarded. A control water sampler was placed in a water column without a mat.

**SCUBA-collected samples:** Water samples were collected directly by a SCUBA diver using a syringe. Samples from mats of high and low density were taken for comparison.

**Sampling frequency.** To determine the changes in the natural nutrient concentra-



Fig. 1. Study site showing the archipelago of southern Fyn, Denmark

tions, samples were collected every 2 to 4 h generally from early morning until late evening. For diel experiments, analyses were completed within 30 h. Sample series were collected 1 to 2 times every month from April until August.

**Sample analyses.** All the water samples were collected in a 10 ml syringe, filtered by pressure (GF/C Whatman filter in a Swinnex holder) and analyzed immediately for oxygen and temperature on an oxygen meter (YSI model 57) and pH (Radiometer PHM 80). The oxygen content was not altered by this pressure filtration and brief exposure to air. The water samples were then stored in polyethylene vials and frozen immediately for further analysis. Samples from the controls were also analyzed. Macroalgal dry weights were determined after drying at 105°C for 12 h. The C:N:P (molar) ratio of the algae was determined. C and N were determined on a Carlo-Erba NA-1500 analyzer and particular phosphorus was determined by using the methods of Strickland & Parsons (1968). Water samples were analyzed for  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$  and  $\text{NO}_3^-$  on an autoanalyzer (Technicon, Autoanalyzer Industrial method Traacs 800). The photon flux at every sampling time was measured on a photon irradiance meter (LICOR LI 185A).

**Rate calculations.** The fluxes of  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , and  $\text{NO}_3^-$  were calculated from differences in nutrient concentration in the water samples, with time. The fluxes from each level of the water column were determined. Algal fluxes were corrected for changes in the controls. Average fluxes were calculated and expressed as  $\mu\text{mol l}^{-1} \text{h}^{-1}$ . All the uptake, mineralization and growth rates were net values. The growth rate of *Cladophora sericea* was determined monthly, by calculating carbon fixation rates based on changes in average oxygen concentrations from the samples ( $\text{PQ} = 1.2$ ). The dark respiration, determined from changes in oxygen content in dark chambers, was added to the oxygen production in the chamber.

## RESULTS

### Profiles of nutrients, day and night

Diel changes of  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{O}_2$ , pH and temperature were measured monthly in water columns containing *Cladophora sericea*. An example of day and night profiles typical for 10 samplings is shown in Fig. 4. There was a peak of the  $\text{NH}_4^+$  in the middle of the mat, during both day and night, indicating a local net mineralization (Fig. 4A). The gradient in the  $\text{NH}_4^+$  (Fig. 4A) and  $\text{PO}_4^{3-}$  (Fig. 4C) concentration, from the sediment to the mat at daytime, indicated a consumption of released sediment nutrients. The same pattern

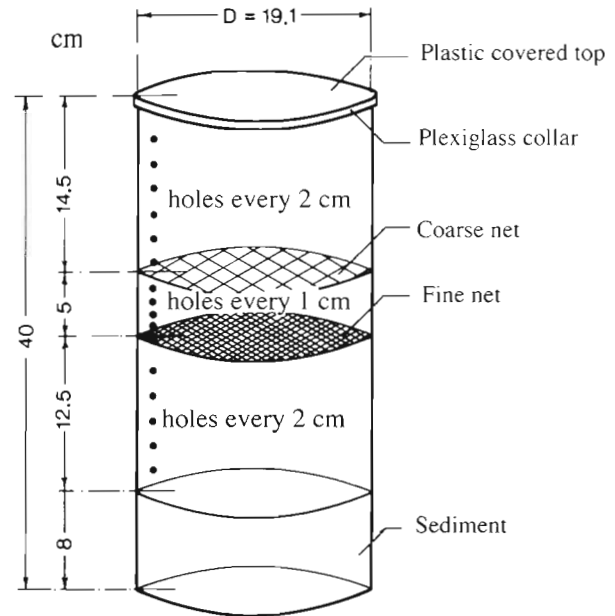


Fig. 2. Incubation chamber. A mat was placed between the 2 nets in a semi-closed system (see text for details)

was not observed for  $\text{NO}_3^-$  (Fig. 4B). There were peaks of  $\text{NO}_3^-$  within the mat both day and night, similar to those of  $\text{NH}_4^+$  but on a smaller scale. The  $\text{PO}_4^{3-}$  concentrations were low in the mat in the daytime, but had a local peak as in the  $\text{NH}_4^+$  and  $\text{NO}_3^-$  profiles (Fig. 4C). The daytime  $\text{O}_2$  (Fig. 4D) and pH (Fig. 4E) profiles

