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Nitrogen release from decomposing seaweeds: species and temperature effects

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Abstract

This study determined the rate at which nitrogen accumulated in seaweeds is released during decomposition and the effect of temperature on their rates of decomposition and nitrogen release. *Gracilaria verrucosa* and *Ulva lactuca* decomposed rapidly in outdoor mesocosms. *Ulva*, but not *Gracilaria*, became nitrogen-enriched during decomposition. Maximal weekly rates of nitrogen release were 5.91 ± 2.23 and 6.37 ± 2.59 g N m^{-2} d^{-1}, respectively for *Gracilaria* and *Ulva*. Temperature had a significant effect on the decomposition rate of *Gracilaria* in a laboratory experiment: decomposition was greater at 30 °C than at 25 °C. No net decomposition was observed at 16 °C. *Gracilaria* became nitrogen enriched at 30 °C, but not at 16° or 25°. The release of stored nutrients from decaying seaweeds should be included in nutrient budgets and models when seaweed standing stocks are significant. Seaweed source-sink relationships are important ecologically and can be applied to attempts at using seaweeds as environmental monitors of anthropogenic eutrophication and to efforts of cultivating seaweeds for the improvement of water quality.

Introduction

In coastal and estuarine systems, seaweeds are important in nutrient cycles, alternately acting as nutrient sources or sinks (Hanisak, 1983; Sfriso *et al.*, 1987; Lavery & McComb, 1991). Seaweeds are capable of assimilating and storing large quantities of nutrients when ambient supplies are higher than what is required for growth (e.g., Chapman & Craigie, 1977; Hanisak, 1979, 1983, 1990; Ryther *et al.*, 1981). When external nutrient levels are low, these internal reserves can sustain growth. Thus, macroalgae are nutrient sinks in the system. Much less known is the fate of nutrients in seaweeds. If seaweeds are not grazed, they die and decompose. Decomposing seaweeds have well-known impacts on oxygen levels, with possible deleterious effects to the whole community, but the impact on nutrient cycling in these systems has been little studied (Williams, 1984; Owens & Stewart, 1983; Lavery & McComb, 1991). When seaweeds decompose, they become sources of nutrients to the system; if seaweeds are abundant, the timing and magnitude of their nutrient releases during decomposition is likely to be ecologically significant.

In particular, few data exist on nutrient release from decaying seaweeds in subtropical and tropical waters. In Florida, seaweeds are abundant in coastal embayments and lagoons, and sharp declines in standing crop often occur during the summer (Dawes *et al.*, 1979; Dawes, 1985; Virnstein & Carbonara, 1985; Hanisak, unpubl. data; R. Johansson, unpubl. data). The cause of these declines is unknown, but there appears to be rapid degradation of populations as temperatures in-

crease to 30 °C. The purpose of this study was (1) to determine the extent to which nitrogen accumulated in seaweeds is released during decomposition and (2) to examine the effect of temperature on their rates of decomposition and nitrogen release.

Materials and methods

Outdoor mesocosm experiment

Two widely distributed seaweeds were collected from Tampa Bay, Florida (USA), for this experiment: the rhodophyte *Gracilaria verrucosa* (Hudson) Papenfuss, a major component of the community, and the chlorophyte *Ulva lactuca* L., a frequent component of the community, particularly in areas where nutrient loading is high. Decomposition rates were measured in three replicate outdoor mesocosms (700-liter concrete tanks, 2.20 m long × 0.70 m wide × 0.45 m deep) for each species at the seaweed cultivation facility at Harbor Branch Oceanographic Institution in Fort Pierce, Florida. The stocking density was 10 kg m^{-2}, a value representative of thick, high-density seaweed beds. Seawater from the adjacent Indian River lagoon flowed through each tank at the rate of 1 volume exchange d^{-1}. The irradiance reaching the tanks was reduced with neutral density screens to ca. 10% of full sunlight (to ca. 200–280 μmol m^{-2} s^{-1}), a value in the typical range for benthic algal communities in coastal embayments and lagoons of Florida. The mean daily water temperature during this experiment ranged from 25–30 °C. At weekly intervals, the biomass (wet weight) of seaweeds in each tank was determined by harvesting them with a dip net, draining the excess water, and weighing. Small samples were harvested for determination of percent dry weight (48 h at 70 °C). Subsamples were analyzed for their carbon and nitrogen content with a CHN elemental analyzer at the Marine Science Institute Analytical Laboratory, University of California, Santa Barbara. Sampling continued for two months until breakdown of the biomass was essentially complete. Seaweed nitrogen pool size (g N $tank^{-1}$) and the weekly rate of nitrogen release during decomposition (g N m^{-2}) were calculated from the measurements of biomass and tissue nitrogen. Negative values for rates of decomposition or nitrogen release indicate an increase in biomass or net uptake of nitrogen by the seaweed, respectively. Data are presented as means ± 1 standard error.

