Response of primary producers to nutrient enrichment in a shallow estuary

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ABSTRACT: Shallow coastal systems worldwide are exhibiting increased algal growth in response to nutrient enrichment. This study evaluates primary production patterns in an estuarine system (Bass Harbor Marsh, ME, USA) receiving low levels of anthropogenic nitrogen. Biomass, areal coverage and *in situ* oxygen production of green macroalgae, *Ruppia maritima*, and phytoplankton were measured over a growing season to determine net ecosystem production. Macroalgae and *R. maritima* exhibited seasonal biomass curves with early summer peaks; however, peak biomass of macroalgae [150 g dry weight (wt) m^{-2}] was substantially greater than *R. maritima* (33 g dry wt m^{-2}). Phytoplankton biomass, measured as chlorophyll *a*, was low (<1 µg l^{-1}) early in the season and peaked (11 µg l^{-1}) following a mid-summer decline in macroalgal biomass, suggesting a competitive interaction with macroalgae. Instantaneous net production rates varied over the growing season for all 3 primary producers. *R. maritima* net production ranged from near zero to 3.7 mg C g^{-1} dry wt h^{-1}, with higher rates during summer and much of the seasonal variability explained by temperature. Macroalgal (0.88 to 5.0 mg C g^{-1} dry wt h^{-1}) and phytoplankton (0 to 28 mg C m^{-3} h^{-1}) net production did not exhibit any clear seasonal signal. Net primary production calculated on an areal basis demonstrated macroalgae's dominance in the lower basin of Bass Harbor Marsh, with peak summer rates (400 mg C m^{-2} h^{-1}) greatly exceeding maximum rates for both *R. maritima* (70 mg C m^{-2} h^{-1}) and phytoplankton (12 mg C m^{-2} h^{-1}). When compared to other New England estuarine sites with short residence times, nutrient loading and peak green macroalgal biomass in Bass Harbor Marsh are relatively low; however, the strong dominance of opportunistic green macroalgae is a pattern that is characteristic of shallow coastal systems undergoing eutrophication.

KEY WORDS: Primary productivity · Eutrophication · Green macroalgae · *Ruppia maritima* · Phytoplankton · Estuary · Maine, USA

INTRODUCTION

As coastal populations grow, eutrophication is becoming a major concern in response to anthropogenic nutrient loading. Studies in Australia (Lavery et al. 1991), Italy (Sfriso et al. 1987), and the United States (Ryther & Dunstan 1971, Thorne-Miller et al. 1983, Valiela et al. 1992, Taylor et al. 1995) have investigated the consequences of nutrient inputs into different coastal systems. However, more information on ecosystem responses to nutrient enrichment, particularly in shallow coastal systems, is needed (Valiela et al.

1992, Harlin 1995). Nixon (1995) has defined eutrophication as 'an increase in the rate of supply of organic matter to an ecosystem'. Eutrophication is often caused by an increase in inorganic nutrients. Elevated levels of organic matter can be supplied by external inputs or by primary producers within the system, and primary production time series measurements are one means of determining if a system is becoming eutrophied.

Coastal systems have exhibited varied patterns of response to nutrient inputs. While some have shown a phytoplankton-dominated response (Ryther & Dunstan 1971), others appear to be dominated by macrophyte growth (Lee & Olsen 1985, Valiela et al. 1992). In shallow eutrophied areas, such as Waquoit Bay (MA, USA) and the Peel-Harvey estuarine system (Australia),

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green macroalgae dominated the response and produced anoxic conditions at times of water column stratification (Lavery & McComb 1991, D'Avanzo & Kremer 1994). Blooms of phytoplankton in Venice Lagoon, Italy, were observed only after macroalgal decomposition had released nutrients into the water column (Sfriso et al. 1987). In nutrient-enriched enclosure experiments, macroalgal suppression of phytoplankton growth has been reported (Fong et al. 1993, Oviatt 1994). However in other enclosure experiments, nutrient additions have initiated phytoplankton blooms with subsequent declines in macrophyte biomass (Taylor et al. 1995). Factors responsible for triggering the different responses are not fully understood.

The objective of this study was to determine dominance in primary production of a marsh-estuarine system receiving low levels of nitrogen enrichment. Located on Mt. Desert Island, Maine, USA, Bass Harbor Marsh lies mostly within the confines of Acadia National Park. One of the freshwater brooks feeding the marsh system is carrying nitrogen leachate from a landfill and residential development near its headwaters. In this study, both biomass and instantaneous production of green macroalgae, *Ruppia maritima*, and phytoplankton were measured in order to estimate net system production. These estimates were used to determine the dominant primary producer on both a seasonal and annual basis. In addition, physical and chemical parameters were measured to evaluate factors controlling the growth and dominance of the different primary producers.

Anthropogenic nitrogen inputs have the potential to enhance primary production in nitrogen limited coastal systems (Howarth 1988, Oviatt et al. 1995). Bass Harbor Marsh offers the opportunity to study the interaction of 3 different primary producers in a system which may be responding to relatively low levels of nitrogen loading.

