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Short communication

The impact of salinity fluctuations on net oxygen production and inorganic nitrogen uptake by *Ulva lactuca* (Chlorophyceae)

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Abstract

In this study, we investigate the impact of rapid fluctuations in salinity on short-term net oxygen production and ammonium (NH_4^+) and nitrate (NO_3^-) uptake by *Ulva lactuca* collected within the Mobile Bay estuary (AL). The salinity regime at the study site was highly variable, remaining mostly between 20 and 30 psu with changes over 3 psu occurring rapidly and frequently. Periodic water sampling revealed a significant inverse relationship between NO_3^- concentration and salinity, but not between NH_4^+ concentration and salinity. Experimental changes in salinity modelled on those observed at the study site resulted in a decline in net oxygen production, while NH_4^+ and NO_3^- uptake rates remained similar. These results suggest that *U. lactuca* maintains the ability to take up NH_4^+ and NO_3^- under conditions of rapidly changing salinity within the salinity range tested and over the short-term scale examined in this study.

Keywords: *Ulva*; Nitrate; Ammonium; Uptake; Salinity; Estuary; Net oxygen production

1. Introduction

The inorganic nutrients that support macroalgal production in estuaries are frequently derived from freshwater inputs (Sawyer, 1965; Valiela et al., 1997). Particularly in oligotrophic estuaries, the delivery of inorganic nutrients from rivers may release macroalgae from nutrient limiting conditions (Lavery and McComb, 1991; Pedersen and Borum, 1996).

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Regardless of nutrient availability, macroalgae in estuaries will often have nutrients delivered in pulses of less saline water primarily in the form of watershed runoff (Lapointe and Clark, 1992). This type of delivery will be more intense in areas where anthropogenic land use has entailed hydrologic change, such as the filling of extensive areas with impervious surfaces, and where rainfall can be quickly channelled into the receiving estuary (Livingston and Duncan, 1979; Millham and Howes, 1994). In addition, physical forcing by winds and tides in shallow estuaries can lead to the rapid replacement of more saline, nutrient-poor marine water with less saline, nutrient-rich estuarine water (Wiseman et al., 1988; Stumpf et al., 1993). The relatively higher nutrient concentrations associated with inputs from these types of events will only be translated into macroalgal production if macroalgae are capable of removing nutrients from the water column in a rapidly changing salinity regime.

The genus *Ulva* is ubiquitous worldwide and often an abundant species in estuaries (Pedersen, 1995; Rivers and Peckol, 1995). Species of the genus *Ulva* are opportunistic macroalgae capable of rapid colonization and growth when conditions are favourable (Littler, 1980). While they exhibit relatively rapid nutrient uptake (Rosenberg and Ramus, 1984; Rivers and Peckol, 1995) and subsequent growth in relation to other macroalgal species, *Ulva* have a limited capacity to store inorganic nutrients (Fujita, 1985). Despite this limitation, the genus *Ulva* comprises highly productive species that are often responsible for a large percentage of total estuarine primary production (Sfriso et al., 1987; Sfriso et al., 1992).

While several investigators have examined inorganic nutrient uptake by *Ulva* spp. (e.g. Rosenberg and Ramus, 1984; Pedersen, 1994; Campbell, 1999) and others have studied how changing salinity affects their growth and photosynthetic capacity (e.g. Steffensen, 1976; Reed, 1983; Einav et al., 1995), no study has yet addressed the influence of rapid changes in salinity on both inorganic nitrogen uptake and net oxygen production. Wang and Dei (1999) have shown enhanced uptake of trace metals by *Ulva lactuca* following a decrease in salinity, but like many other studies investigating salinity fluctuations (Steffensen, 1976; Reed, 1983; Floreto et al., 1994), some acclimation time (3 days) was allowed before measurements were taken.

In this paper, we investigate the effect of rapid fluctuations in salinity on short-term net oxygen production and ammonium (NH_4^+) and nitrate (NO_3^-) uptake by *U. lactuca* collected from the Mobile Bay estuary (AL, USA). We consider our measurements short-term because they are taken over a short period immediately after the salinity manipulations. To assess the natural occurrence of the rapid salinity fluctuations tested in the laboratory; salinity was monitored at the collection site from January to July 2000. In addition, dissolved inorganic nutrient concentrations (NO_3^-, NH_4^+) were periodically measured at the collection site to assess the relationship between salinity and nutrient levels.

