



Light dependence of *Zostera marina* annual growth dynamics in estuaries subject to different degrees of eutrophication

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Abstract

We examined the coupling between eelgrass growth dynamics and surface irradiance over an annual cycle in four shallow estuaries of the Waquoit Bay system (MA, USA) that have similar physical characteristics, but are subject to different land-derived nitrogen loading rates and eutrophication. Contrary to our hypothesis, the results show that most measures of eelgrass demographics were positively correlated with surface irradiance in all four estuaries. Of the 45 regression models adjusted between irradiance and demographic variables (density, plastochrone intervals, and above- or belowground biomass, growth, and production, on both a per shoot and areal basis), only nine were non-significant, and only six of those corresponded to the eutrophic estuaries. There was a lack of correlation between shoot density and irradiance in the eutrophic estuaries, in contrast to the strong coupling in estuaries with the lowest nitrogen loads. Severe light limitation and other deleterious impacts imposed by macroalgal canopies on newly recruiting shoots in the eutrophic estuaries likely contributed to the lack of correlation between shoot density and irradiance at the water's surface. Because the range in eutrophication included the range of conditions at which eelgrass can survive, the relatively consistent temporal coupling between surface irradiance and most eelgrass demographic variables found here may also be a feature of other shallow temperate systems undergoing eutrophication, and indicates a measure of plant recruitment (density) to be one of the first parameters to become uncoupled from light reaching the water's surface.

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1. Introduction

Eelgrass (*Zostera marina* L.) is a dominant producer in shallow, temperate waters of the North Atlantic, the eastern Pacific and around Japan, the Arctic Circle, the Mediterranean Sea, and the Black Sea. Eelgrass is primarily a subtidal species, with the upper limit of distribution controlled by physical factors, including desiccation, wave action, and ice scouring (Robertson and Mann, 1984). The lower limit of eelgrass distribution and growth is primarily controlled by light availability (Backman and Barilotti, 1976; Dennison, 1987; Duarte, 1991; Koch and Beer, 1996); eelgrass requires 6–8 h day⁻¹ of photosynthetic-saturating irradiance to survive (Dennison and Alberte, 1985).

Light availability is also an important control of eelgrass seasonality (Setchell, 1929; Sand-Jensen, 1975; Penhale, 1977; Marsh et al., 1986; Dennison, 1987). In temperate populations, the timing of peak biomass or productivity occurs near the annual peak in irradiance (Sand-Jensen, 1975; Jacobs, 1979; Aioi, 1980; Nienhuis and de Bree, 1980; Wium-Andersen and Borum, 1984; Orth and Moore, 1986; Thom, 1990; Marbà et al., 1996; Sfriso and Ghetti, 1998), and interannual variations in productivity may even correspond to interannual variations in irradiance resulting from variable sky cover (Sand-Jensen, 1975; Jacobs, 1979; Sand-Jensen and Borum, 1983; Kentula and McIntire, 1986). In addition, numerous experimental manipulations have repeatedly demonstrated light availability determines the timing and magnitude of eelgrass growth in temperate environments (Backman and Barilotti, 1976; Penhale, 1977; Dennison and Alberte, 1982; Short et al., 1995).

Anthropogenic impacts that enhance turbidity in estuarine waters, such as dredging or algal overgrowth induced by

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eutrophication, may uncouple the tight temporal correspondence between surface irradiance and eelgrass growth seasonality that is often observed in pristine, temperate environments. For instance, increased algae, promoted by increased delivery of land-derived nutrients, may intercept a large percentage of incident light before it reaches the leaf canopy and prevents increase in eelgrass growth, despite increasing irradiance at the water surface (Short et al., 1995; Hauxwell et al., 2001, 2003). Though many reports qualitatively describe the temporal coupling between eelgrass growth and light availability (Jacobs, 1979; Aioi, 1980; Nienhuis and de Bree, 1980; Wium-Andersen and Borum, 1984; Orth and Moore, 1986; Thom, 1990; Marbà et al., 1996; Sfriso and Ghetti, 1998), the relationship between eelgrass demographic variables and irradiance at even the air–water interface has rarely been quantified, impeding our ability to recognize instances in which established, quantified annual patterns might fail as eutrophication increases. Furthermore, it is not known whether an uncoupling between surface irradiance and demographic variables would affect seagrass above- and belowground compartments to the same extent, or whether shoot-based changes (expressed on a shoot basis) are more important than areal changes (expressed per m^2). Determining whether increased eutrophication can effectively uncouple eelgrass growth dynamics from the seasonal pattern of surface irradiance and, if so, understanding the nature of that uncoupling is important in understanding propagated effects on the ecology of estuaries and in developing adequate management practices.