MATERIALS AND METHODS

Study area. Situated on the southwest coast of Mt. Desert Island, Maine, Bass Harbor Marsh encompasses 349 ha (Fig. 1). It is connected to the ocean through Bass Harbor, where a road causeway and a natural bedrock sill near the marsh mouth dampen the tidal range from 3 m in the harbor to 0.3 m within the marsh. Depths are shallow, generally less than 0.5 m at low tide. The system is well flushed, with a residence time of less than 3 d. The main marsh creek meanders for
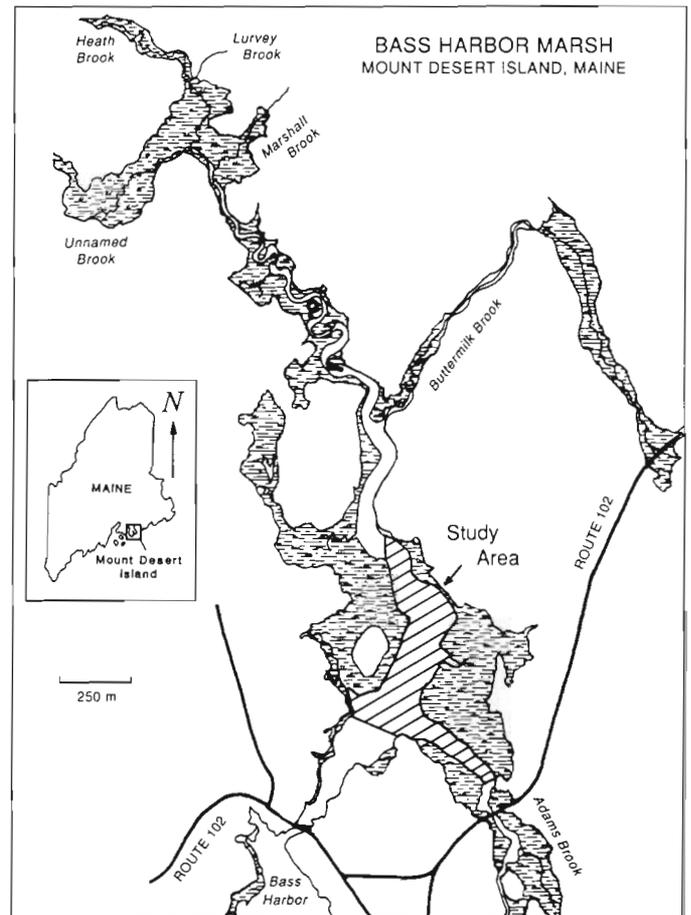

Fig. 1. Bass Harbor Marsh, located on Mt. Desert Island, off the Maine coast. Note the 20 ha study site in the lower marsh basin

approximately 3 km and is fed by 7 freshwater brooks. Salinities range from freshwater at the upstream tidal end to 32 parts per thousand (ppt) near the mouth. Total dissolved inorganic nitrogen loading from both the freshwater brooks and the ocean is 2.20 mmol m^{-2} d^{-1} (Doering et al. 1995). The developed Marshall Brook drainage (landfill, residences) accounted for 74% of total freshwater nitrate-nitrite loading to Bass Harbor Marsh.

The marsh surface is dominated by short form *Spartina alterniflora* and other plants characteristic of saline to brackish-water systems. In the submerged portions of the lower marsh basin, *Ruppia maritima*, a few patches of *Zostera marina*, and green macroalgae species, principally *Enteromorpha prolifera* and *E. flexuosa*, all co-occur. *E. intestinalis*, *Rhizoclonium riparium*, as well as the the yellow-green alga *Vaucheria* sp. and the blue-green *Microcoleus lyngbyaceus* are also found.

All sampling was conducted in the lower marsh basin, a 200 000 m^2 area near the mouth where maxi-

mum macroalgal growth occurred (Fig. 1). During the period from early April to late November, 1995, water temperatures in the lower basin ranged from 2.8 to 25.5°C, and mid-day light extinction coefficients were variable due to wind and tidal scour in the shallow water column (Table 1).

Biomass sampling and mapping. Green macroalgal and *Ruppia maritima* biomass were sampled 11 times (April 4 and 25, May 25, June 6 and 20, July 6 and 25, August 15, September 14, October 18, and November 28) in 1995. Twenty *R. maritima* and 20 macroalgal quadrats were randomly collected along transects within the study area. A 0.05 m² circular quadrat was inserted into the sediment and all belowground, aboveground and floating plant material harvested. Harvested material was washed on a 2 mm mesh sieve and all visible animals and non-target plant species removed. *R. maritima* leaves were separated from the rest of the plant. All plant samples were rinsed with deionized water and dried to constant weight at 60°C. Dried samples were weighed and biomass calculated as grams dry weight (g dry wt) of plant tissue m⁻² (g dry wt m⁻²). At the time of biomass sampling, areal plant coverage was mapped. The study area was surveyed by canoe, and the presence or absence of green macroalgae and *R. maritima* recorded on a base map derived from vertical aerial photographs (scale 1:9600). A range finder was used to help estimate distances within the 200 000 m² study area.

In situ **productivity incubations.** Instantaneous production of green macroalgae (*Enteromorpha prolifera* and *E. flexuosa*), *Ruppia maritima* and phytoplankton was measured within 24 h of each biomass survey with the exception of the April 4 sampling. That sample date occurred immediately after ice-out and prior to

the appearance of green macroalgae and *R. maritima* in the marsh; therefore only phytoplankton were incubated. Benthic microalgal production was not included in this study because a previous investigation found it to be a minor component of primary production in Bass Harbor Marsh (Farris 1996).

