Macrophyte abundance in Waquoit Bay:

Effects of land-derived nitrogen loads on seasonal and multi-year biomass patterns

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Abstract

Anthropogenic inputs of nutrients to coastal waters have rapidly restructured coastal ecosystems. To examine the response of macrophyte communities to land-derived nitrogen loading, we measured macrophyte biomass monthly for six years in three estuaries subject to different nitrogen loads owing to different land uses on the watersheds. The set of estuaries sampled had nitrogen loads over the broad range of 12 to 601 kg N ha^{-1} y^{-1}. Macrophyte biomass increased as nitrogen loads increased, but the response of individual taxa varied. Specifically, biomass of *Cladophora vagabunda* and *Gracilaria tikvahiae* increased significantly as nitrogen loads increased. The biomass of other macroalgal taxa tended to decrease with increasing load, and the relative proportion of these taxa to total macrophyte biomass also decreased. The seagrass, *Zostera marina*, disappeared from the higher loaded estuaries, but remained abundant in the estuary with the lowest load. Seasonal changes in macroalgal standing stock were also affected by nitrogen load, with larger fluctuations in biomass across the year and higher minimum biomass of macroalgae in the higher loaded estuaries. There were no significant changes in macrophyte biomass over the six years of this study, but there was a slight trend of increasing macroalgal biomass in the latter years. Macroalgal biomass was not related to irradiance or temperature, but *Z. marina* biomass was highest during the summer months when light and temperatures peak. Irradiance might, however, be a secondary limiting factor controlling macroalgal biomass in the higher loaded estuaries by restricting the depth of the macroalgal canopy. The relationship between the bloom-forming macroalgal species, *C. vagabunda* and *G. tikvahiae*, and nitrogen loads suggested a strong connection between development on watersheds and macroalgal blooms and loss of seagrasses. The influence of watershed land uses largely

overwhelmed seasonal and inter-annual differences in standing stock of macrophytes in these

temperate estuaries.

Keywords: eutrophication, macroalgae, bloom, nitrogen, estuarine, *Gracilaria, Cladophora*

Introduction

Recent human activities in coastal zones have led to rapid eutrophication of estuarine

systems, largely as a result of increased nitrogen inputs (Nixon 1995; Duarte 1995). Land-

derived nutrient loading to coastal waters often results in higher nutrient concentrations in

estuaries (Nixon 1995; Valiela et al. 1997), which stimulate primary production (Nixon 1992;

Howarth 1988). This eutrophication of estuarine and coastal waters leads to increases in

phytoplankton concentrations (Tomasky et al. 1999), and to changes in biomass and species

composition of the macroalgal canopies (Lavery et al. 1991; Valiela et al. 1997; Rafaelli et al.

1998; Hauxwell et al. 2001). Increased primary production owing to increased nutrient supply

can control higher trophic levels in both benthic and pelagic food webs (Rafaelli et al. 1998;

Ware and Thompson 2005). Macroalgal blooms, in particular, have had further consequences,

often shading and replacing seagrass meadows (McGlathery 2001; Hauxwell et al. 2001), as well

as fostering of hypoxic conditions (D'Avanzo and Kremer 1994; Diaz 2001) that decrease

abundance of invertebrates (Hauxwell et al. 1998; Oesterling and Pihl 2001) and fish (Baden et

al. 1990; Deegan et al. 2002).

Macrophyte biomass may be controlled by temperature, light availability, nutrients, and

grazers (Lapointe and Duke 1984; Geertz-Hansen et al. 1993; Duarte 1995; Peckol and Rivers

1995; Hauxwell et al. 1998). Opportunistic species of macroalgae, such as *Cladophora*

vagabunda and *Gracilaria tikvahiae*, are better able to take advantage of light and nutrients than other non-blooming species (Lapointe and O'Connell 1989; Peckol and Rivers 1995; Borum and Sand-Jensen 1996; Hauxwell et al. 2001). *Ulva* spp. are also opportunistic macroalgae that are proliferating in coastal waters worldwide (Sfriso et al. 1989; Campbell 2001; Fong et al. 1996). Efficient uptake, assimilation, and storage of nitrogen of bloom-forming species allows for the rapid growth and high biomass accumulation (Peckol and Rivers 1995; Pedersen and Borum 1996, 1997; Teichberg et al. 2007), which may further increase competition for space (Peckol and Rivers 1995). In temperate estuaries, controlling variables such as nutrients and light vary across seasons and among years, and might create seasonal and multi-year changes in standing crops of coastal subtidal macrophytes.