2. Methods

Submerged *U. lactuca* was collected from the east end of Dauphin Island at the mouth of Mobile Bay, AL, USA (30°15.02′N, 88°04.76′W). Salinity measurements collected every 30 min from 1 January to 31 July 2000 by a Hydrolab H2O (Hydrolab Corporation, Austin, TX, USA) maintained by the Dauphin Island Sea Lab were used to describe the salinity

regime at the collection site over successive 30 min intervals. Water samples were periodically taken at the collection site, GFC-filtered, and frozen at −20 °C for later analysis of NO_3^- and NH_4^+ concentrations on a Sans^{plus}Systems autoanalyzer (SKALAR, Norcross, GA, USA) according to the protocol outlined in the SKALAR operations manual (SKALAR, 1996).

The *U. lactuca* used in this study was collected in June (2000) towards the end of the growing season. Following collection, the algae were quickly rinsed to remove sediment and invertebrates and transported back to the laboratory in filtered seawater (FSW; 1 μm felt bag filter; Aquatic Ecosystems Inc., Apopka, FL, USA). To reduce the time between collection and the start of each experiment (less than 30 min), salinity treatments were prepared prior to collection.

In order to ensure that the treatments differed only in salinity, FSW collected at the site was diluted with deionized water to the lowest salinity prescribed in the experimental design. Using a super-saturated artificial seawater solution (Instant Ocean®, Aquarium Systems Inc., Mentor, OH, USA) with a salinity of 250 psu, the salinity of the diluted FSW was then raised to the desired experimental values. Five salinity treatments (19, 22, 25 (ambient), 28 and 31 psu) were prepared for the net oxygen production experiment and three salinity treatments (20, 25 (ambient), and 30 psu) were prepared for the NH_4^+ and NO_3^- uptake experiments. *U. lactuca* was collected only when salinity at the collection site was 25 psu.

The effect of changing salinity on net oxygen production was measured using 60 ml biological oxygen demand (BOD) bottles. The prepared salinities were poured into BOD bottles and the initial dissolved oxygen concentration measured using a salinity adjusted Orbisphere Laboratories dissolved oxygen meter (model 2607, Orbisphere, Vésenaz, Switzerland). Four sample (containing algae) and two control (without algae) bottles were set up for each salinity treatment. The algal thalli were fragmented into small pieces (~2.5 cm^2), firmly pressed between two paper towels, weighed (FW), and introduced into the sample bottles. Work with *Entermorpha* sp., another macroalgal chlorophyte with a thallus type similar to *U. lactuca*, indicates that neither net oxygen production nor inorganic nitrogen uptake rates are affected by this fragmentation (Lartigue, unpublished data). Between 0.02 and 0.04 g FW of algae was added to each sample bottle. The BOD bottles were then incubated outdoors under conditions similar to the collection site (200 μmol m^{-2} s^{-1} of shaded sunlight at 28 °C) and mixed by inverting each bottle once every 10 min. All replicates were run simultaneously and light varied less than 2 μmol m^{-2} s^{-1} over the area where the bottles were incubated and less than 10 μmol m^{-2} s^{-1} over the course of the incubation. After 1 h, final oxygen concentrations were measured and net oxygen production calculated (μmol O_2 g^{-1} FW h^{-1}) after correcting for the controls and normalizing to the amount of algal tissue enclosed. Treatment means were compared with a one-way ANOVA, after testing for normality and homoscedasticity, and pairs of treatment means compared with a Tukey's post hoc test. To assess differences in carbon availability among the salinity treatments, dissolved inorganic carbon (DIC) concentrations were measured for the 19, 25, and 31 psu treatments using a Shimadzu TOC-5000 (Shimadzu Scientific Instruments Inc., Shimadzu America, Columbia, MD, USA). In order to determine a DW to FW conversion factor, separate samples of *U. lactuca* of a known FW were dried for 24 h at 80 °C and weighed again to determine DW ($n = 36$, DW:FW $= 0.24 \pm 0.01$, mean ± S.E.).