Five-liter chambers (15 cm diameter, 30 cm height) were constructed of clear polycarbonate for the incubations. Three different treatments (phytoplankton, *Ruppia maritima* and macroalgae) were incubated, with each treatment containing 3 light chambers and 3 chambers made dark with opaque tape. In the *R. maritima* treatment, 0.1 to 0.6 g dry wt of leaf material were added to each chamber and, in the macroalgae treatment, 0.3 to 1.1 g dry wt of algae thalli. This amount of tissue was comparable to the range of macrophyte densities found in the field, except during peak macroalgal growth. More than 1.1 g dry wt of macroalgae per chamber was not used to avoid CO_2 and nutrient deficiency during the incubations (Johnston 1969). Only the leaves of *R. maritima* (the photosynthetic portion of the plant) were placed in the chambers. Inclusion of whole plants may have resulted in internal oxygen utilization (Thursby 1984a), making it difficult to use change in dissolved oxygen as a means of measuring oxygen production.

Initial oxygen samples were collected for each treatment and fixed immediately using the azide oxygen method (American Public Health Association 1980). Incubations were conducted during mid-day (09:30 to 15:30 h), and the chambers were suspended 25 cm below the surface with clear plastic buoys. The 30 cm high chambers encompassed over half the mean 0.5 m water column. Chambers with only ambient water were incubated 5 to 6 h. The water was unfiltered, including the entire water-column community; however, because primary producers were the focus of this study, this treatment is referred to as the phytoplankton treatment. *Ruppia maritima* was incubated 3 to 6 h, and macroalgae 2 to 5 h, with shorter times used during the warm summer months. The macrophyte tissue used was sparsely epiphytized, and thus the incubations represent a community response. The chambers were shaken every 30 to 60 min to avoid stratification and the depletion of nutrients in the water immediately surrounding the plants (Littler 1979). During the incubations, 2 to 3 light profiles (µE m⁻² s⁻¹) were taken adjacent to the chambers with a Li-Cor LI-1000 light meter (LI-192SA and LI-190SA radiation sensors). Ambient water temperature and salinity were measured with a mercury thermometer and refractometer, respectively.

Table 1. Physical parameters measured during the productivity experiments. Light data from mid-day light profiles are presented. Surface irradiance refers to measurements in air; bottom indicates measurements in water near 0.5 m depth. Ext. coeff.: extinction coefficient. All data are from 1995. ND: no data

Date	Water temp. (°C)	Salinity (ppt)	Irradiance (µE m⁻² s⁻¹) Surface	Bottom	Ext. coeff. (m⁻¹)
Apr 4	2.8	8	ND	ND	ND
Apr 25	6.0	18	1900	1120	1.4
May 25	21.5	18	1448	917	1.1
Jun 6	17.0	18	1085	289	2.2
Jun 20	20.5	24	1869	564	2.6
Jul 6	25.5	30	1781	856	1.4
Jul 25	22.0	20	682	245	1.7
Aug 15	21.0	31	531	233	1.4
Sep 14	19.0	32	303	153	1.4
Oct 18	13.0	20	1056	322	3.3
Nov 28	6.0	27	323	186	1.6

Immediately following the incubation, four 60 ml biological oxygen demand bottles were filled from each chamber and fixed. Plant material was then collected from the chambers, rinsed with deionized water, and dried to constant weight at 60°C. Dried plant tissue was ground to a fine powder and stored frozen for later organic carbon and nitrogen analysis on a Carlo-Erba NA 5000 CHN analyzer.

Initial chlorophyll a samples collected for each treatment were filtered the day of collection through Whatman GF/F glass fiber filters, preserved with magnesium carbonate solution, and stored frozen for less than 1 mo before being analyzed. Chlorophyll a concentrations were determined using acetone extraction and fluorometric analysis on a Turner design series 10 Fluorometer (Strickland & Parsons 1972). Initial nutrient samples were filtered the day of collection, preserved with chloroform and frozen until the time of analysis. Concentrations of nitrite+nitrate, ammonium and phosphate were determined colorimetrically on a Technicon II autoanalyzer (Strickland & Parsons 1972).

Productivity calculations. Oxygen production and respiration were calculated as mg O_2 g^{-1} dry wt h^{-1} for the macrophytes and as g O_2 m^{-3} h^{-1} for phytoplankton. To facilitate comparison with the literature, oxygen production was converted to carbon production using photosynthetic quotients of 1.2 (Oviatt et al. 1986, Valiela 1995), 1.25 (Murray & Wetzel 1987) and 1.2 (Arnold & Murray 1980, Peckol & Rivers 1996) for phytoplankton, *Ruppia maritima*, and macroalgae, respectively. For the macrophytes, carbon production on an areal basis was determined by combining the incubation results (mg C g^{-1} dry wt h^{-1}) with the biomass results (g dry wt m^{-2}) to yield mg C m^{-2} h^{-1}. *R. maritima* leaf biomass was used in these calculations because only the leaves were incubated. System production for the study area was calculated using the mapping results (m^2 of macrophyte cover/system) and was expressed as mg C system^{-1} h^{-1}. Phytoplankton net production was also calculated on an areal and system-wide basis using depth profiles to determine water volume within the study area. Hourly net production rates were converted to daily rates using Vollenweider's (1965) methods. For each incubation day, day length (sunrise to sunset) was divided into 5 equal periods, with each period having a different percentage of total daily production. Hourly incubation rates were then converted to daily (daylight, not 24 h) rates based on the duration and timing of the incubation. Although developed for phytoplankton, this calculation was applied to macroalgae and *R. maritima* as well since phytoplankton, macroalgae and seagrass have a similar relationship between light and photosynthetic

rates (Valiela 1995). To estimate net annual daylight production, daily rates were then plotted against time and the area under the curve integrated.