Temperature experiment

Six 57-liter aquaria containing *Gracilaria verrucosa*, at a stocking density of 10 kg m^{-2} (based on the side of the aquaria facing the light source), were set up in a light- and temperature-controlled room. Light was provided by high-output cool-white fluorescent tubes on a 12:12 h light:dark photoperiod. The lights were arranged adjacent to the aquaria to provide unidirectional light along the back side of the aquaria (0.18 m^2). Irradiance at a central point adjacent to the light-exposed side was 465 μmol m^{-2} s^{-1}. Temperature was controlled in each aquarium with a heat exchanger system. Water was circulated by gentle aeration. Two replicate aquaria were set up in batch mode (50 l, no exchange of seawater) at each of three temperatures: 16, 25 and 30 °C. These values approximate average temperatures for winter, spring/autumn and summer in the coastal waters of Florida. The biomass (wet weight), percent dry weight, carbon and nitrogen contents and decomposition rates were measured or calculated as previously described at weekly intervals for four weeks. Water samples for nutrient analyses were taken at weekly intervals, filtered through GFF 0.45 μm filters, and frozen until analyses were performed. Inorganic nitrogen (nitrate, nitrite, ammonium) were analyzed with an Alpkem Autoanalyzer.

Results

Mesocosm experiment

Both species decomposed rapidly (Fig. 1). Initially, *Gracilaria* broke down faster (maximal weekly rate per tank = 5.13 ± 0.98 kg wet weight)

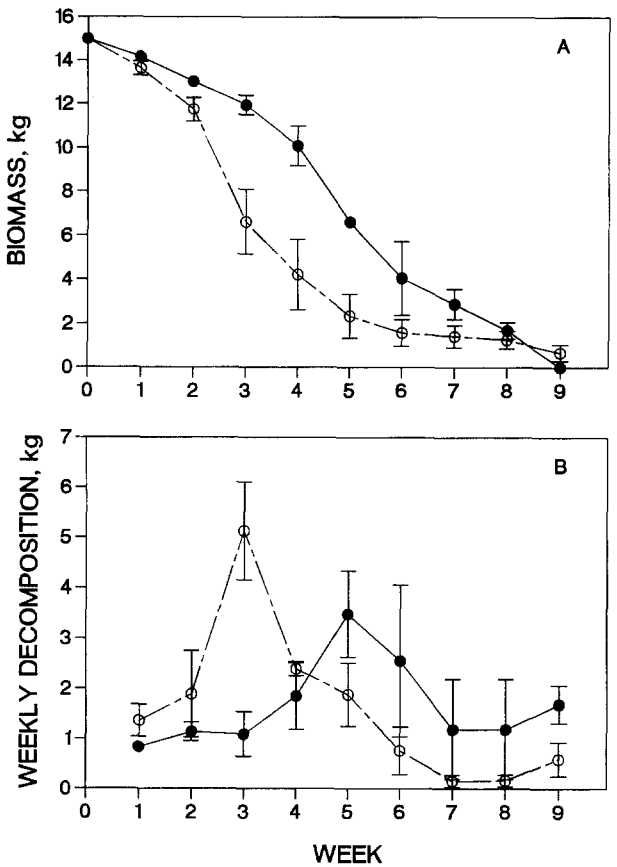

Fig. 1. Reduction of biomass (A), as kg wet weight per tank, and weekly decomposition (B), as kg wet weight per tank, for *Gracilaria* (open circles) and *Ulva* (filled circles) during the outdoor mesocosm experiment. Each point is the mean of three replicates for each species; the vertical bars indicate one standard error.