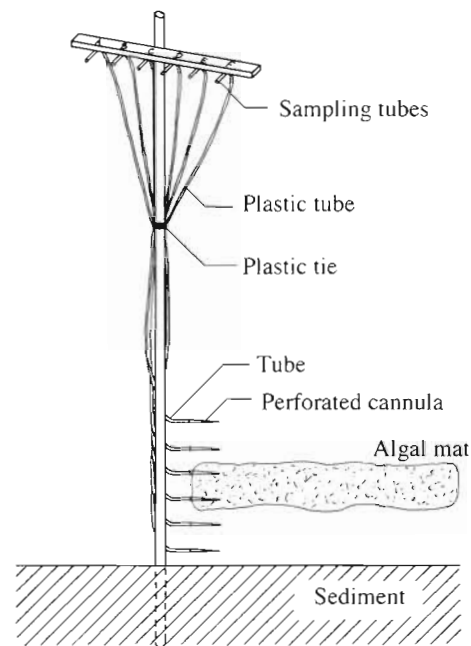


Fig. 3. Water sampling manifold. The rod was placed in a mat *in situ* (see text for details)

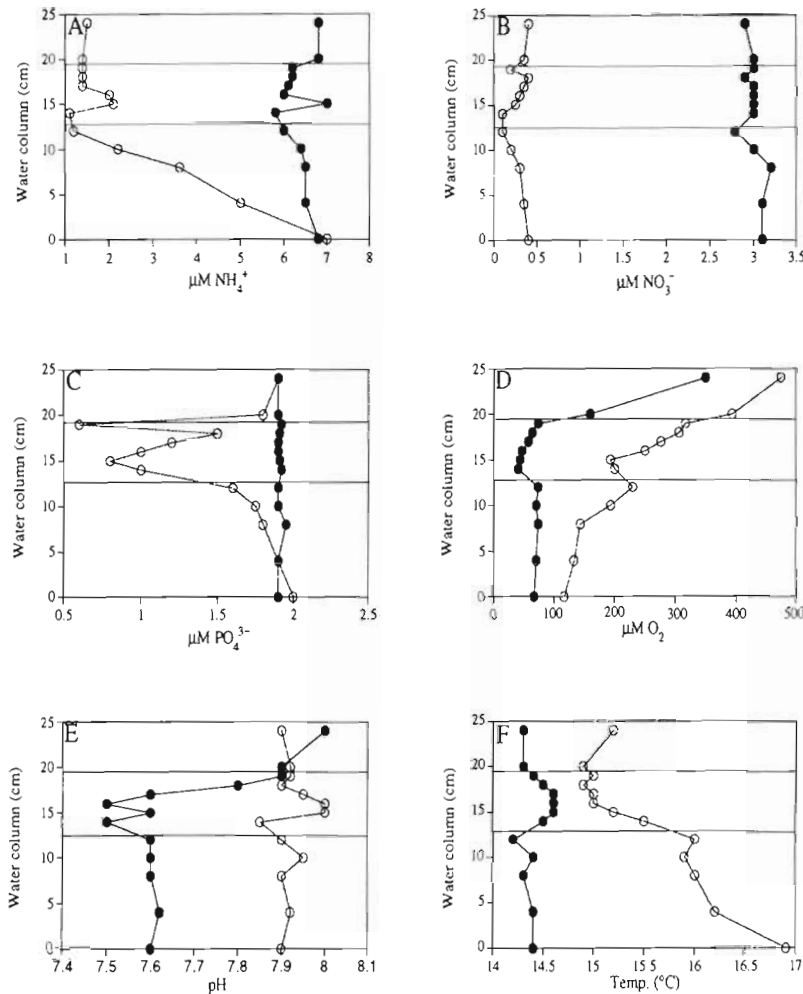


Fig. 4. Day and night profiles of nutrient concentrations, oxygen, pH and temperature in an incubation chamber. The lines 13 and 20 cm above the sediment represent the 2 nets containing a mat. 0 cm represents the sediment. Data are from 7–8 June 1989, from 13:00 h (○), and 01:00 h (●)

reflected the local  $\text{NH}_4^+$  increase in the mat. At night, there was a higher temperature in the inner mat (Fig. 4F).