To test the influence of salinity shifts on NH_4^+ and NO_3^- uptake, *U. lactuca* was incubated in the presence of NH_4^+or NO_3^- in 2 l of FSW. Air was bubbled through the water to maintain thorough circulation and the containers were placed under shaded sunlight (200 μmol m^{-2} s^{-1}) at 28 °C. In the NH_4^+ uptake experiment, the concentration of NH_4^+ was raised to approximately 30 μM with the addition of 5 ml of 12 mM NH_4Cl to each of the experimental containers. In the NO_3^- uptake experiment, 5 ml of 12 mM $NaNO_3$ was added to each container to raise the NO_3^- concentration to 30 μM. Four sample containers containing algae and one control containing no algae were included in each salinity treatment. Between 0.85 and 1.4 g FW of *U. lactuca* sectioned into ~2.5 cm^2 pieces was added to each sample container and an initial water sample (50 ml) taken using a 50 ml syringe. Over the next 4 h, water samples were taken every 30 min. Again, all replicates were run simultaneously to ensure similar light level. All water samples were immediately frozen at −20 °C for later analysis.

Ammonium concentration in the water samples from the NH_4^+ uptake experiment was determined using the phenol-hypochlorite method described in Grasshoff et al. (1983). Uptake rate over each 30 min interval was then calculated using the equation

$$\text{uptake rate } (\mu\text{mol g}^{-1}\text{ FW min}^{-1}) = \frac{(S_0 - S_t)((V_0 + V_t)/2)}{tM} \quad (1)$$

where S_0 and S_t are the substrate concentrations in μmol l^{-1} at the beginning and end of a 30 min interval, V_0 and V_t the water volumes in l at the beginning and end of the same

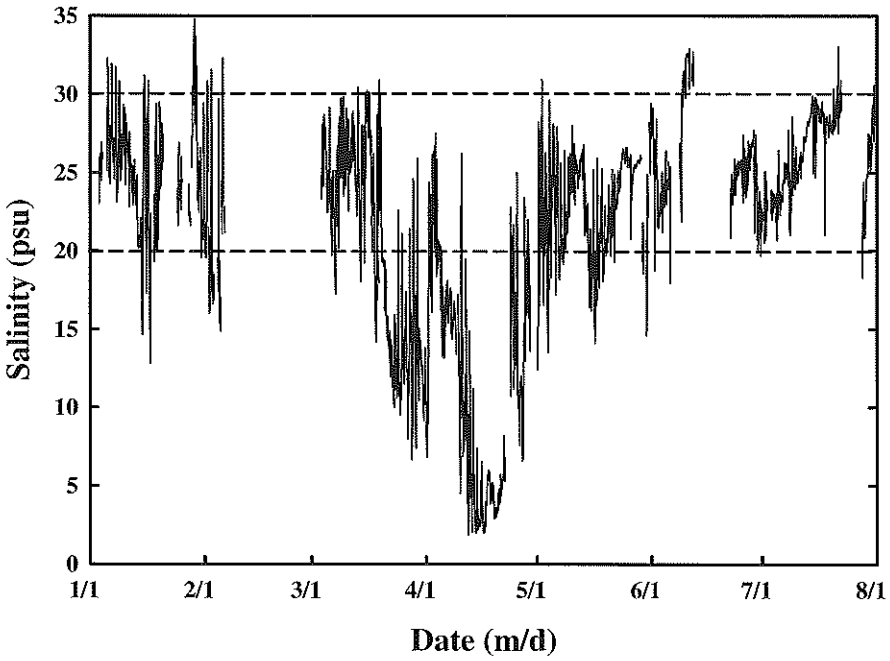

Fig. 1. Salinity recorded by a Hydrolab H2O near the collection site from 1 January to 31 July 2000. Dotted lines indicate the range of salinity values tested in the NH_4^+ and NO_3^- uptake experiments.