than *Ulva*; after four weeks, only 28% of the *Gracilaria* and 67% of the *Ulva* remained. Thereafter, the decomposition of *Ulva* was faster (maximal weekly rate per tank = 3.48 ± 0.85 kg wet weight); by the end of the experiment, no *Ulva* was recoverable from the tanks, and only 5% of the initial biomass of *Gracilaria* remained.

After an initial value of 1.98%, the tissue nitrogen of *Gracilaria* (Fig. 2A) ranged from 2.21–2.67%, with the exception of week 4 (3.10%). In contrast, the tissue nitrogen of *Ulva*, initially 1.25%, increased during decomposition to a maximal value of 4.02% at the end of the experiment. C:N ratios were inversely related to tissue nitrogen (Fig. 2B). C:N ratios of *Gracilaria* ranged between 8.32–9.87, with the exception of week 4 (6.92), while the C:N ratio of *Ulva* decreased from 20.10 to 4.81. The total seaweed nitrogen (Fig. 3A) in the tanks decreased as decomposition occurred. While the absolute magnitude of nitrogen release was similar for the two species, differences occurred in their temporal release of nitrogen (Fig. 3B); more nitrogen was released by *Gracilaria* during the first month, but more was released by *Ulva* during the second month. Maximal weekly rates of nitrogen release were 5.91 ± 2.13 and 6.37 ± 2.59 g N m^{-2}, respectively for *Gracilaria* (week 5) and *Ulva* (week 6). At the end of the two-month experiment, 93% and 100% of the original seaweed nitrogen had been lost by *Gracilaria* and *Ulva*, respectively.

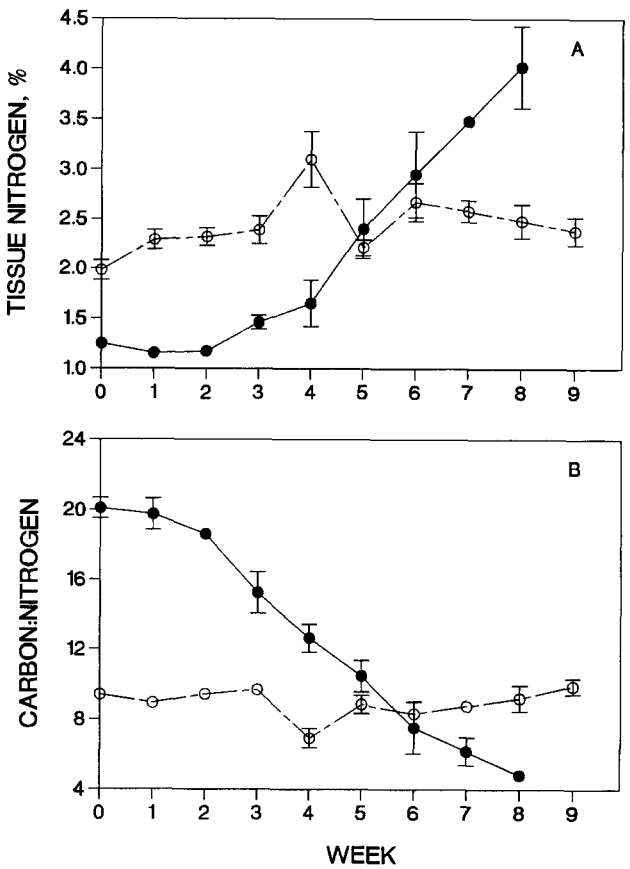

Fig. 2. Tissue nitrogen (A), as percent of dry weight, and carbon:nitrogen ratio (B) for *Gracilaria* (open circles) and *Ulva* (filled circles) during the outdoor mesocosm experiment. Each point is the mean of three replicates for each species; the vertical bars indicate one standard error.