#### Profiles of $\text{NH}_4^+$ changes within the mat during day and night

The  $\text{NH}_4^+$  changes within a mat were measured monthly. In Fig. 5, typical monthly data are shown (June 1989). The  $\text{NH}_4^+$  depletion was always greatest in the lower part of the mat at noon, as exemplified in Fig. 5Aa. At night there was a net  $\text{NH}_4^+$  increase in the mat (Fig. 5Ba). There was always a marked difference in the profiles of high and low density mats as shown in Fig. 6. There were greater differences in oxygen and

pH above, within and below the high density mat (Fig. 6Aa, c) compared to the low density mat (Fig. 6Ba, c). Beneath the high density mat, oxygen concentrations were  $< 31 \mu\text{M}$  (in June), levels critical for fish and benthos (Fig. 6Aa). The highest concentrations of oxygen were always observed above the mat, up to  $525 \mu\text{M}$  (in May). The high density mat had a higher night temperature (Fig. 6Ab).

#### Integrated diel changes in $\text{NH}_4^+$ , $\text{NO}_3^-$ and $\text{PO}_4^{3-}$ concentrations in water

Representative integrated diel changes in  $\text{NH}_4^+$  and  $\text{NO}_3^-$  concentrations are shown in Fig. 7A, B (note the different scales). Both rates varied with photon flux. Between 14:00 and 16:00 h on the first day and between 12:00 and 14:00 h on the following day, the photon fluxes were  $950 \mu\text{E m}^{-2} \text{s}^{-1}$  and  $290 \mu\text{E m}^{-2} \text{s}^{-1}$  respectively. At night there was a small decrease of  $\text{NH}_4^+$  (Fig. 7A). Phosphate fluxes were infrequently determined, because the phosphate concentrations were too low to be measured accurately. In June, an average uptake rate of  $0.10 \mu\text{mol l}^{-1} \text{h}^{-1}$  ( $1.33 \text{ mmol m}^{-2} \text{d}^{-1}$ ) was found in the incubation chambers.

In both low light and dark chambers, the rate of  $\text{NH}_4^+$  appearance was initially high followed by a decrease.

This pattern was consistent for 10 out of 10 sample series. In Fig. 7A, the highest appearance of  $\text{NH}_4^+$  ( $2.48 \mu\text{mol l}^{-1} \text{h}^{-1}$ ) was between 19:00 and 20:00 h when the photon flux decreased from  $178$  to  $113 \mu\text{E m}^{-2} \text{s}^{-1}$ . As darkness increased, however, there was a negative rather than a positive  $\Delta\text{NH}_4^+$ . A small increase of  $\text{NO}_3^-$  between 16:00 and 04:00 h on the following day (Fig. 7B) was found. At night, the average  $\text{NO}_3^-$  increase in June was  $0.15 \mu\text{mol l}^{-1} \text{h}^{-1}$  by water sampler, and  $0.20 \mu\text{mol l}^{-1} \text{h}^{-1}$  in the incubation chamber.

The average daily  $\text{NH}_4^+$  efflux from the sediment was  $0.83 \text{ mmol m}^{-2} \text{d}^{-1}$  in June. This was determined in dark chambers without mats.

In a dark incubation (Fig. 8) as opposed to the onset of night, the  $\Delta\text{NH}_4^+$  was  $2.73 \mu\text{mol l}^{-1} \text{h}^{-1}$ , followed by rates of around zero. Higher initial  $\Delta\text{NH}_4^+$  rates of  $4.10 \pm 0.72 \mu\text{mol l}^{-1} \text{h}^{-1}$ , followed by almost zero rates,

were also found in May 1989 in light and dark incubations respectively.

#### Integrated monthly changes of $\Delta\text{NH}_4^+$ , $\Delta\text{NO}_3^-$ and $\Delta\text{PO}_4^{3-}$ concentrations in water