RESULTS AND DISCUSSION

Macrophyte biomass

Ruppia maritima and macroalgae exhibited strong seasonal trends in biomass during 1995. Macroalgal biomass increased from zero in April to an early summer peak of 150 g dry wt m^{-2}, followed by a sharp decline during July and August (Fig. 2). In fall, macroalgal biomass maintained a density of about 15 g dry wt m^{-2}. *R. maritima* was similar to macroalgae in seasonality, but it had much lower biomass. *R. maritima* biomass increased from zero in early April to a July maximum of 33 g dry wt m^{-2}, followed by a gradual decline through the remainder of the growing season (Fig. 2).

Biomass of macroalgae and *Ruppia maritima* in Bass Harbor Marsh falls within the range of values reported in other coastal areas (Table 2). While peak *R. maritima* biomass seen in this study is comparable to those observed in Rhode Island (USA) coastal ponds and in Chesapeake Bay (VA, USA), it is an order of magnitude lower than peak values measured in the previous 1991 Bass Harbor Marsh study (Doering et al. 1995). However, in the 1991 study, *R. maritima* was collected further upstream, and differences in hydrology, nutrient dynamics, and other environmental factors may be driving the different biomass levels. Furthermore the 1991 site was free of macroalgae.
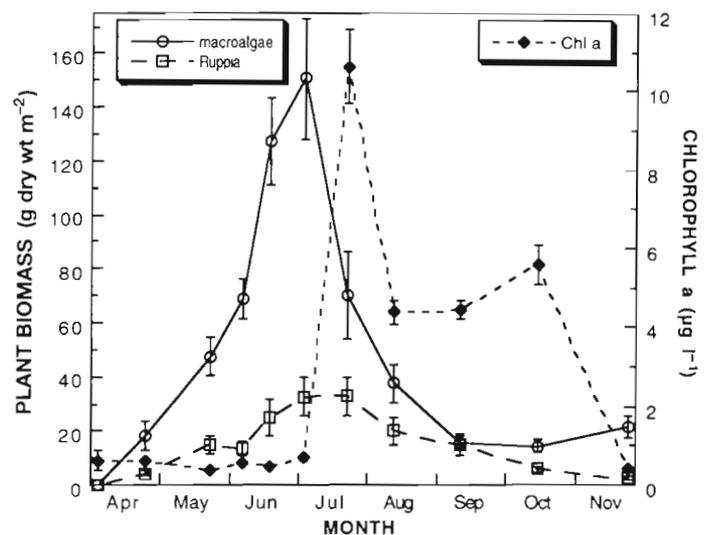

Fig. 2. Macroalgae, *Ruppia maritima*, and phytoplankton (chlorophyll a). Biomass measured over the growing season. Mean ± standard error (n = 20 for macroalgae and *R. maritima*; n = 6 for chlorophyll a) is presented

Table 2. *Ruppia maritima* and green macroalgae. Comparison of biomass values (peak and/or annual means) for shallow coastal sites in New England and the Mid-Atlantic. Different genera of green macroalgae are included, principally *Enteromorpha*, *Cladophora*, and *Ulva*

Site (Source)	Biomass (g dry wt m^{-2})		
	R. maritima Peak	Green macroalgae Peak	Mean
Bass Harbor Marsh, ME (This study)	33	150	57
Bass Harbor Marsh, ME (Doering et al. 1995)	233	171	92
Childs River, MA (Valiela et al. 1992)			220
Quashnet River, MA (Valiela et al. 1992)			85
Sage Lot Pond, MA (Valiela et al. 1992)			36
Ninigret Pond, RI (Thorne-Miller et al. 1983)	21	300	
Green Hill Pond, RI (Thorne-Miller et al. 1983)	10	400	
Mumford Cove, CT (French et al. 1989)[a]		865 63	
Branford River, CT (Welsh 1980)		185	
Chesapeake Bay, VA (Murray & Wetzel 1987)	87		

[a] Mumford Cove biomass values are from before (865) and after (63) the diversion of a sewage treatment outfall pipe

As with *Ruppia maritima*, green macroalgal biomass in this study is comparable to other New England sites (Table 2) except those with high nutrient loading (Childs River, MA, USA, and Mumford Cove, CT, USA). In addition, peak green macroalgal biomass in the nutrient-enriched Venice Lagoon, Italy (1060 g dry wt m^{-2}; Sfriso et al. 1987), and Peel Inlet, Australia (1250 g dry wt m^{-2}; Lavery et al. 1991), greatly exceeded levels found in Bass Harbor Marsh.

Mumford Cove provides an interesting example of the effects of reduced nutrient supply. Nutrient inputs from a waste water treatment facility had encouraged a virtual monoculture of *Ulva lactuca*, covering 74% of this shallow estuary in 1987 (French et al. 1989, Harlin 1995). Following diversion of the sewage outfall pipe in 1987, *U. lactuca* areal coverage sharply declined to 3% with a dramatic drop in biomass (Table 2). The immediate response of *U. lactuca* to nutrient reduction points to the opportunistic and potentially ephemeral behavior of green macroalgae species. Studies in Waquoit Bay showed that *Cladophora vagabunda* growing in a more nutrient-enriched environment (Childs River) actually had higher nitrogen uptake and photosynthetic rates than *C. vagabunda* from a less

enriched site, indicating a physiological adaption to higher nutrient concentrations (Valiela et al. 1992). Because of this opportunistic behavior, green macroalgae can colonize areas receiving excess nutrients and outcompete other primary producers in the system. When Harlin & Thorne-Miller (1981) fertilized seagrass beds in Ninigret Pond (RI), green macroalgal growth dominated the response. Nitrate additions enhanced the growth of *U. lactuca* and *Enteromorpha* spp. but not *Ruppia maritima*. When ammonium was added, *R. maritima* biomass actually declined while *U. lactuca* and *Enteromorpha* spp. biomass increased. These manipulative field experiments further support the hypothesis that green macroalgae species are the competitive dominants in shallow nitrogen-enriched coastal systems.