In this paper we assess whether differences in land-derived nitrogen loading rates lead to differences in macrophyte community structure and in seasonal and multi-year patterns of macroalgal biomass. To evaluate the response of macrophytes to nitrogen supply, we sampled macroalgal biomass in a set of subestuaries (Childs River, Quashnet River, and Sage Lot Pond) of the Waquoit Bay estuarine system that are subject to different land-derived nitrogen loads imparted from different land uses on their watersheds (Bowen and Valiela 2001). The Childs River watershed is suburbanized, and delivers 601 kg N ha^{-1} y^{-1} to the estuary. The Quashnet River is subject to an intermediate nitrogen load from its watershed, 403 kg N ha^{-1} y^{-1}. The watershed of Sage Lot Pond comprises mainly a forested state park, and delivers only 12 kg N ha^{-1} y^{-1} to the estuary. This range of nitrogen loads encompasses approximately 75% of the range of reported values to estuaries worldwide (Nixon 1992). Although there were differences among the Waquoit Bay subestuaries, previous publications showed that the differences in nitrogen loading received from land overwhelm the influence of other potential controls on water

chemistry, primary production, and trophic interactions (Valiela et al. 1997; McClelland et al. 1997; Hauxwell et al. 1998; Thompson and Valiela 1999).

This study of macrophyte biomass in Waquoit Bay provides important quantitative data on macrophyte community changes in response to increasing nitrogen inputs from land-derived sources.

Methods

To evaluate the response of macrophyte communities to nitrogen supply, we sampled macrophytes in ten stations in each of three subestuaries (Childs River, Quashnet River, and Sage Lot Pond) of the Waquoit Bay estuarine system that are subject to the different land-derived nitrogen loads imparted from their watersheds (Fig. 1; Bowen and Valiela 2001). Stations were distributed to representatively include shallow as well as deeper portions of the estuaries (0.5 – 3 m), as well as lower to higher salinities (10 – 32 ppt). The number of sample stations was determined from an earlier study examining the stability of the variance across different number of replicate stations (Hersh 1996). Hersh (1996) found that mean macrophyte biomass of ten sample stations adequately represented biomass within each estuary when data were pooled over longer time intervals than days, for example seasonally, annually, or inter-annually. At each station, a random sample was collected using a 15 cm x 15 cm benthic grab. The collected material was rinsed through a 1 mm sieve to remove mud. Samples were later sorted to genus or species, dried at $60^{\circ}C$ for 48 hours, and weighed for dry weight (d.w.).

To measure seasonal and inter-annual changes in biomass of each species of macroalgae in the three subestuaries of Waquoit Bay, macrophyte samples were collected at each station approximately once a month from June 1994 through June 2000.

To explore whether changes in irradiance and temperature were related to the seasonal or inter-annual patterns of macroalgal biomass, we examined the relative effects of nutrient supply, temperature, and light availability on macroalgal biomass patterns. We obtained surface irradiance and air temperature data for our sampling period from records kept by Robert Payne of the Woods Hole Oceanographic Institution (http://www.whoi.edu/climate). To relate the irradiance and temperature data to the crop of macroalgae, for each date of macroalgal sampling, we averaged irradiance and temperature across four weeks prior to each macroalgal sampling date.

Results and discussion

Macrophyte taxa and biomass—The major macrophyte species in the estuaries of Waquoit Bay, Cape Cod, MA, during 1994 - 2000, were the chlorophyte, *Cladophora vagabunda*; the rhodophyte, *Gracilaria tikvahiae*; and the seagrass, *Zostera marina* (Table 1). *C. vagabunda* contributed 70, 55, and 21 %, *G. tikvahiae*; made up 25, 32, and 19 %, and *Z. marina* contributed 0, 0, and 47 % of total macrophyte biomass in Childs River, Quashnet River, and Sage Lot Pond, respectively. A dozen additional algal taxa contributed smaller proportions, 5, 12, and 13 % of biomass in Childs, Quashnet, and Sage Lot Pond, respectively; we will refer to these taxa as "other algae" for brevity.

Macrophyte biomass differed among estuaries, within seasons, and among years. Within estuaries, there was considerable variation in macroalgal biomass among stations, shown by the vertical error bars for each month (Fig. 2). Pilot work on a time series analysis of the biomass data of Fig. 2 did not reveal additional information to aid in interpretation of the differences and variation in the dataset, and its results are not shown here. Instead, below we examine the

response of macrophyte communities to nitrogen loads, and identify seasonal and inter-annual effects that may arise from differences in irradiance and temperature.