Average diel changes of  $\text{NH}_4^+$  concentration through the spring and summer were measured in an incubation chamber (Fig. 9A) and by water sampling (Fig. 9B). The negative (uptake)  $\Delta\text{NH}_4^+$  increased from April until June. In July the uptake declined rapidly. Before April, no *Cladophora sericea* was found. The average *in situ* daytime uptake rate was  $0.06 \mu\text{mol l}^{-1} \text{h}^{-1}$  for  $\text{PO}_4^{3-}$ ,  $0.12 \pm 0.05 \mu\text{mol l}^{-1} \text{h}^{-1}$  for  $\text{NO}_3^-$  and  $0.29 \pm 0.09 \mu\text{mol l}^{-1} \text{h}^{-1}$  for  $\text{NH}_4^+$  in June, using the water sampler. There was a complete disappearance of filamentous algae at the end of July or the beginning of August. Within a few days, no mats were found. Average values of  $\text{NH}_4^+$  uptake in June were  $0.09 \mu\text{mol l}^{-1} \text{h}^{-1}$  in dark chambers,  $0.07 \mu\text{mol l}^{-1} \text{h}^{-1}$  in night measurements of light chambers, and  $0.14 \mu\text{mol l}^{-1} \text{h}^{-1}$  in water sampler measurements.

#### Growth

The carbon fixation rate rose through spring and summer and declined to zero in August. Representative data from every month are shown in Fig. 10. The changes in biomass were coincident. At the end of July/beginning of August, no mats were found. The average C:N:P concentration ratio in the algae, from April to June, was 304:18:1.

#### DISCUSSION

The main purpose of the investigation was to determine the mat growth, to make diurnal, monthly, seasonal budgets and to examine 2 new methods for *in situ* sampling. The study was based on measuring changes in *in situ* nutrient concentrations with no enrichment, whereas most determinations of filamentous algal growth are from laboratory studies, or from *in situ* nutrient enrichment studies using glass bottles (Wallentinus 1984), or plastic bags (Lavery & McComb 1991). The problems associated with measurement and interpretation of *in situ* nutrient uptake rates have been discussed by McCarthy (1981). Growth was estimated from changes in the concentration of nitrogen ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) with time. These changes were observed in chambers attached to the sediment or in samples of the vertical profiles in the water column (controls subtracted). Both methods, based on net changes

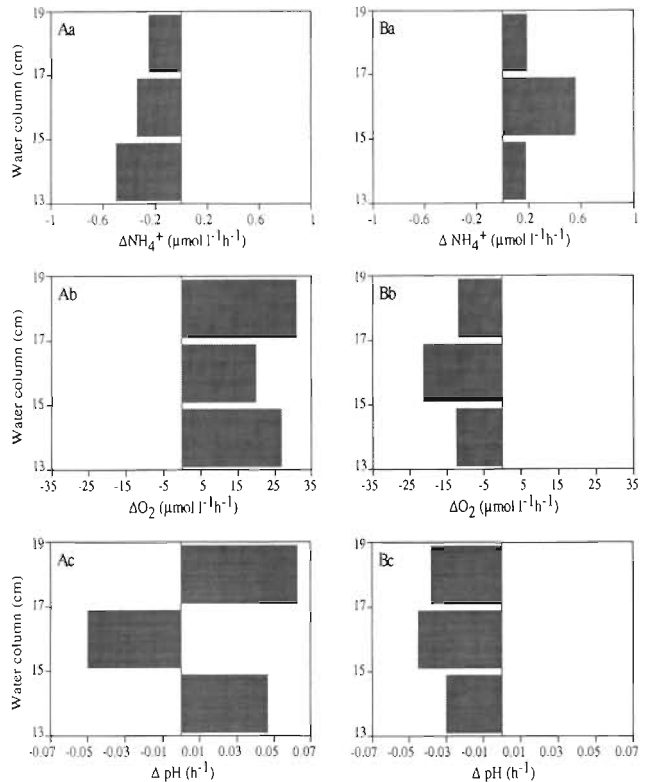


Fig. 5. Day and night changes in  $\text{NH}_4^+$ ,  $\text{O}_2$  and pH in a chamber incubation. The mat was placed between 13 and 19 cm above the sediment. Data are from 7 June 1989, (A) between 10:00 and 13:00 h and (B) between 22:00 and 01:00 h

in concentrations, gave estimates of net growth. Any concentration change could be due to a change in either production rate of the nutrient (increased nutrient concentration with time), or in uptake rate by the mat (decreased nutrient concentration with time). In general, it can be assumed that the rate of  $\text{NH}_4^+$  production did not alter in response to light or dark. Predation was not considered, as the aim was to give *in situ* nutrient fluxes for algal mat systems.