30 min interval, t the time in min, and M the algal mass in g FW. A mean uptake rate for each replicate was then calculated by averaging all the uptake rates for that replicate. A One-way ANOVA was then used to test for differences among the mean uptake rates for each salinity treatment. Initial NO_3^- concentrations in the NH_4^+ uptake experiment were determined using a Sans^{plus} Systems.

Nitrate concentrations in the NO_3^- uptake experiment were determined using a Sans^{plus} Systems autoanalyzer. Nitrate uptake was then calculated and treatments compared using the same method described above for NH_4^+ uptake. To assess whether NH_4^+ inhibition of NO_3^- uptake occurred during the NO_3^- uptake experiment, we also measured NH_4^+ concentration during the NO_3^- uptake experiment using the Sans^{plus} Systems autoanalyzer.

3. Results

A total of 7109 salinity values were recorded from January to July 2000 (Fig. 1). Gaps in the data set correspond to periods when the station was shut down for routine maintenance or repair. Salinity oscillated between 20 and 30 psu with the exception of late March and April when spring rainfall led to salinities consistently below 15 psu (Fig. 1). When comparing successive salinity values (values taken 30 min apart), the values differed from one another, reflecting a change in salinity, 78.5% of the time (Fig. 2). Although 87.2% of these changes were less than 1 psu, greater changes also occurred. Overall, 0.5% of the salinity changes were ≥5 psu and 2.9% of the salinity changes were ≥3 psu (Fig. 2). With forty-eight 30 min

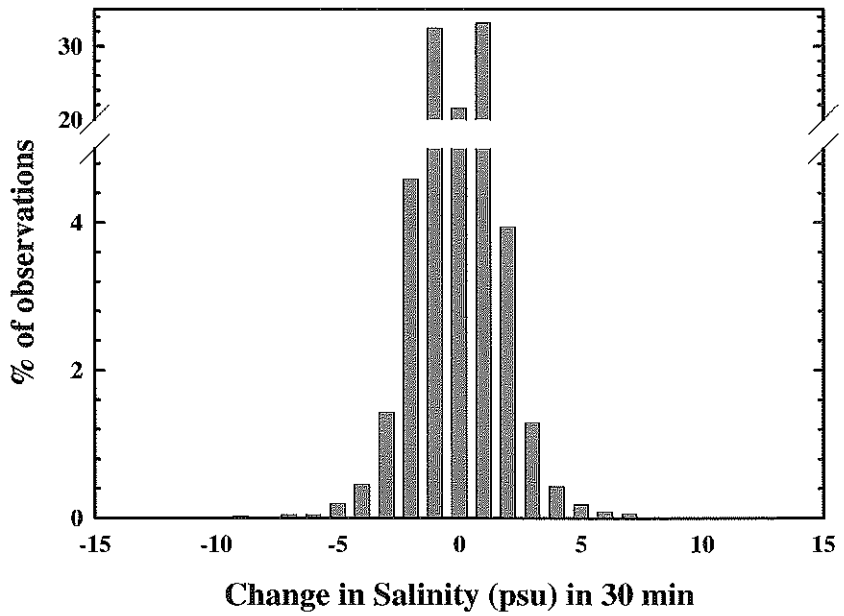

Fig. 2. Histogram of salinity changes over successive 30 min intervals measured from 1 January to 31 July 2000 near the collection site.