Nitrogen loads— Total macroalgal biomass increased with increasing nitrogen load, more than tripling from the low- to high-loaded estuaries (Table 1). Total macroalgal biomass had the highest maximum biomass in the high nitrogen load estuary (approximately 1847, 1708, and 429 g d.w. m^{-2}, for Childs, Quashnet, and Sage Lot, respectively). The two dominant macroalgae (*C. vagabunda* and *G. tikvahiae*) showed evident across-estuary effects, with greater biomass in the higher-loaded estuaries (Table 1). *C. vagabunda* was the most abundant macrophyte in the two higher-loaded estuaries, while *Z. marina* dominated the low-loaded estuary (Table 1). The response of *C. vagabunda* to nitrogen load was an approximately 6-fold increase in biomass from low to high load, while *G. tikvahiae* biomass more than doubled. "Other algae" were a small proportion of the macroalgae in the higher-loaded estuaries, but they represented nearly one-third of the macroalgal biomass in the low load estuary. The responses of the individual species that we pooled into "other algae" were variable: *Ulva lactuca* increased with increasing nitrogen load, but *Polysiphonia* spp. and *Agardhiella subulata* decreased (Table 1). The biomasses of the remaining taxa were too low to ascertain a response to load. While the relative biomass of different taxa of macroalgae varied among estuaries, the number of macrophyte taxa did not (Table 1). The species which make up the "other algae" constitute most of the taxa in each estuary (Table 1). This finding is contrary to theory that nutrient enrichment reduces species richness (Worm et al. 2002; Herbert et al. 2004; Harpole and Tilman 2007).

Z. marina was present only in Sage Lot Pond, the low load estuary (Table 1). Although we have found *Z. marina* seed coats buried in recent sediments of the other estuaries (Safran et al. 1998), eelgrass has functionally disappeared from the heavily loaded estuaries within the last

20 years (Short and Burdick 1996; Valiela et al. 1997; Hauxwell et al. 2001). Shading of the

seagrasses by other primary producers is almost certainly responsible for the elimination of

eelgrass beds in Waquoit Bay (Hauxwell et al. 2001, 2003). Macroalgal canopies, stimulated by

land-derived nitrogen, have replaced seagrasses in the higher loaded estuaries. Other causes of

eelgrass declines include high ammonium concentrations remineralized from senescent

macroalgal canopies which may be toxic to new shoots (van Katwijk et al. 1997), low oxygen

concentrations within the macroalgal canopy can lower oxygen concentration around the

seagrass meristem (Greve et al. 2003), and lower oxygen concentrations can lead to higher

concentrations of hydrogen sulfide which may inhibit photosynthesis (Goodman et al. 1995).

To assess the effect of nitrogen load on macroalgal biomass, we plotted biomass versus

estimates of nitrogen loads for the three estuaries as calculated by Bowen and Valiela (2001).

Biomass of total macroalgae, *C. vagabunda*, and *G. tikvahiae* significantly increased as nitrogen

loads increased (Table 1, Fig. 3). "Other algae" biomass did not respond to increases in load

(Fig. 3). This suggests a connection between urban development of coastal landscapes and the

appearance of macroalgal blooms. This coupling is mediated by the transport of nitrogen from

land to receiving estuaries, as has been shown by mass balance and stable isotopic evidence for

Waquoit Bay (Valiela et al. 1997a; 2004; McClelland and Valiela 1998; Martinetto et al. 2006).

In Waquoit Bay, increases in nitrogen loads have taken place as watersheds have become

urbanized over time (Bowen and Valiela 2001). If we assume that the Waquoit estuaries

constitute a reasonable space-for-time substitution (Pickett 1989), the results of Fig. 3 can be

interpreted to mean that macroalgal biomass increases as nitrogen loads increase across decades.

Cladophora spp. and *Gracilaria* spp. are common macroalgae that have been shown to

proliferate in response to increased anthropogenic nutrient inputs to coastal waters worldwide

(Baden et al. 1990; Lavery et al. 1991; Barile 2004). It is therefore not surprising to find these taxa blooming in sites where nutrient loads are high, such as Childs and Quashnet rivers. The lack of response by other species may be a result of competitive interactions that prevent blooms of the less competitively dominant taxa (Pearse and Hines 1979). *Ulva* spp. are also fast-growing macroalgae that are proliferating in coastal waters worldwide (Sfriso et al. 1989, 1993; Campbell 2001; Fong et al. 1996). These algae have been shown to use rapid uptake and assimilation of nutrients, and high growth rates to efficiently take advantage of available nutrients in the water column (Bjornsater and Wheeler 1990; Pedersen and Borum 1996, 1997; Teichberg 2007). In high nutrient environments, interactions among species lead to domination by a few highly competitive taxa that are able to proliferate to form macroalgal blooms.