There were marked diurnal changes in the concentration of  $\text{NH}_4^+$  in the profile through a mat in the incubation chamber (Fig. 4). It was clear that the sediment was a source of  $\text{NH}_4^+$ , but a higher concentration of  $\text{NH}_4^+$  in the middle of the mat was seen in both dark and light. This indicated a higher rate of mineralization in the middle of the mat. The  $\text{NO}_3^-$  profile showed a similar trend, but less pronounced. There was no evidence that the sediment was a source of  $\text{NO}_3^-$ . The same pattern was seen for  $\text{PO}_4^{3-}$ , but with a peak in the light only. The sediment was a source of  $\text{PO}_4^{3-}$ . The decrease in oxygen concentration in the mat, again suggested high mineralization activity. The pH profiles were consistent with photosynthesis during the day (high pH) and mineralization at night (low pH). The

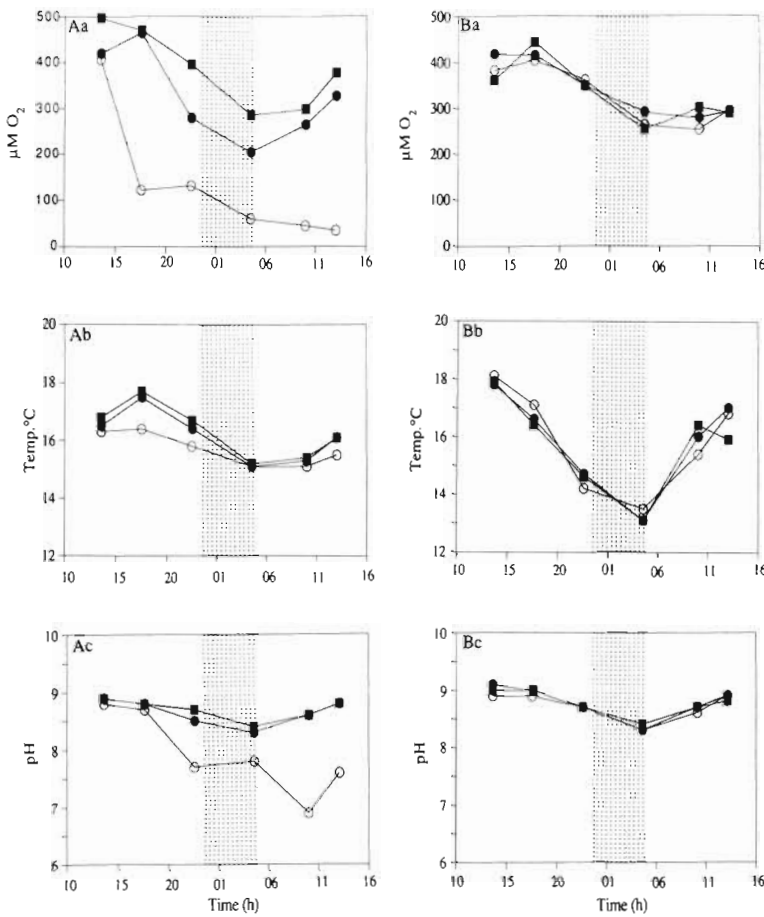


Fig. 6. Diel changes in O<sub>2</sub>, temperature and pH samples taken by SCUBA diver on 7–8 June 1989. Samples are (A) from a high density mat and (B) from a low density mat, and taken from the middle (●), above (■) and below (○) the mat. Stippled area represents darkness

temperature profiles showed that the daytime temperature was maintained in the middle of the mat at night, but not in the remainder of the water column. This suggested that the structure of the mat restricted exchange of water nutrients from above and below. It was seen from the profiles (Fig. 4), that the mat exerted some influence on the water column below the mat, for example O<sub>2</sub> decreased at night. In the water column without mat a minor O<sub>2</sub> decrease was seen due to sediment uptake (data not shown).

Rates of change in NH<sub>4</sub><sup>+</sup>, O<sub>2</sub> and pH within the mat, measured over a 3 h period, are shown in Fig. 5. There was a large negative  $\Delta$ NH<sub>4</sub><sup>+</sup> in the lower part of the mat during the day, indicating a higher net algal growth at the bottom of the mat, compared to the top. Presumably this can be attributed to a greater availability of NH<sub>4</sub><sup>+</sup> from the sediment. Reduced photon flux was not a limiting factor, as the water depth did not exceed 1.2 m. This is in accordance with Bach &