The estuaries of Waquoit Bay (MA, USA) offer an opportunity to examine the coupling between irradiance and eelgrass growth under a range of eutrophication intensity and light interception by algae. In the Waquoit Bay system, different land use patterns within watersheds of various estuaries with otherwise similar physical characteristics (i.e. size, depth, water residence time) have generated a range of nitrogen loading rates delivered to the estuaries (Valiela et al., 1997, 2000a). At the time of our surveys, eelgrass beds occur only in four estuaries of the system: Timms Pond, Sage Lot Pond, Hamblin Pond, and Jehu Pond. Timms and Sage Lot Ponds have forested watersheds and receive 5.3 and 7.6 $kg\ N\ ha^{-1}$ (of estuarine + salt marsh area) $year^{-1}$ from land, respectively. Hamblin and Jehu Ponds have somewhat urbanized watersheds and receive 3.5–6-fold higher loads of land-derived nitrogen (28.4 and 30.1 $kg\ N\ ha^{-1}\ year^{-1}$, respectively). In these higher nitrogen estuaries, eelgrass has declined substantially over the last decade as a result of light limitation or biogeochemical alterations imposed by algal overgrowth (Hauxwell et al., 2001, 2003). Eelgrass has disappeared from the three additional estuaries that receive the highest nitrogen loading rates, ranging from 62.7 (Eel Pond) to 407 (Childs River) $kg\ N\ ha^{-1}\ year^{-1}$. Refer to Hauxwell et al. (2003) for additional information on the Waquoit Bay estuarine system, its estuaries, intensity of anthropogenic eutrophication and eelgrass and algal abundance.

In this paper, we first examined the temporal dynamics of shoot density and biomass; above- and belowground areal

biomass; and leaf, rhizome and root growth and areal production rates over an annual cycle in the four Waquoit Bay estuaries where eelgrass was still present. Second, we explored the degree of coupling between eelgrass demographic variables and surface irradiance by quantifying the relationship between surface irradiance and each eelgrass variable measured over the annual cycle. We expected an uncoupling between surface irradiance and many demographic parameters in declining populations (i.e. Jehu and Hamblin Ponds), where relatively higher nitrogen inputs may have stimulated algal growth capable of sequestering increased quantities of light between the air–water interface and eelgrass canopy.

2. Methods

We conducted the field study from November 1997 to 1998, with measurements taken every 2–8 weeks in eelgrass meadows located in the Waquoit Bay estuaries of Timms (41.553°N, 70.540°W), Sage Lot (41.554°N, 70.508°W), Hamblin (41.576°N, 70.505°W), and Jehu Ponds (41.566°N, 70.499°W). Depth ranged 1.3–1.7 m (MLW + 0.5-m tidal range). Water residence times for the estuaries ranged 1.5–2.7 days. Salinity within the eelgrass meadows ranged 25–30‰.

A non-destructive method was employed to quantify density of shoots within each meadow. SCUBA divers counted the number of vegetative shoots within randomly tossed 0.25- m^2 quadrats. In Sage Lot, Timms, and Jehu Ponds, where spatial distributions of shoots were reasonably homogenous, we took three to four measurements of shoot density in each visit. In Hamblin Pond, we took 6–12 measurements in each visit because spatial distribution was patchy.

Leaf growth rates were measured using the marking technique of Zieman and Wetzel (1980). On each visit and for each estuary, 25 shoots randomly chosen within a 0.25- m^2 area were tagged and marked for growth with a 23-gauge hypodermic needle by SCUBA divers. Shoots were retrieved ~2–6 week later with as much intact rhizome/root material as possible, and new shoots were tagged and marked; this continuous mark/retrieval provided 12 sets of measurements throughout the study period. Shoots were brought to the laboratory and frozen until measurements of shoot biomass and above- and belowground growth rates could be made.