Phytoplankton biomass

Phytoplankton biomass measured as chlorophyll *a* exhibited a different seasonal trend than the macrophytes (Fig. 2). Chlorophyll levels were very low (<1 µg l^{-1}) until late July when they peaked at 11 µg l^{-1} and then remained relatively high (4 to 5 µg l^{-1}) until late November. The sharp increase in chlorophyll *a* coincided with the decrease in macroalgal biomass, suggesting a competitive dynamic between macroalgae and phytoplankton. This inverse relationship may be a result of macroalgae outcompeting phytoplankton for nutrients. Nutrients remineralized during macroalgal decay may have triggered the phytoplankton bloom. Similarly in the highly eutrophied Venice Lagoon, successive peaks of chlorophyll *a* (>100 µg l^{-1}) coincided with high water column nutrient concentrations resulting from decomposing *Ulva rigida* (Sfriso et al. 1987).

The competitive dominance of macroalgae reported in field studies has also been documented in enclosure experiments. Fong et al. (1993) found that with high levels of nitrate loading, algal mats outcompeted phytoplankton, as evidenced by a 10-fold reduction in chlorophyll *a*. Similarly, Oviatt (1994) reported that macroalgae outcompeted phytoplankton in nitrogen-enriched mesocosms. In other enclosure experiments, the results have been quite different. A study conducted in mesocosms, designed to simulate Rhode Island coastal lagoons, produced a phytoplanton-dominated response to nutrient enrichment (Taylor et al. 1995). A sharp increase in phytoplankton biomass (up to 160 µg l^{-1}) in nitrogen and phosphorus addition tanks reduced light to below the light saturation levels for eelgrass and *Cladophora* sp. Competition for light became a key factor in the decline of both eelgrass and macroalgae under nutrient-enriched conditions.

In Bass Harbor Marsh, peak chlorophyll a levels of 11 µg l^{-1} were well below levels reported in the Rhode Island nutrient addition tanks. Though phytoplankton biomass in the marsh peaked when macroalgal biomass declined, levels still remained fairly low throughout the entire growth season (Fig. 2). When compared with the Waquoit Bay sites (Valiela et al. 1992), mean chlorophyll a levels in Bass Harbor Marsh (2.6 mg m^{-3}) were similar to the mean concentrations found in Quashnet River, MA (5.9 mg m^{-3}) and Sage Lot Pond, MA (3.9 mg m^{-3}) and lower than those in Childs River (25.5 mg m^{-3}), the most nutrient-enriched site. While competition with macroalgae for either nutrients or light may be the controlling factor in Bass Harbor Marsh, flushing rate may also be maintaining a low phytoplankton biomass. In the mesocosm experiment (Taylor et al. 1995), residence time was on the order of 3 wk, while in Bass Harbor Marsh, residence time is much shorter—less than 3 d. In the marsh, phytoplankton may be flushed from the system before bloom conditions can develop.
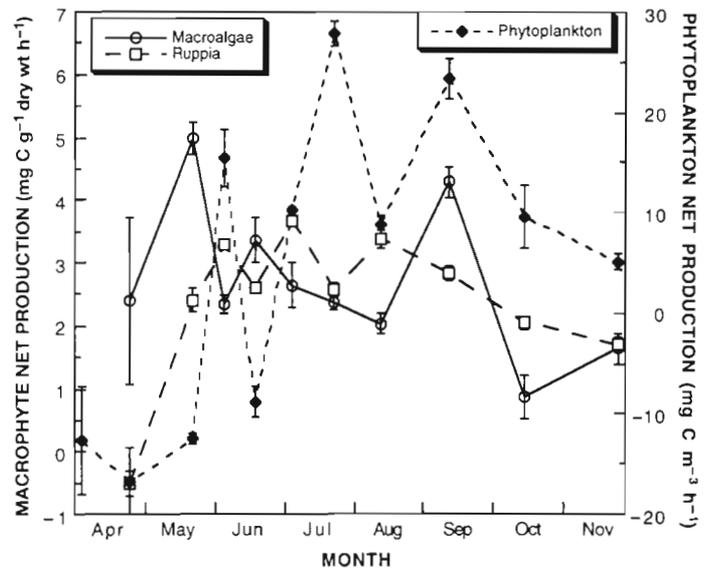

Fig. 3. Macroalgae, Ruppia maritima and phytoplankton. In situ net production rates expressed in carbon, over the growing season. Mean ± standard error (n = 3) is presented

Primary productivity

Instantaneous production and respiration rates varied over the growing season for all 3 primary producers (Table 3). Only Ruppia maritima exhibited a distinct seasonal cycle with consistently higher net productivity during the summer months. Over the growing season, R. maritima net production ranged from near zero in late April to a maximum of 3.7 mg C g^{-1} dry wt h^{-1} in

early July (Fig. 3). Because R. maritima was incubated without macroalgae, these net production rates likely represent maximum values due to lack of shading. Temperature, which ranged from 6.0 to 25.5°C, explained over 60% of the seasonal variability in R. maritima's net production (R^2 = 0.63, p < 0.0001), while temperature and ammonium concentrations combined accounted for over 80% of the variability ($y = 0.66x_1 + 2.88x_2 - 5.76$, R^2 = 0.84, p < 0.0001). The Bass Harbor Marsh net production rates measured for R. maritima were similar to the maximum photosynthetic rates