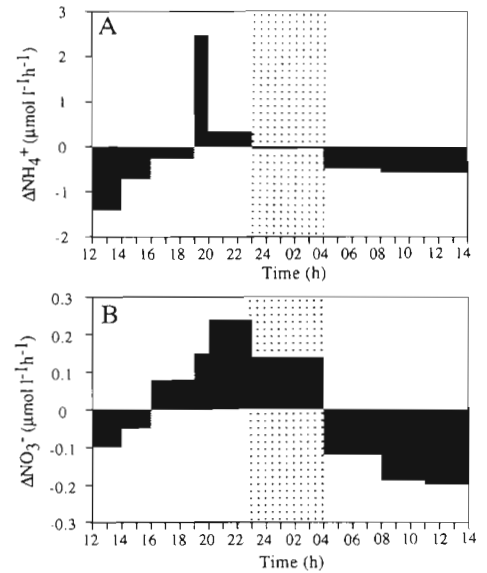


Fig. 7. Diel changes in (A) NH<sub>4</sub><sup>+</sup> and (B) NO<sub>3</sub><sup>-</sup> concentrations in a mat. Samples were taken with the manifold on 11–12 June 1990. Stippled area represents darkness

Josselyn (1978), where reduction in growth of *Cladophora prolifera* was first observed at 3 to 4 m water depth. It was clear that NH<sub>4</sub><sup>+</sup> production occurred in the mat (difference between Fig. 5Aa and 5Ba). The lower part of the mat received some NH<sub>4</sub><sup>+</sup> from the sediment source, but the upper part of the mat was probably dependent on NH<sub>4</sub><sup>+</sup> recycling. The rates of change in the O<sub>2</sub> and pH are consistent with this interpretation. The

results seen in Figs. 4 & 5 were obtained in the incubation chamber for both ease of sampling, and to get finer profiles. A similar diurnal experiment was performed *in situ*, with 2 naturally occurring mats of differing density (Fig. 6). The oxygen concentration

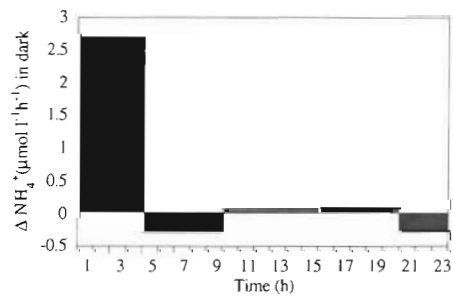


Fig. 8. Changes in dark chamber NH<sub>4</sub><sup>+</sup> concentration in a mat, 7–8 June 1989

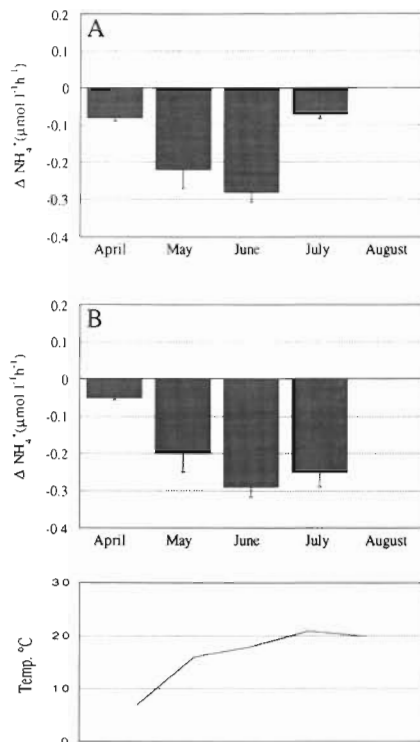


Fig. 9. Monthly changes in the average diel  $\Delta\text{NH}_4^+$  concentration in a mat comparing the 2 sampling methods: (A) incubation chamber, 1989; and (B) water sampler, 1990. Average water temperature is shown. Error bar = 1 SD, n = 5

associated with the high density mat (Fig. 6Aa) had the same distributions as seen in Fig. 4D. There was a decrease in concentration in the dark, and the above-mat concentration was highest and fell least. The below-mat concentration was lowest, while the within-mat concentration was intermediate, but had the largest changes. These  $\text{O}_2$  changes were not so obvious in the thinner mat (Fig. 6Ba), there being little difference between the mat layers, but there was a fall at night and an increase during the day. The diurnal changes in pH, temperature and  $\text{O}_2$  indicated that the structure of both mat types tended to isolate the mat from its surroundings. Thus, changes within the mat reflected mat events, rather than general changes in the environment.