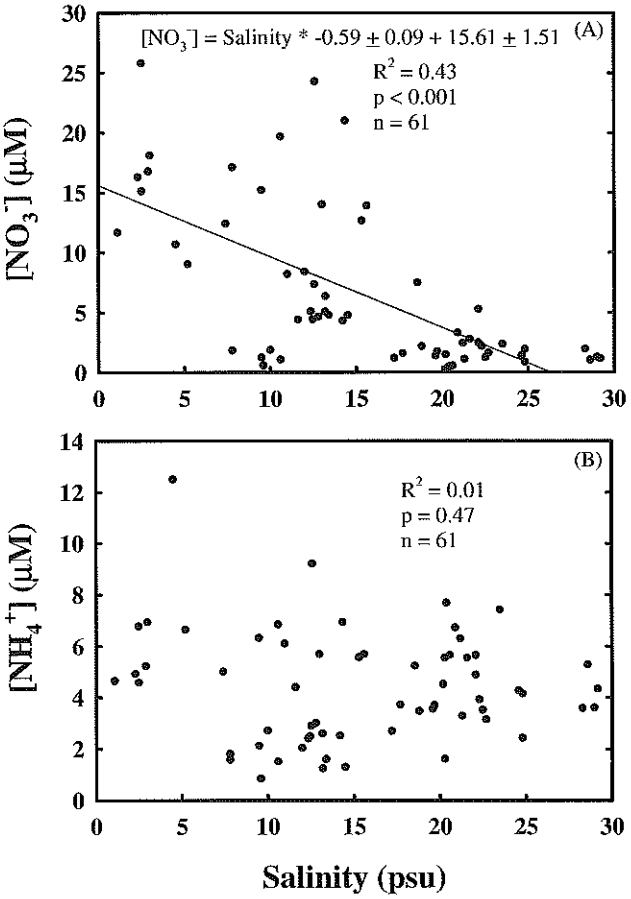

Fig. 3. Nitrate (NO_3^-) and ammonium (NH_4^+) concentration versus salinity for the collection site periodically measured between 1 January to 31 July 2000: (A) NO_3^- concentration versus salinity; (B) NH_4^+ concentration versus salinity.

intervals in a day, this frequency implies that, on average, *U. lactuca* was subject to a $\geq$5 psu change over a 30 min period once every 4.2 days and to a $\geq$3 psu change over a 30 min period once every 0.7 days.

Water samples taken in the cove between January and July 2000 revealed a significant inverse relationship between NO_3^- concentration and salinity (Fig. 3A), but no significant relationship between NH_4^+ concentration and salinity (Fig. 3B).

The raised (28 and 31 psu) and lowered (19 and 22 psu) salinity treatments exhibited depressed net oxygen production compared to the ambient treatment (ANOVA, d.f. = 19, $F = 10.66$, $P < 0.001$; Tukey's test, $P < 0.05$; Fig. 4). The amount of oxygen drift in the controls was less than 2%. DIC concentrations in the 19, 25, and 31 psu treatments were 1255.18 μmol ± 11.72 μmol C kg^{-1} SW, 1275.28 μmol ± 7.33 μmol C kg^{-1} SW, and 1301.94 μmol ± 14.83 μmol C kg^{-1} SW, respectively (mean ± S.E., $n = 3$).