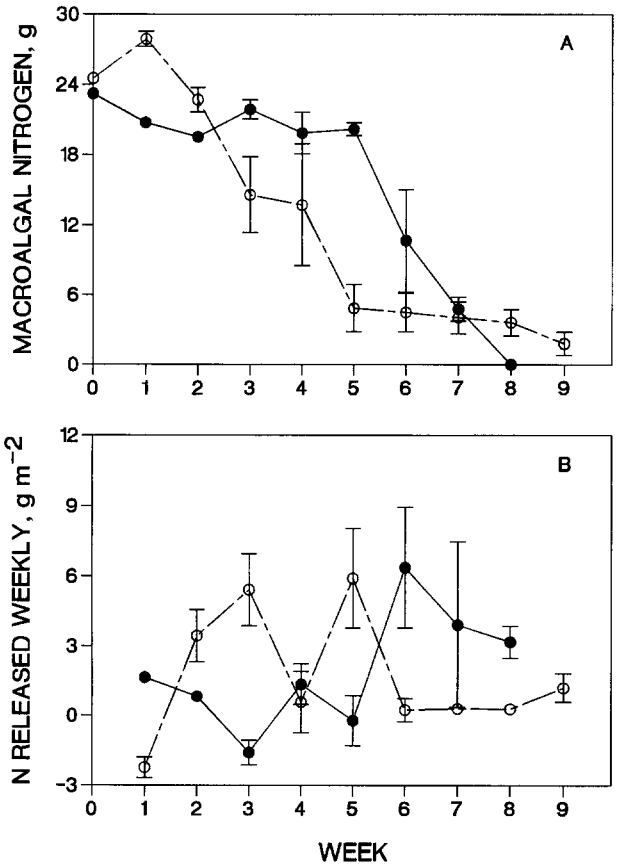

Fig. 3. Macroalgal nitrogen (A), as g nitrogen per tank, and nitrogen released weekly (B), as g m^{-2} for *Gracilaria* (open circles) and *Ulva* (filled circles) during the outdoor mesocosm experiment. Each point is the mean of three replicates for each species; the vertical bars indicate one standard error.

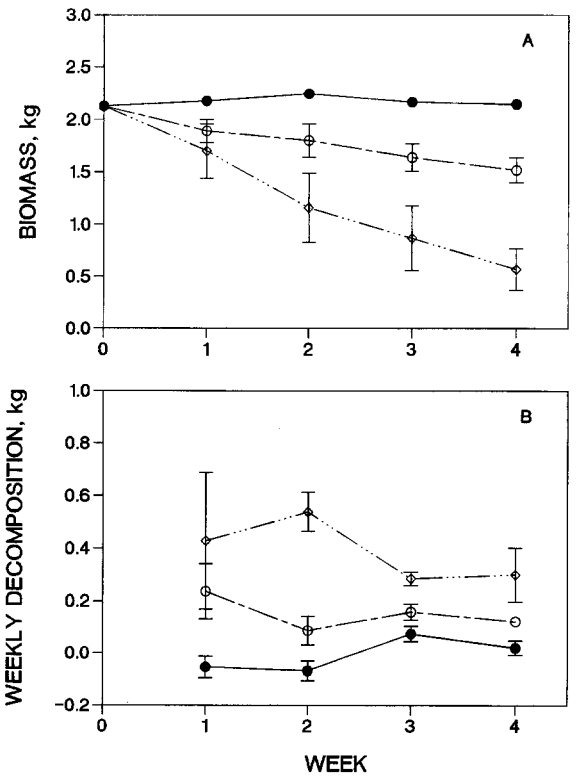

Fig. 4. Reduction of biomass (A), as kg wet weight per tank, and weekly decomposition (B), as kg wet weight per tank, for *Gracilaria* at 16 (filled circles), 25 (open circles) and 30 °C (diamonds). Each point is the mean of two replicates for each temperature; the vertical bars indicate one standard error.