Seasonal and inter-annual patterns— To examine seasonal variation in each estuary, we averaged mean biomass for each month across all six years of sampling (Fig. 4). The seasonal pattern was similar in the three estuaries. Total macroalgal biomass peaked during May-June (Fig. 4, line graphs in left panels), and was lowest in the fall. The highest mean monthly biomass over a six year period for total macroalgae was measured in the high nitrogen load estuary (230 g d.w. m^{-2} for Childs), with lower abundances in the other estuaries (approximately 130 and 80 g d.w. m^{-2}, for Quashnet, and Sage Lot, respectively).

Nitrogen loads influenced several other aspects of the seasonal cycle (Fig. 4). The greater the nitrogen load, the larger the difference between maximum and minimum monthly mean total biomass (approximately 150, 80, and 40 g d.w. m^{-2}, respectively, for Childs, Quashnet, and Sage Lot). Although larger biomass ranges were found in estuaries with higher nitrogen loads, the relative change (coefficient of variation) among the monthly means for the three estuaries did not differ for any macroalgal group (Table 2). The minimum mean total biomass was also higher

where nitrogen loads were highest (approximately 80, 50, and 20 g d.w. m^{-2}, respectively, for Childs, Quashnet, and Sage Lot; Fig. 4).

These contrasts suggest that higher land-derived nitrogen loads, not only lead to more biomass of algae, but also to larger seasonal differences, and a consistently larger crop of macroalgal biomass during the seasonal low. Since nutrient storage in mean annual macroalgal biomass can store 25% - 250 % of the annual inputs (Hersh 1996), the larger fluctuations and seasonal lows have implications for the concentration of nutrients in the water column, as well as effects on other ecosystem components (Valiela et al. 1997).

The seasonal pattern of total macroalgal biomass in Waquoit Bay was, in general, less marked than that found elsewhere (Fig. 4). For example, mean macrophyte biomass in Bass Harbor Marsh, ME, USA, varied 0-150 g d.w. m^{-2} within a year (Kinney and Roman 1998), and biomass of *Enteromorpha* spp. in Coos Bay, OR, USA, varied 0-300 g d.w. m^{-2} within a year (Pregnall and Rudy 1985). Mean macroalgal biomass in Waquoit Bay showed a persistent year-round macroalgal canopy in each estuary (Fig. 4). The nitrogen stored in macroalgal biomass is a substantial portion of annual inputs of land-derived nitrogen entering the water column (Hersh 1996, Valiela et al. 1997). Since biomass does not disappear at any time of year, the macroalgae may be buffering nitrogen concentrations in the water column during all seasons (Hauxwell et al. 2001). The buffering effect may be largest in early summer when total macroalgal biomass is highest (Fig. 4), and nutrient concentrations in the water column are low (Holmes 2008).

The seasonal patterns of biomass for each macrophyte taxon were less distinct than for total macroalgal biomass. *C. vagabunda* did not show a seasonal pattern in any estuary, and had similar biomass across the year with only a slight decrease in winter (Fig. 4, left panel). *G. tikvahiae* and the "other algae" peaked in late spring in the high nitrogen load estuary, and

showed two peaks, late spring and late fall, in the low load estuary (Fig. 4, middle, right panel).

The second peak of macroalgal biomass in fall may be due to increased regeneration of nutrients

from sediments to the water column that may be occurring in late summer in these estuaries

(Valiela et al. 2004). In Sage Lot Pond, the estuary receiving the lowest nitrogen load, *Z. marina*

was present and exhibited a clear seasonal peak in summer (Fig. 4, bottom). The peak of eelgrass

biomass coincided with the lowest biomass of total macroalgae in Sage Lot Pond.

Seasonal patterns in mean monthly biomass described above were repeated in each of the

six years from 1994 - 2000 (Fig. 2). There was a clear lack of seasonality in *C. vagabunda*

biomass across all years. The patterns in Fig. 4 for *G. tikvahiae* and "other algae," described

above, can be seen in all years of this study (Fig. 2). Two major inter-annual patterns emerged,

an increase in *C. vagabunda* biomass in Quashnet River and an increase in *G. tikvahiae* biomass

in Childs River over the years of this study.

Effects of irradiance and temperature— Total macroalgal and *Z. marina* biomass were

affected by seasonal and inter-annual effects, possibly related to changes in irradiance and

temperature across the year and among years.