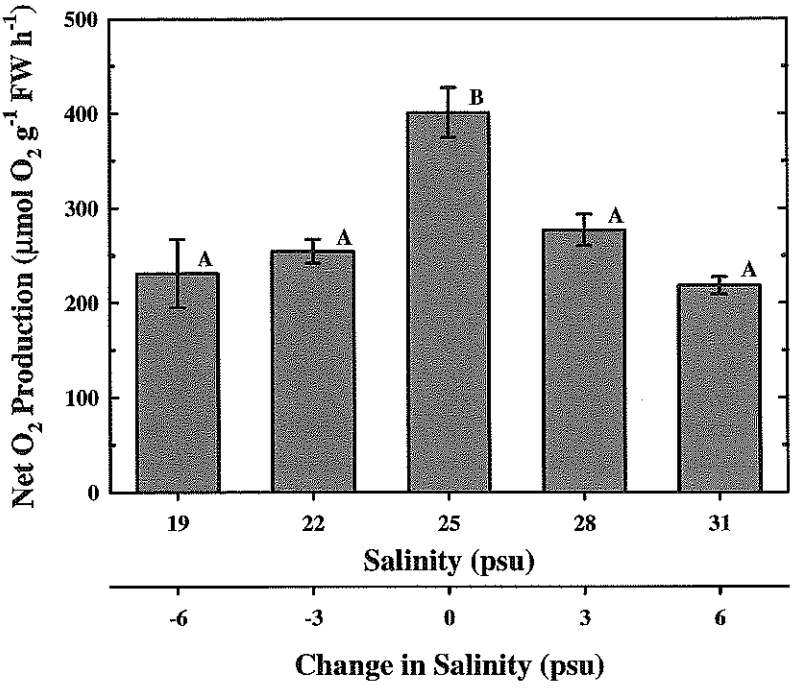

Fig. 4. Net oxygen production in the five salinity treatments. Bars are mean values ± S.E. ($n = 4$). Salinity at the collection site was 25 psu. The top x-axis indicates the salinity for each treatment and the bottom x-axis indicates the change in salinity imposed by each treatment relative to the ambient salinity of 25 psu. Letters denote treatments that are significantly different (Tukey's test, $P < 0.05$).

We found a marginal tendency for ammonium uptake rate to differ among salinity treatments (ANOVA, d.f. $= 11$, $F = 4.374$, $P = 0.047$; Table 1). The weakness of this tendency was supported by the results of the pair-wise comparisons which could not differentiate between pairs at $\alpha = 0.05$, (Tukey's post hoc test; 20 psu versus 25 psu, $P = 0.063$; 20 psu

Table 1
Mean values ± S.E. ($n = 4$) for ammonium or nitrate uptake by *Ulva lactuca* exposed to the three salinity treatments

Salinity (change) (psu)	Uptake rate (μmol g^{-1} FW h^{-1})
Ammonium uptake rate	
20 (−5)	12.36 ± 1.97
25 (0)	6.81 ± 0.62
30 (+5)	7.18 ± 1.53
Nitrate uptake rate	
20 (−5)	5.63 ± 0.83
25 (0)	5.39 ± 0.45
30 (+5)	3.69 ± 0.54

Values in parenthesis correspond to the salinity change imposed by the treatment relative to the ambient salinity (25 psu).

versus 30 psu, $P = 0.082$; 25 psu versus 30 psu, $P = 0.984$). At most, these comparisons suggest a possible trend towards higher uptake at the lowered salinity. The FSW used for the NH_4^+ uptake experiments contained less than 1 μM NO_3^-.

Nitrate uptake rate did not differ among the salinity treatments (ANOVA, d.f. = 11, $F = 2.814$, $P = 0.112$; Table 1). The FSW used for the NO_3^- uptake experiments initially contained ~6 μM NH_4^+. The algae took up this NH_4^+ during the experiment, leaving less than 1 μM after 120 min except in the controls (no algae enclosed). Incidentally, in all three treatments, nitrate uptake rate gradually increased over the first 120 min before remaining roughly constant.

4. Discussion

With the exception of late March and April, salinity mainly ranged between 20 and 30 psu. This salinity range was very close to the range covered in our experiments. Nevertheless, *U. lactuca* growing in the Mobile Bay estuary frequently experiences shifts in salinity greater than 3 psu that are sudden, occurring over 30 min or less. These shifts occur throughout the growing season and are probably the result of several factors. Wind stress has been shown to drive water exchange between the shelf and the shallow estuary, which averages 3 m in depth, and may explain some of the oscillations (Wiseman et al., 1988; Stumpf et al., 1993). Tidal forcing, which brings relatively more saline water into the bay, may also contribute to these changes. Finally, river discharge into Mobile Bay, which ranges from 223 to 13,977 $m^3 s^{-1}$, results in a freshwater residence time of 3–166 days (Anon, 1989). Although the river effect is more likely to account for long-term trends in salinity, it may combine with wind and tidal forcing to produce rapid changes in salinity (Wiseman et al., 1988). When salinity does decline, NO_3^- concentrations tend to increase and vice versa. In contrast, NH_4^+ and salinity are not correlated, which points to NH_4^+ sources other than freshwater input, such as regeneration from the sediments (Cowan et al., 1996).