Temperature experiment

Temperature had a significant effect on decomposition over the four-week experiment (Fig. 4). At 16 °C, no signs of decomposition were evident in the aquaria throughout the experiment. At 25 °C, biomass decreased relatively slowly, but steadily, with a total loss of 29%; decomposition clearly exceeded growth (maximal weekly decomposition per tank = 0.24 ± 0.10 kg wet weight, week 1). At 30 °C, there was a rapid breakdown of biomass; by week 4, only 27% of the initial quantity remained (maximal weekly decomposition per tank = 0.54 ± 0.07 kg wet weight, week 2).

The tissue nitrogen (Fig. 5A) of *Gracilaria* ranged from 1.40 to 1.61% and 1.42 to 1.82%, respectively, at 16 and 25 °C. In contrast, the tissue nitrogen of *Gracilaria* increased from 1.61 to 2.64% at 30 °C. C:N ratios (Fig. 5B) increased from 11.28 to 16.37 and 15.79, respectively, at 16 and 25 °C, but decreased to 8.30 at 30 °C. Seaweed nitrogen per tank (Fig. 6A) was relatively constant (3.1–3.6 g N $tank^{-1}$) at 16 °C throughout the experiment, but decreased at higher temperatures as decomposition occurred. Overall, losses from the initial seaweed nitrogen were 8, 38 and 48%, in that order, for 16, 25, and 30 °C. Maximal weekly rates of nitrogen release (Fig. 6B) were 1.89 ± 0.20, 4.67 ± 0.24 and 3.94 ± 1.53 g N m^{-2}, in that order, for 16, 25 and 30 °C.

Significant increases in dissolved inorganic nitrogen (initial values < 1 μM) occurred at all temperatures. Values ranged from 3.54 to 13.6 μM at

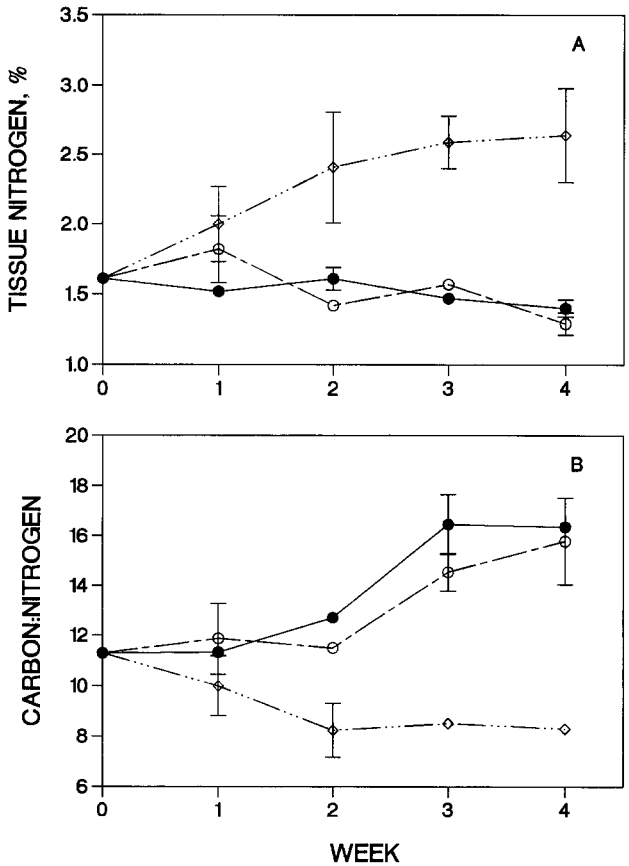

Fig. 5. Tissue nitrogen (A), as percent of dry weight, and carbon:nitrogen ratio (B) for *Gracilaria* at 16 (filled circles), 25 (open circles) and 30 °C (diamonds). Each point is the mean of two replicates for each temperature; the vertical bars indicate one standard error.