To see if the seasonal changes in biomass in Fig. 4 were to some degree associated with

changes in light and temperature, we plotted biomass versus surface irradiance data and local air

temperature, averaged for 4 weeks before the macrophyte sampling dates, for all the multi-year

data (Fig. 5). Despite the seasonal pattern in total macroalgal biomass in all three estuaries (Fig.

4), there was no apparent relationship between biomass of macroalgae and irradiance or

temperature (Fig. 5, top panels). Biomass of each algal taxa were also not related to temperature

or light, so data are not shown here [Appendix 3, Stieve (2001)].

Z. marina, in contrast to macroalgae, showed increased biomass with higher irradiances

and temperatures (Fig. 5, bottom panels). We cannot separate the effect of irradiance or temperature on *Z. marina* because the two variables were correlated ($r = 0.91$), as they are in most temperate climates. Biomass of *Z. marina* was highest during summer, following the seasonal pattern typical of many plants in temperate climates, taking advantage of summer's high irradiances and temperatures.

In the case of macroalgae, the role of irradiation as a limiting factor might be complicated. Perhaps self-shading plays a role in restricting the canopy height of the macroalgal mats, and hence may limit biomass accumulation. As much as 99% of surface irradiance can be lost within a macroalgal canopy only 9 cm thick (Hauxwell et al. 2001). Peckol and Rivers (1996) found that net production in *C. vagabunda* mats reached zero only 2 cm below the surface of the canopy, and growth of fronds below 2 cm depth may be photosynthetically restricted. In thick canopies of drift macroalgae with no holdfasts, the survival of fronds depends on the rate at which the canopy is turned over and exposed to ambient light by turbulent water movement, which may occur in Waquoit Bay approximately every 2 weeks (P. Peckol, unpublished data). Macroalgal fronds are able to survive that long in darkness (Peckol and Rivers 1996). Thus, macroalgal biomass may be controlled by the turbulence of the water column that exposes buried portions of the canopy to light rather than by total irradiance entering the water column or temperature.

To explore these possible relationships, we calculated the thickness of *C. vagabunda* mats in our sample sites by using the relationship of macroalgal biomass and canopy thickness from Peckol and Rivers (1996). We used annual peaks in biomass to calculate how thick the mat became each year. Every year of this study, peak canopy thickness of *C. vagabunda* in Childs River was greater than the 2 cm (Fig. 6), the thickness of a photosynthetically active mat (Peckol

and Rivers 1996). In Quashnet River the canopy was less than 2 cm at the start of the study and increased over the six years, approaching, but not exceeding, Childs River values. In Sage Lot Pond, the estuary subject to the lowest nitrogen load and with the lowest macroalgal biomass, peak canopy height remained below 2 cm during all years. If the macroalgal canopies were not nutrient-limited and allowed to proliferate, according to Peckol and Rivers (1996) the macroalgae would be light-limited under a 2 cm canopy. Since canopies in Waquoit Bay were greater than 2 cm, the macroalgae are overcoming light limitation by turning over in turbulent water, associated with wind, tides, or anthropogenic activities. The degree to which water movement can turn over a macroalgal mat may impose a ceiling on the proliferation of macroalgal canopies: there may be sufficient nutrients to go on growing, but only the upper layers may photosynthesize sufficiently.

If self-shading under high nitrogen loads is an important control on macroalgal canopy height, we would expect that light limitation in other estuaries would create similar constraints on macroalgal biomass. Peak summer biomass in Waquoit estuaries (80-230 g d.w. m^{-2}; Fig. 4) were within the range of reported values in estuaries dominated by *Cladophora* sp. and *Gracilaria* sp. (Conover 1958; Bach and Josselyn 1979; McComb et al. 1979; Thorne-Miller et al. 1983; Thybo-Christiansen et al. 1993). This may be evidence that such ceilings as we posit do exist. For other species of macroalgae, with higher photosynthetic affinities, these ceilings may differ and photosynthesis might be possible deeper within the macroalgal canopy. Estuaries dominated by *Ulva*, *Enteromorpha,* and *Chaetomorpha* spp. may attain much larger biomasses of 2400-3600 g d.w. m^{-2} (Sfriso et al. 1989; Sfriso and Facca 2007; wet weight converted by 12% dry:wet weight in Morand and Briand 1996).

This analysis of macroalgal biomass and canopy height in the three Waquoit Bay

estuaries, as well as data presented in Peckol and Rivers (1996), suggest that peak macroalgal accumulation may be spurred by increased nitrogen supply, but ultimately the canopy is limited by light availability. Since macroalgal biomass in Waquoit Bay falls within the range of that of many estuaries worldwide, it seems that similar processes may be occurring elsewhere. As urbanization of the Waquoit Bay watersheds progresses, we would therefore anticipate that macroalgal biomass would increase gradually and then plateau as self-shading restricts the rate of photosynthesis deeper in the macroalgal canpopy. In estuaries where biomass is orders of magnitudes higher than in Waquoit, it may be that canopy turnover (in the case of drift algae) is more frequent, or the specific macroalgae involved may have more efficient photosynthetic abilities.