The net production of 401 μmol ± 26 μmol O_2 g^{-1} FW h^{-1} (mean ± S.E.) measured at the ambient salinity was similar to the value of 312.5 μmol O_2 g^{-1} FW h^{-1} obtained by Riccardi and Solidoro (1996) under similar light levels for *Ulva curvata*, but higher than the 65 μmol ± 10 μmol O_2 g^{-1} FW h^{-1} (mean ± S.D.) measured by Del Rio et al. (1995) for *U. rigida*. Overall, the net oxygen production at the ambient salinity was significantly greater than net oxygen production at any other salinity level suggesting that abrupt changes in salinity involve a reduction in net oxygen production by *U. lactuca*. Similar to our findings, Einav et al. (1995) found that five species of macroalgae including, *U. lactuca*, exhibited a decline in net oxygen production following a sudden change in salinity.

Under exposure to hypotonic or hypertonic conditions, algal cells may alter their internal osmotic pressure by pumping ions across cell membranes or by interconverting monomeric and polymeric metabolites (Hellebust, 1976; Dickson et al., 1980, 1982; Ritchie, 1988; Lobban and Harrison, 1994). Work by Ritchie (1988) suggests that, when salinity is stable, ion transport in *U. lactuca* consumes about 8% of the total energy available under light-saturating conditions and possibly as much as 50% of the available energy in the dark. Under fluctuating salinity and osmotic stress, ion transport and osmotic regulation via the

synthesis and degradation of organic osmolytes may well require an even larger percentage of the available energy. As a result, respiration rates may increase to provide this energy leading to depressed net oxygen production (Lobban and Harrison, 1994). However, we did not measure respiration in this study to confirm this hypothesis.

Several authors have attributed a drop in net oxygen production following exposure to less saline conditions to the lower availability of carbon (dissolved carbon dioxide and bicarbonate) in less saline water (Hammer, 1968; Gessner and Schramm, 1971). DIC concentrations in our 19, 25, and 31 psu treatments differed by less than 5%. Using the CO2SYS program developed by Lewis and Wallace (1998), which derives the fraction of DIC represented by carbon dioxide, bicarbonate, and carbonate from the measured DIC, pH, salinity, and temperature, we calculated that differences in dissolved carbon dioxide and bicarbonate were less than 2% among the treatments. We, therefore, conclude that the observed decline in net oxygen production is due to the change in salinity and that the contribution of DIC availability to the differences observed is minor.

The NH_4^+ uptake rates measured for the ambient salinity treatment lie within the low end of the range published for *Ulva* spp. at a starting NH_4^+concentration near 30 μM. The mean uptake rate (±S.E.) for the ambient salinity treatment was 6.81 μmol ± 0.61 μmol NH_4^+ g^{-1} FW h^{-1} or, using our 0.24 conversion factor for DW:FW, 28.38 μmol±2.54 μmol NH_4^+ g^{-1} DW h^{-1}. This rate is substantially lower than the ~270 μmol NH_4^+ g^{-1} DW h^{-1} obtained by Rosenberg and Ramus (1984) for *U. curvata* starting at 40 μM NH_4^+, but closer to the ~108 μmol NH_4^+ g^{-1} DW h^{-1} found by Campbell (1999) for *Ulva* sp. starting at 28.6 μM NH_4^+ and the ~60 μmol NH_4^+ g^{-1} DW h^{-1} estimated from a regression by Pedersen (1994, Fig. 3A) for uptake by *U. lactuca* over 300 min at a starting concentration of 30 μM NH_4^+.

Overall, the results from the NH_4^+ uptake experiment suggest that within the salinity range tested *U. lactuca* is able to maintain similar NH_4^+ uptake rates when salinity rapidly increases and may even increase NH_4^+ uptake when salinity rapidly declines. However, it is important to again mention that the difference in NH_4^+ uptake between salinity treatments was marginal. At any rate, it seems that the salinity fluctuations, at the least, did not decrease NH_4^+ uptake rates. We are unaware of any previous work on NH_4^+ uptake by *U. lactuca* or any other species of macroalgae under similar salinity fluctuations.