Table 3. Macroalgae, Ruppia maritima and phytoplankton. Net production and respiration in Bass Harbor Marsh. Standard error is included in parentheses (n = 3). Negative net production values indicate net O$_2$ respiration in the light chambers. Zeros indicate no measurable respiration in the dark chambers. ND: no data. On April 4, macroalgae and R. maritima had not yet appeared in the marsh

Date	Net production			Respiration		
	Macroalgae (mg O$_2$ g^{-1} dry wt h^{-1})	R. maritima (mg O$_2$ g^{-1} dry wt h^{-1})	Phytoplankton (g O$_2$ m^{-3} h^{-1})	Macroalgae (mg O$_2$ g^{-1} dry wt h^{-1})	R. maritima (mg O$_2$ g^{-1} dry wt h^{-1})	Phytoplankton (g O$_2$ m^{-3} h^{-1})
Apr 4	ND	ND	−0.040 (0.017)	ND	ND	0.036
Apr 25	7.69 (4.22)	−1.70 (0.70)	−0.054 (0.011)	2.14 (0.69)	3.65 (0.49)	0.058 (0.006)
May 25	16.00 (0.84)	8.03 (0.61)	−0.040 (0.002)	0.99 (0.06)	4.27 (0.46)	0.046 (0.003)
Jun 6	7.50 (0.49)	10.92 (0.17)	0.049 (0.009)	2.27 (0.07)	1.84 (0.25)	0
Jun 20	10.75 (1.17)	8.69 (0.13)	−0.028 (0.005)	1.66 (0.14)	2.93 (0.08)	0.025 (0.002)
Jul 6	8.44 (1.14)	12.16 (0.13)	0.033 (0.001)	3.75 (0.06)	2.76 (0.08)	0
Jul 25	7.61 (0.40)	8.56 (0.40)	0.089 (0.004)	1.34 (0.07)	1.76 (0.11)	0
Aug 15	6.48 (0.50)	11.23 (0.46)	0.028 (0.003)	2.63 (0.35)	1.40 (0.21)	0
Sep 14	13.74 (0.78)	9.45 (0.40)	0.075 (0.006)	2.86 (0.04)	0.84 (0.18)	0
Oct 18	2.82 (1.11)	6.81 (0.31)	0.031 (0.010)	3.33 (0.23)	2.62 (0.44)	0.013 (0.001)
Nov 28	5.25 (0.77)	5.71 (0.32)	0.016 (0.003)	0.85 (0.09)	0	0

(P_{max}: 0.96 to 3.85 mg C g^{-1} dry wt h^{-1}) calculated for *R. maritima* in Chesapeake Bay over a temperature range of 1 to 28°C (Wetzel & Penhale 1983). In that study, *R. maritima* production also correlated with temperature.

Macroalgal net production rates were more variable over the growth season and not easily explained by the measured parameters (light, temperature, salinity, % tissue N, nitrate, nitrite, ammonium, and phosphate). Rates ranged from 0.88 to 5.00 mg C g^{-1} dry wt h^{-1} (Fig. 3). The maximum rate was measured at an ambient water temperature of 21.5°C and is lower than the peak net photosynthetic rate (7.3 mg C g^{-1} dry wt h^{-1} at 21°C) determined for *Enteromorpha intestinalis* in laboratory experiments (Arnold & Murray 1980). The only measured parameter which explained, albeit weakly, some of the variability in macroalgal net production was percent tissue nitrogen ($y = -1.68x_1 + 12.03$, $R^2 = 0.23$, $p = 0.004$). The negative regression coefficient indicates that higher rates of production were measured at times of lower tissue nitrogen content. This may be due to the greater utilization of stored nitrogen at times of higher production. Several studies with green macroalgae have found low tissue nitrogen during summer, suggesting that higher growth depleted internal nitrogen stores (Hanisak 1979, Birch et al. 1981).

Aside from late April when *Ruppia maritima* net production was near zero, both *R. maritima* and macroalgae had measurable net daytime production throughout the growth season. Phytoplankton showed no measurable net daytime production in April, May or late June (Table 3). At other times, net production rates varied from 0.016 to 0.089 g O_2 m^{-3} h^{-1} (5.0 to 27.8 mg C m^{-3} h^{-1}; Fig. 3). As with chlorophyll, these rates are comparable to phytoplankton production measured in Waquoit Bay's Sage Lot Pond (10 to 50 mg C m^{-3} h^{-1}), but not to rates found in the more nutrient-enriched Childs River (100 to 200 mg C m^{-3} h^{-1}; Valiela et al. 1992). In Bass Harbor Marsh, maximum phytoplankton net production occurred in late July, when chlorophyll *a* peaked in the system (Fig. 2). The relationship between phytoplankton net production and chlorophyll *a* was significant over the course of the study ($R^2 = 0.45$, $p < 0.0001$). As described earlier, chlorophyll *a* concentrations in Bass Harbor Marsh were low (mean = 2.6 µg l^{-1}). It is not surprising that net phytoplankton production was also low or at times zero in the marsh because of competition with macroalgae and a high flushing rate.