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Figure Legends

Fig. 1. Map of Waquoit Bay, MA and the three subestuaries with different land-derived nitrogen loads sampled during this study (bottom): Childs River, Quashnet River, and Sage Lot Pond with nitrogen loads of 601 kg N ha^{-1} y^{-1}, 403 kg N ha^{-1} y^{-1}, 12 kg N ha^{-1} y^{-1}, respectively. The sampling stations are indicated by the ten points in each estuary.

Fig. 2. Mean ± se of monthly macrophyte biomass across twelve month intervals (June-May) from June 1994 through June 2000 for the different macrophyte groups in each of the three subestuaries receiving different land-derived nitrogen loads, Childs River, Quashnet River, and Sage Lot Pond with nitrogen loads of 601 kg N ha^{-1} y^{-1}, 403 kg N ha^{-1} y^{-1}, 12 kg N ha^{-1} y^{-1}, respectively.

Fig. 3. Response of macroalgae to increasing N load. Macroalgal biomass of different macroalgal groups for each of the six years of study versus nitrogen load for each of the three estuaries, Childs River, Quashnet River, and Sage Lot Pond with nitrogen loads of 601 kg N ha^{-1} y^{-1}, 403 kg N ha^{-1} y^{-1}, 12 kg N ha^{-1} y^{-1}, respectively.

Fig. 4. Seasonal variation in macrophyte biomass (mean ± s.e.) for total macroalgae (line, left panel), *Cladophora vagabunda* (bars, left panel), *Gracilaria tikvahiae* (middle panel), and "other algae" (right panel) in the three Waquoit Bay estuaries. Data for Sage Lot macrophytes, total algae and *Zostera marina* biomass are shown in bottom panel. Data for each month was averaged across the six years of sampling; and the standard error for each month of the year was calculated across the six years.

Fig. 5. Macrophyte biomass versus surface irradiance and local air temperature averaged over the four week interval prior to sampling for each of the three Waquoit Bay estuaries. Temperature and irradiance data were obtained from the Falmouth Monthly Climate Report

(http://www.whoi.edu/climate).