The NO_3^- uptake rates found for *U. lactuca* at the ambient salinity are within the range of published values for *Ulva* spp. at a starting concentration near 30 μM. Nitrate uptake at the ambient salinity was 5.39 μmol ± 0.45 μmol NO_3^- g^{-1} FW h^{-1} or, using our 0.24 conversion factor for DW:FW, 22.46 μmol ± 1.88 μmol NO_3^- g^{-1} DW h^{-1} (mean ± S.E.). This uptake rate is less than the ~66 μmol NO_3^- g^{-1} DW h^{-1} found by Rosenberg and Ramus (1984) for *U. curvata* at a starting NO_3^- concentration of 30 μM, but higher than the 17.52 μmol NO_3^- g^{-1} FW h^{-1} found by Pedersen and Borum (1997, Fig. 3) for *U. lactuca* at 30 μM NO_3^- and the 0.84 μmol ± 0.36 μmol NO_3^- g^{-1} FW h^{-1} found by Riccardi and Solidoro (1996) for *U. rigida* exposed to 22 μM NO_3^- and 3 μM NH_4^+.

Overall, the sudden salinity changes had no significant effect on NO_3^- uptake rates. The suppression of NO_3^- uptake until NH_4^+ concentration had declined suggests that NH_4^+ inhibition of NO_3^- uptake occurred during our experiment. However, the pattern of NO_3^-

uptake over time was similar in all the salinity treatments. So while it is possible that NO_3^- present in less saline pulses of water may not be fully available to *U. lactuca* due to NH_4^+ inhibition, a changing salinity regime alone, even if sudden, does not appear to diminish the alga's capacity to remove NO_3^- from the water column.

To our knowledge, this study is the first account of NO_3^- uptake by *Ulva* spp. under sudden salinity fluctuations. Rueter and Robinson (1986) found that NO_3^- uptake by euryhaline *Fucus distichus* was stimulated by a sudden decline in salinity. Based on the outcome of experiments where ionic strength was kept constant and sodium ions substituted for potassium ions, they hypothesized that NO_3^- uptake was dependent on the potassium ion efflux gradient and not on ionic strength. We did not find any evidence of a gradient in uptake rates over the range and type of salinity shifts we tested.

The uptake and assimilation of NH_4^+ and NO_3^- are processes that require energy and reduced carbon skeletons both derived from photosynthesis (Turpin et al., 1997). Since high levels of NH_4^+ are toxic to algal cells, NH_4^+ is not stored in large quantities and the active uptake (Balch, 1986) and assimilation of NH_4^+ does not continue in the absence of available energy and reduced carbon skeletons. Nitrate uptake via active transport (Boyd and Gradmann, 1999), NO_3^- reduction, and NO_3^- assimilation also require energy and reduced carbon skeletons. As a result, these processes do not continue in the absence of energy and reduced carbon skeletons either. However, the decline we observed in net oxygen production likely did not result in a decline in nitrogen uptake rates, because over the short-term scale of our uptake experiments (4 h) *U. lactuca* has sufficient reserves of energy and carbon skeletons to maintain inorganic nitrogen uptake.

5. Conclusion

This report provides novel results as to how sudden fluctuations in salinity comparable to those measured in the field may affect short-term net oxygen production and inorganic nitrogen uptake rates. In spite of reduced oxygen evolution, *U. lactuca* seems to maintain the capacity to take up NH_4^+ and NO_3^- under sudden, short-term $\leq$5 psu changes within the 20–30 psu range. Whether inorganic nitrogen uptake would continue to remain similar under frequent and prolonged exposure to a change in salinity, however, remains to be seen. Since large amounts of energy and carbon skeletons are needed to assimilate inorganic nitrogen (Turpin et al., 1997), it is doubtful that uptake rates would remain unchanged if conditions that lead to a decline in net oxygen production persist for more than a few hours. However, the high levels of biomass and production reached by *U. lactuca* at our estuarine site and others (Valiela et al., 1997) suggest that this species may adapt to both short- and long-term salinity changes of varying intensity. Clearly more work must be conducted before broader conclusions about the impact of salinity fluctuations on macroalgal metabolism and growth can be made. Research aimed at elucidating how estuarine algae respond seasonally to sudden changes in salinity (e.g. spring rainfalls) and recover from the short-term impacts of an intense, sudden salinity change would be particularly relevant as would work that investigates whether the relationship between fluctuating salinity, inorganic nutrient uptake, and net oxygen production is dependent on the light regime and photosynthetic activity.

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