The *in situ* changes in nutrient concentrations within the mat (e.g. Fig. 6) were integrated to give a whole mat and diel rate of change (Fig. 7). Integrated  $\text{NH}_4^+$  concentration changes indicated uptake in light, declining from noon to 19:00 h,

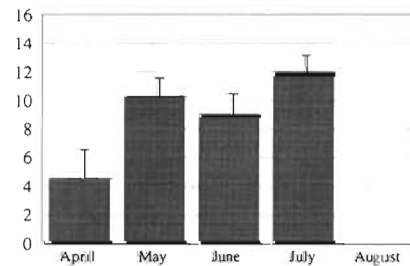


Fig. 10. Monthly C-fixation rates in a mat based on  $\Delta\text{O}_2$ . Error bar = 1 SD, n = 5

after which time  $\Delta\text{NH}_4^+$  was positive until 23:00 h. The most unusual event was the very high rate of  $\text{NH}_4^+$  appearance between 19:00 and 20:00 h (Fig. 7A). This was not observed in Fig. 5 (chamber experiment), because those data did not cover that time period. This apparent  $\text{NH}_4^+$  production always occurred and was probably due to the release of loosely bound  $\text{NH}_4^+$  from the mat at low photon fluxes, rather than to an increase in detrital mineralization (Thybo-Christesen & Blackburn 1993). This  $\text{NH}_4^+$  disappeared, presumably by algal uptake even at low photon fluxes. In the dark,  $\text{NH}_4^+$  uptake continued, resulting in a negative  $\Delta\text{NH}_4^+$ . The same trend was observed using  $^{15}\text{NH}_4^+$  (Thybo-Christesen & Blackburn 1993). Other *Cladophora* spp. are also able to take up  $\text{NH}_4^+$  in the dark (Bach & Josselyn 1978, Gordon et al. 1981).

$\Delta\text{NO}_3^-$  indicated uptake between 04:00 and 16:00 h with production at other times, in low light or dark (Fig. 7B). It is not known if  $\text{NO}_3^-$  production was constant during the diel cycle, but quantitatively it is of much less importance than  $\text{NH}_4^+$ , as seen from the difference in scales (Fig. 7A, B). The lack of  $\text{NO}_3^-$  uptake in the dark is consistent with the energy required for  $\text{NO}_3^-$  reduction (Fujita et al. 1989, Flynn 1991).

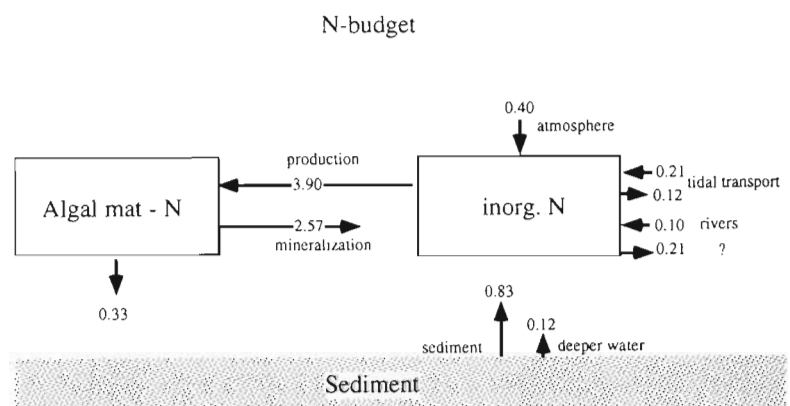


Fig. 11. Nitrogen budget for the shallow water in the archipelago of southern Fyn in June (see text for details). Values in  $\text{mmol m}^{-2} \text{d}^{-1}$

The high positive  $\Delta\text{NH}_4^+$  observed in Fig. 7A was investigated in a chamber experiment in which a mat was incubated in the dark (Fig. 8). There was an immediate 'release' of  $\text{NH}_4^+$ , very similar to the release between 19:00 and 20:00 h (Fig. 7A). Following this release there was evidence for uptake of  $\text{NH}_4^+$ , resulting in a negative  $\Delta\text{NH}_4^+$ , similar to the diel 23:00 to 04:00 h uptake.

The integrated monthly  $\Delta\text{NH}_4^+$  rates, measured in the incubation chamber (Fig. 9A) and by *in situ* sampling (Fig. 9B), were essentially the same, with small standard deviations. This verifies that the water sampling manifold was suitable for measurements of *in situ* changes in nutrient concentrations, and thus to estimate growth rate. The difference in the values of  $\Delta\text{NH}_4^+$  for July in Fig. 9A, B was because of a later onset of algae decay in 1990 than in 1989. An independent calculation of growth rate was made based on  $\Delta\text{O}_2$  (Fig. 10). A calculation based on changes in pH values gave similar results (data not shown).