Fig. 6. Calculated canopy thickness of *Cladophora vagabunda* in each of the three subestuaries receiving different land-derived nitrogen loads, Childs River, Quashnet River, and Sage Lot Pond with nitrogen loads of 601 kg N ha^{-1} y^{-1}, 403 kg N ha^{-1} y^{-1}, 12 kg N ha^{-1} y^{-1}, respectively. Values for each year, from June 1994 through June 2000, were averaged over twelve month intervals. The dashed line at 2 cm indicates the compensation point for production and respiration within the macroalgal mat, from Peckol and Rivers (1996).
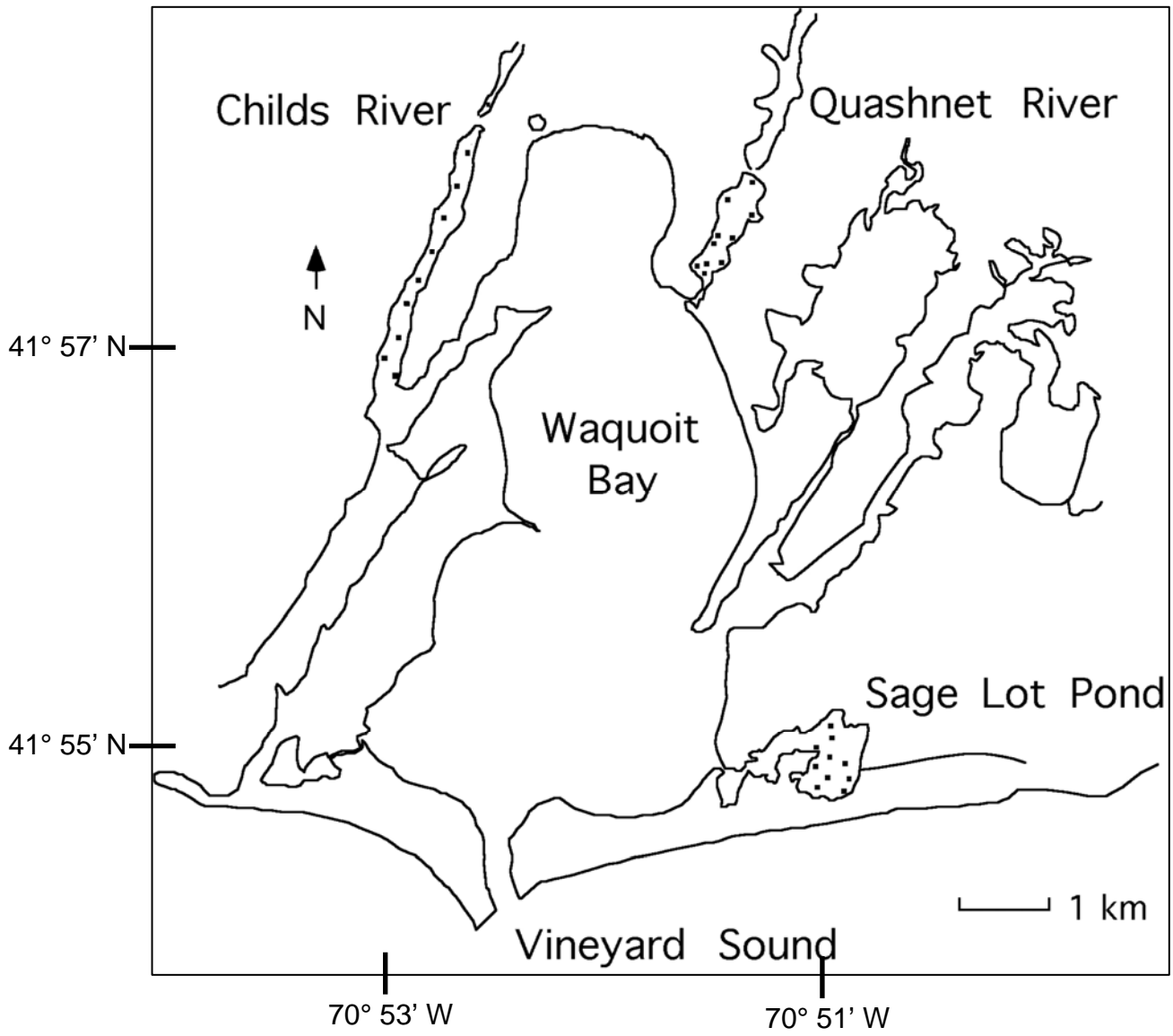
Table 1. Mean ± s.e. macrophyte biomass (g d.w. m^{-2}) and maximum single sample biomass of the macrophyte taxa in each estuary with different land-derived N loads (kg N ha^{-1} y^{-1}) over the 6 year study from 1994 - 2000.

| Taxon | Estuary | | | | | |
| | Childs (601) | | Quashnet (403) | | Sage Lot (12) | |
	Mean ± s.e.	Max	Mean ± s.e.	Max	Mean ± s.e.	Max
Total macroalgae	165.4 ± 12	1846.8	91.2 ± 5.8	1707.6	50.0 ± 2.3	428.9
Cladophora vagabunda	115.7 ± 11.3	1763.2	50.6 ± 5.3	1625.6	19.3 ± 1.5	385.3
Gracilaria tikvahiae	41.9 ± 3.5	1306.3	29.5 ± 1.8	408	18.2 ± 1.3	256.4
Other algae	7.7 ± 1.1	386.5	11.1 ± 1.5	669.1	12.5 ± 1.2	401.8
Ulva lactuca	2.6		1.3		0.1	
Ulva spp. *	0.5		—		0.1	
Codium fragile	—		—		1.7	
Sargassum filipendula	trace		—		—	
Acrothrix gracilis	—		0.1		—	
Ectocarpus sp.	—		0.003		—	
Polysiphonia spp.	1.3		1.1		2.9	
Agardhiella subulata	1		0.4		3.9	
Spyridia filamentosa	0.5		0.2		0.1	
Ceramium spp.	trace		0.002		—	
Unidentified	1		2.8		7.8	
Z. marina	—		—		43.7 ± 3.3	580

*formerly *Enteromorpha* spp.

Table 2. Coefficient of variation of mean monthly macroalgal biomass (g d.w. m^{-2}) in three subestuaries of Waquoit Bay with different land-derived N loads (kg N ha^{-1} y^{-1}).				
Estuary (N load)	Total macroalgae	*Cladophora vagabunda*	*Gracilaria tikvahiae*	Other algae
Childs (601)	26.2	24.9	45.1	85.4
Quashnet (403)	23.4	34.9	24.8	60.0
Sage Lot (12)	32.9	28.1	43.0	79.6

Fig. 1.