Conversion of net production rates to an areal basis allows for comparison between the different primary producers and their relative contribution to system productivity. Macroalgal net production clearly dominated, with peak summer rates exceeding 400 mg C m^{-2} h^{-1} (Fig. 4). *Ruppia maritima* peak net production
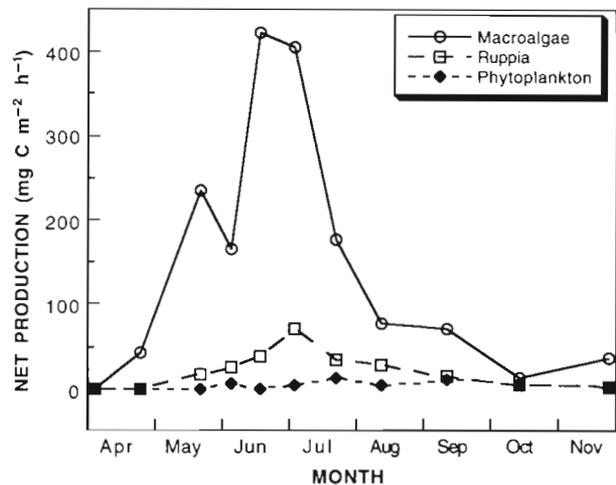

Fig. 4. Macroalgae, *Ruppia maritima* and phytoplankton. Net production calculated on an areal (per m^2) basis over the growing season

was 70 mg C m^{-2} h^{-1}, while phytoplankton's was only 12 mg C m^{-2} h^{-1}. When converted from a m^2 to a system-wide basis for the 20 ha lower basin, macroalgal net production (0 to 61 kg C $system^{-1}$ h^{-1}) still dominated that of *R. maritima* (0 to 3.9 kg C $system^{-1}$ h^{-1}) and phytoplankton (0 to 2.7 kg C $system^{-1}$ h^{-1}).

Macroalgal annual net daylight production was 305 g C m^{-2} yr^{-1}, greatly exceeding annual rates for both *Ruppia maritima* (46 g C m^{-2} yr^{-1}) and phytoplankton (11 g C m^{-2} yr^{-1}). Macroalgal production represented 84% of the total net production of the water column autotrophs, with *R. maritima* contributing 13% and phytoplankton only 3%. In Waquoit Bay, annual macroalgal production varied by a factor of 2.5 between Sage Lot Pond (443 g C m^{-2}) and the nutrient-enriched Childs River (1094 g C m^{-2}; Peckol & Rivers 1996). Annual net production in Bass Harbor Marsh was similar to that in Sage Lot Pond. However, in Sage Lot Pond (Valiela et al. 1992), the seagrass *Zostera marina* appeared to be a co-dominant while in Bass Harbor Marsh, macroalgae clearly dominated primary production.

In the Rhode Island salt ponds, shallow macrophyte-based communities similar to Bass Harbor Marsh, annual production rates were comparable, though the relative contributions of the plant communities differed. Annual primary production averaged 300 g C m^{-2} yr^{-1}, with seagrasses contributing over 50%, macroalgae and benthic microalgae 40%, and phytoplankton only 10% (Thorne-Miller et al. 1983, Lee & Olsen 1985). The salt ponds did not exhibit the macroalgal dominance evident in Bass Harbor Marsh and in areas such as Childs River, Waquoit Bay. Instead, seagrasses were the dominant autotrophs in the system. However, as indicated by the nutrient-enrichment experiment

conducted by Harlin & Thorne-Miller (1981), increases in nutrient loading could change the dominance patterns in salt pond communities by encouraging the proliferation of green macroalgae.

Competitive interactions

While low phytoplankton production is typical of a number of shallow coastal systems (Lee & Olsen 1985, Murray & Wetzel 1987, Valiela et al. 1992, Bass Harbor Marsh, this study) the relatively low *Ruppia maritima* production in Bass Harbor Marsh is more intriguing. What is driving macroalgal dominance over *R. maritima* in the lower basin of Bass Harbor Marsh? Because light and nutrients are both critical to photosynthesis, an examination of how these resources are partitioned provides insight into the competitive dynamics of water column production in the estuary.

Patterns in tissue nitrogen content differed between macroalgae and *Ruppia maritima* (Fig. 5). Over the course of the season, macroalgal %N varied from 0.5 to 4.1% while *R. maritima* %N was more constant, ranging from 2.8 to 4.9%. The critical level for tissue nitrogen, defined as the point where growth becomes limited, is 2.0% for macroalgae (Hanisak 1979, O'Brien & Wheeler 1987), while *R. maritima*'s critical %N is 2.5 to 3.0% (Thursby 1984b). For much of the summer, macroalgal growth was nitrogen limited, with % tissue N lower than the critical level (Fig. 5). *R. maritima* tissue N was never limiting. Macroalgae can only utilize nutrients dissolved in the water column, as supported by a similar seasonal trend of dissolved inorganic nitrogen and tissue N (Fig. 5). In contrast, *R. maritima* has access to both nitrogen and phosphorus in the sediments, and the predominance of root-to-shoot nutrient translocation has been demonstrated (Thursby & Harlin 1984). In the lower basin, phosphate is consistently low ($<0.5~\mu$mol l^{-1}) in the water column, while dissolved inorganic nitrogen is low during summer and early fall ($<2.0~\mu$mol l^{-1}). Therefore the sediments must constitute an important nutrient reservoir for *R. maritima*, particularly as it must compete with opportunist green macroalgae, which are capable of rapid nutrient uptake and growth rates (Fong et al. 1994).