Cambridge et al. (1990b) have indicated a correlation between growth of *Cladophora sericea* and an increase in water temperature. A similar relationship is seen in Fig. 9, but this should be interpreted with caution; because of the correlation between light, temperature and stratification of the water, it is unwise to attempt to make a close connection between mat production and temperature. All evidence from the present investigation points to light limitation in the spring, and nutrient limitation during the summer.

There is considerable uncertainty regarding N and  $\text{PO}_4^{3-}$  uptake rates by different, or the same, species of filamentous algae, because of differences in intracellular nutrient pools, growth history and environmental factors (Harlin & Craigie 1978, Topinka 1978, Lapointe & Tenore 1981, Wallentinus 1984). Comparison of growth rates with literature values can, therefore, only be tentative. The *in situ*  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and  $\text{PO}_4^{3-}$  net uptake rates in June were factors of 400, 1000 and 30 respectively below the  $V_{\text{max}}$  maximum rates (*Cladophora albidula*; Gordon et al. 1981). A prehistory of  $\text{PO}_4^{3-}$  starvation resulted in a  $\text{PO}_4^{3-}$   $V_{\text{max}}$  300 times higher than in our study (*Chaetomorpha linum*; Lavery & McComb 1991). The  $\text{NH}_4^+$  uptake rate, which was calculated by applying Michaelis-Menten kinetics,  $K_m$  (half saturation constant) and  $V_{\text{max}}$  constants for *Cladophora glomerata* (Wallentinus 1984), at an *in situ*  $\text{NH}_4^+$  concentration of  $1.4 \mu\text{mol l}^{-1}$  (Fig. 4A) was 60 times the actual rate. A connection between nitrogen and  $\text{PO}_4^{3-}$  uptake has been shown for *Cladophora prolifera*, where  $\text{PO}_4^{3-}$  deficiency inhibited growth in spite of N enrichment (Lapointe & O'Connell 1989). A similar explanation could account for the low uptake rates in the present study.

It is probable that *Cladophora sericea* in Lunkebugten suffered from nitrogen deficiency, as the C:N

ratio for all months was 17 compared to published values of 7 (Atkinson & Smith 1983). This is consistent with the low  $\text{NH}_4^+$  concentrations in the water, particularly in the summer. The June uptake C:N ratio of 33 was even higher, the resulting C:N in the cells was  $37 \pm 4.4$  in June, based on 60 measurements (Thybo-Christesen & Blackburn 1993).

A nitrogen budget in June for the shallow waters (0 to 2 m) in the archipelago of southern Fyn was made on the basis of reports of the contribution from the atmosphere, rivers, purifying plants, tidal transport, and deeper waters (J. Sehested Hansen & C. Jørgensen pers. comm.), and from biomass assays, and ship and SCUBA divers' collections (Rasmussen et al. 1993). The present study contributed with the net uptake rate and sediment efflux. The mineralization rate was from the same day and year (Rasmussen et al. 1993). The N-budget (Fig. 11) showed an accumulated input of  $4.23 \text{ mmol N m}^{-2} \text{ d}^{-1}$ , or  $139 \text{ mmol C m}^{-2} \text{ d}^{-1}$ . By comparison, the C-production rate in June for *Cladophora* spp. in the Northern Baltic Sea is  $103.5 \text{ mmol C m}^{-2} \text{ d}^{-1}$  (Jansson 1977).

The consumption by the filamentous algae accounted for up to 95% of the available N and 85% of the available P (data not shown). It was concluded that the clear water, found under the mat, was a result of nutrient uptake by the filamentous algae. The mat was an almost closed system, with 63% of its N requirement being supplied by internal recycling and the remainder coming from the sediment, lateral advection and atmospheric precipitation (Fig. 11). The mat system had a relatively high biomass in June ( $87.05 \text{ g dry wt m}^{-2}$ ) with an active breakdown ( $2.57 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ) and resynthesis ( $3.90 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ). During the growing season, there must have been some new mat production and export from the mat, but this caused no obvious environmental problems. At the end of the growing season, however, the mat either sank locally or was exported to the shore, or to deeper waters, where degradation could lead to problems associated with decaying organic matters.

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