Fig. 2.

CHILDS QUASHNET SAGE LOT

C. vagabunda

G. tikvahiae

Other algae

Z. marina

Biomass (g d.w. m^{-2})

Year

Fig. 3.

Total macroalgae

y = 0.187x + 39.551

F = 45.7 ***

C. vagabunda

y = 0.1503x + 10.082

F = 37.9 ***

G. tikvahiae

y = 0.0372x + 16.35
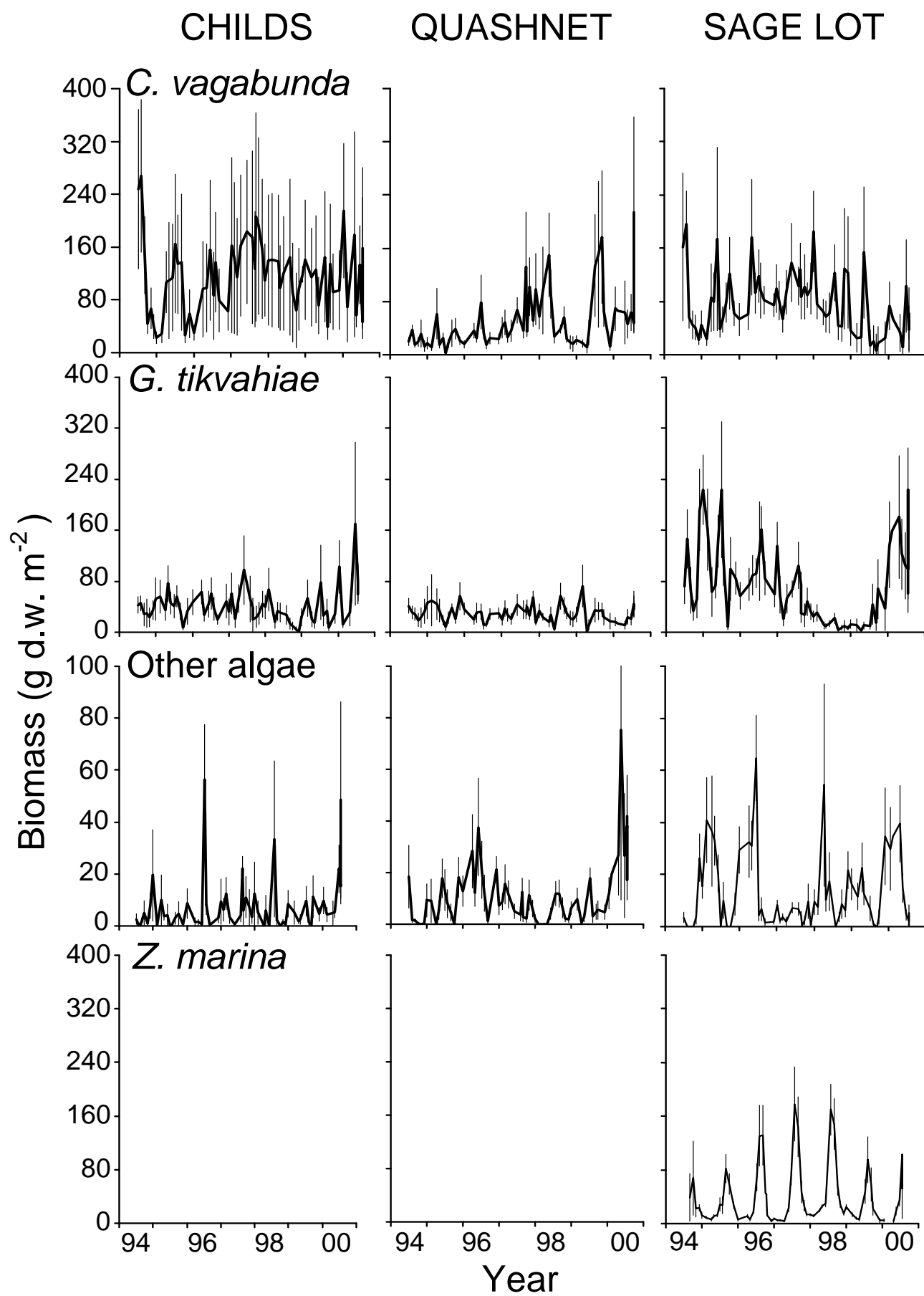
F = 19.2 ***

Other algae

not significant

Mean Biomass (g d.w. m^{-2})

N load (kg N ha^{-1} y^{-1})

Fig. 4.

Fig. 5.

Fig. 6.