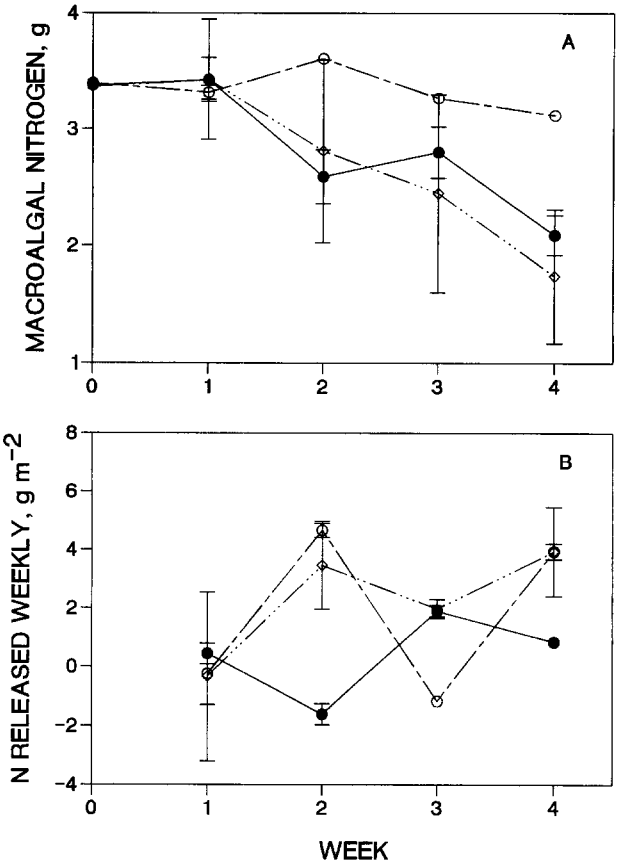

Fig. 6. Macroalgal nitrogen (A), as g nitrogen per tank, and nitrogen released weekly (B), as g m^{-2}, for *Gracilaria* at 16 (filled circles), 25 (open circles) and 30 °C (diamonds). Each point is the mean of two replicates for each temperature; the vertical bars indicate one standard error.

16 °C, 8.31 to 12.4 μM at 25 °C, and 14.66 to 157 μM at 30 °C. Most of the dissolved inorganic nitrogen was in the form of ammonium: mean values were 75%, 77% and 92%, in that order, for 16, 25 and 30 °C. However, only a small portion (4%, <1% and 7%, in that order, for the three temperatures) of the nitrogen lost from the macroalgae was measured as inorganic nitrogen in the seawater medium.

Discussion

Gracilaria initially broke down more quickly than *Ulva*, but thereafter the decomposition rate of *Ulva* rapidly accelerated and ultimately exceeded that of *Gracilaria*. This is consistent with previous measurements of the digestibility of the two genera in fermenters for biogas production (Habig *et al.*, 1984; Habig & Ryther, 1984). Differences in decomposition rates between macrophytes are probably a result of differences in biochemical compositions (Buchsbaum *et al.*, 1991). These differences may be related both to phylogenetic differences in structural and storage carbohydrates and pigment systems and to morphological differences in thallus complexity. The thallus of *Ulva* is two cell layers thick, and all cells are photosynthetic and in direct contact with the surrounding medium. *Gracilaria* has a greater amount of structural cells, which are non-

photosynthetic and not in immediate contact with the medium. The initially quicker decomposition of *Gracilaria* may be a result of an increased respiratory demand of the structural cells.

In the mesocosm experiment, *Ulva* but not *Gracilaria,* became nitrogen-enriched during decomposition, a phenomenon commonly observed in other macrophytes, presumably as a result of microbial enrichment or binding activities of detrital cell wall constituents (Buchsbaum *et al.*, 1991). While the absolute magnitude of nitrogen release was similar for the two species, differences between species occurred in the temporal release of nitrogen. This difference, in both the concentration and release of nitrogen during decomposition, is probably ecologically significant, not only in terms of nitrogen release to the system but in terms of nutritional value to detritivores.