Because of *Ruppia maritima*'s higher tissue nitrogen content and access to sediment reservoirs, competition for nutrients is likely not the factor limiting its growth. Instead, light is probably the critical factor. In nutrient-enriched natural and experimental systems
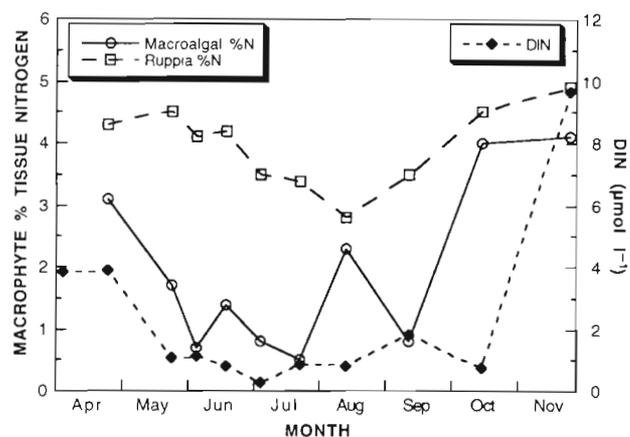

Fig. 5. Macroalgae and *Ruppia maritima*. Macrophyte percent tissue nitrogen and water column dissolved inorganic nitrogen (DIN) presented over the growth season

where seagrasses have declined, nutrients triggered blooms of either macroalgae (Harlin & Thorne-Miller 1981, Valiela et al. 1992) or phytoplankton (Twilley et al. 1985, Taylor et al. 1995), with consequent seagrass shading. The photosynthetic saturation intensities for *R. maritima* are around 250 to 500 μE m^{-2} s^{-1} (Wetzel & Penhale 1983). In Bass Harbor Marsh, light levels at the bottom were generally at or above these intensities in areas free of macroalgae (Table 1). Therefore, water column light attenuation did not appear to limit *R. mar-*
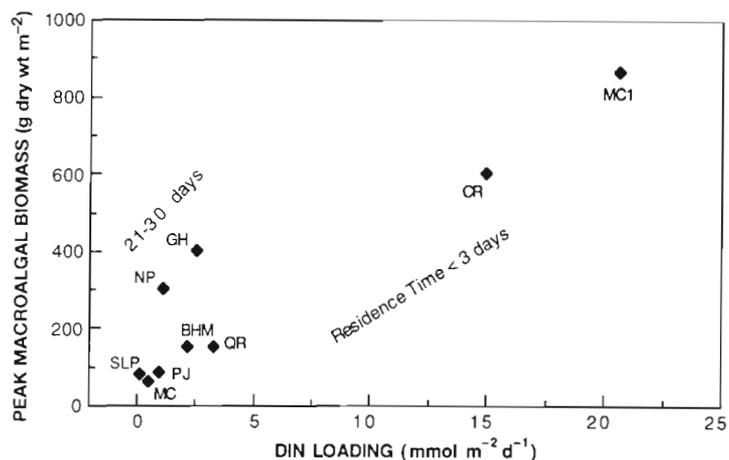

Fig. 6. Relationship between peak green macroalgal biomass and dissolved inorganic nitrogen (DIN) loading for shallow estuarine sites in New England with short and long residence times. BHM: Bass Harbor Marsh (this study). CR: Childs River, MA; QR: Quashnet River, MA; SLP: Sage Lot Pond, MA (D'Avanzo et al. 1996, Hersh 1996). GH: Green Hill Pond, RI; NP: Ninigret Pond, RI; PJ: Pt. Judith Pond, RI (Isaji & Spaulding 1981, Thorne-Miller et al. 1983, Lee & Olsen 1985). MC: Mumford Cove, CT, after diversion of sewage outfall pipe; MC1: Mumford Cove, CT, before diversion of sewage outfall pipe (French et al. 1989). DIN loading for MC1 was calculated by multiplying sewage-based total nitrogen loading by 0.85 (Nixon 1992)

itima survival. However, the dominant macroalgal biomass shades *R. maritima* throughout the growth season. In this way, macroalgae may be outcompeting *R. maritima* for light and thereby dominating primary production in the lower basin.

CONCLUSIONS

Small shallow systems are often the first to be affected by nutrient enrichment (Valiela et al. 1992). In various sites around New England, there appears to be a relationship between nitrogen loading and green macroalgal biomass in shallow embayments (Fig. 6). Sites with low nitrogen inputs and rapid flushing, such as Bass Harbor Marsh, have low algal biomass relative to estuarine sites with high loading (Childs River, Mumford Cove). The concept that residence time influences the response of estuaries to nutrient loading has been previously discussed (D'Avanzo et al. 1996). Although Ninigret and Green Hill Ponds (RI) have low nitrogen loading rates, high biomass in those sites may be a result of long residence time. Poor tidal flushing may limit the dilution of nutrients brought in by freshwater sources.

Although peak green macroalgal biomass in Bass Harbor Marsh is relatively low, the estuary is displaying productivity patterns characteristic of eutrophied sites. Opportunistic green macroalgae dominated primary production in the lower marsh basin, with net areal production rates far exceeding those of either *Ruppia maritima* or phytoplankton. Anthropogenic nitrogen may have promoted macroalgal growth, negatively impacting other autotrophs in the lower basin. Thus, Bass Harbor Marsh represents a shallow estuarine system that may be responding to relatively low levels of nutrient enrichment.

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