One of the first benefactors of nitrogen release from seaweed decomposition may be other seaweeds. Rapid cycling of nutrients within seaweed communities may be an important mechanism by which high standing crops are maintained. *In situ* measurements of productivity and nitrogen cycling of most seaweeds are not adequately known, but the rate of nitrogen release during decomposition is more rapid than the rate of nitrogen acquisition during growth. For example, under nitrogen sufficient conditions, a short-term (7 weeks, summer conditions) *in situ* productivity of *Gracilaria* of 24 g dry weight m^{-2} d^{-1} was measured in the Indian River lagoon, Florida (Hanisak, 1990). However, the productivity of *Gracilaria* appears to be frequently nitrogen-limited in Florida waters; e.g., the mean tissue nitrogen for *Gracilaria verrucosa* in Tampa Bay (Hanisak, unpubl. data, $n = 34$) was 1.67%, a value sufficient to sustain a productivity of ca. 12 g dry weight m^{-2} d^{-1} (based on Hanisak, 1990). The nitrogen requirement for this productivity would be 0.2 g N m^{-2} d^{-1}. Comparison of the nitrogen release rates obtained during this study (maximal rates during decomposition were equivalent to 0.3 to 0.9 g N m^{-2} d^{-1}) with the nitrogen requirements for growth indicates that nitrogen released during decomposition is more than adequate to sustain significant levels of seaweed productivity. Moreover, these seaweeds are well-adapted for rapid accumulation of nitrogen from pulses in the environment (Ryther *et al.*, 1981; Hanisak, 1990).

Temperature is important in determining the rate of seaweed decomposition and nitrogen release. Warmer temperatures (30 °C) were the most favorable for decomposition. These data are consistent with observations that seaweed biomass in the coastal embayments and lagoons of Florida drops precipitously (Dawes *et al.*, 1979; Virnstein & Carbonara, 1985; R. Johansson, unpubl. data) during the later part of the summer. Laboratory cultures of these species have demonstrated that growth rates decline rapidly above 30 °C (Hanisak, 1987). As the rate of decomposition exceeds the growth rate, seaweeds are no longer a nutrient sink in the system, but a source. The largest nitrogen pulses into coastal waters would be expected to occur during the second half of the summer (August/September); not only would decomposition rates be maximal, but the reduced growth potential of macroalgae at higher temperatures would limit their direct recycling of nitrogen. The decomposition rate is likely to be accelerated during years of high terrestrial runoff because of the associated high turbidity (i.e., reduced light for benthic photosynthesis) and elevated nutrients (which increase phytoplankton blooms and further reduce available light to the benthic community).

Although there has been substantial interest in the adaptive strategy of macroalgae in storing nitrogen for use when external sources are limited (e.g., references previously cited), there has been little appreciation of the magnitude of this nitrogen sink and its flux at the ecosystem level. This study has demonstrated the potential importance of decaying seaweeds as an important nitrogen source in coastal waters. The magnitude of this nutrient reservoir in coastal systems is unquantified because of a lack of a better spatial and temporal resolution of both macroalgal standing crop and nutrient cycling. In these systems, seaweeds are an important factor in determining nutrient availability, not only because of their enormous

uptake and storage capabilities relative to other components, e.g., phytoplankton, but also because of an even more rapid release of nutrients during decomposition. The seaweed source-sink relationship should be included in nutrient budgets and models whenever seaweed standing stocks are significant. Moreover, the dynamic aspect of nutrient cycling within the seaweed community itself has not been widely appreciated (Owens & Stewart, 1983). This phenomenon may be particularly important in maintaining nutrients within subtropical and tropical communities where seaweed productivity is more likely to be nutrient limited than in the temperate zone (Wheeler & Björnsäter, 1992; Lapointe *et al.*, 1992).

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