We measured leaf growth as the distance between the sheath and marked holes on the leaves of tagged shoots. We also measured leaf length and width. We used only those shoots for which we could accurately measure leaf growth; that is, we discarded the shoot if any leaf of the shoot was not intact and holes were not observed on the remaining portion. We also determined leaf-specific weight ($mg\ dry\ weight\ cm^{-2}$ of leaf surface) to convert the measurements of leaf length and width into dry weight and derive values of aboveground shoot biomass ($mg\ dry\ weight\ shoot^{-1}$) and leaf growth rates per shoot ($mg\ dry\ weight\ shoot^{-1}\ day^{-1}$). Weight-specific leaf growth rates were determined by dividing growth rates per shoot by aboveground shoot biomass.

Horizontal rhizome and root material from marked shoots were separated according to internode rank (only for fully-formed rhizome segments), dried, and weighed. Plastochrone intervals (i.e. number of days between the appearance of consecutive leaves) were calculated by dividing the number of days elapsed between initial marking and retrieval of shoots by the mean total number of new leaves (i.e. bearing no holes) produced per shoot. Since each node on the horizontal rhizome corresponds to the insertion of one leaf sheath into the rhizome, these measurements allowed us to calculate rhizome growth for each marked shoot during each sampling interval, as the weight of the rhizome segment between the shoot and a number of nodes equal to the number of new leaves produced during the given interval (Sand-Jensen, 1975; Pedersen and Borum, 1992, 1993). Similarly, we could also derive conservative estimates of root growth from the weight of roots attached to the new rhizome formed during the interval (Duarte et al., 1998). Those estimates are conservative because they do not account for root biomass turnover between sampling dates or for root growth on rhizome formed during previous sampling intervals.

We multiplied mean aboveground shoot biomass by the corresponding mean shoot density to estimate mean aboveground shoot biomass. Due to the destructive nature of belowground biomass sampling, we chose not to take those measurements in all estuaries, but report data on areal belowground biomass for Sage Lot Pond, where a long-term monitoring program has been conducted since 1994 (Hersh, 1996; Hauxwell et al., 1998). Ten samples of belowground biomass were taken monthly within the meadow using a Eckman grab (15 cm × 15 cm). Areal leaf, rhizome, and root production was derived by multiplying growth rates per shoot by the corresponding shoot density. Annual estimates were derived by summing the production during all sampling intervals between November 1997 and 1998.

Vertical solar energy flux data, collected by R. Payne of the Woods Hole Oceanographic Institution, were measured at 10-s intervals by an Eppley PSP pyranometer (stationed on land within 10 km of our sites), averaged over an hour by a Campbell data logger, and summed for daily totals. Mean daylight irradiance was determined for each day of the year by dividing daily total solar energy flux data by the number of daylight hours (sunrise minus sunset, plus 1). Water temperature data were collected by the Waquoit Bay National Estuarine Research Reserve Baywatchers Program. Measurements of bottom water were taken every ~3 week in seven sites in the Waquoit Bay system.

3. Results

Irradiance was highest between late June and early July, when the mean monthly daylight irradiance (above the water's surface) was $420 \text{ J m}^{-2} \text{ s}^{-1}$ (Fig. 1). Bottom water temperatures for the Waquoit Bay system ranged from 2 to 25 °C and were similar among sites (Fig. 1; for all sites, mean standard error < 0.5°). The peak in temperature (mid August) was offset from that in irradiance by ~1.5 months.

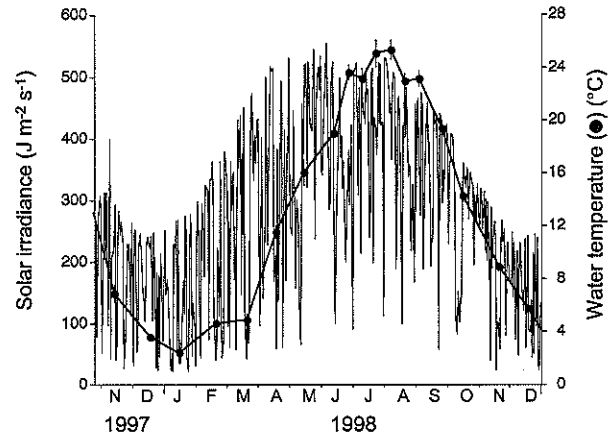


Fig. 1. Daily surface irradiance (mean for daylight hours, above the water's surface) and bottom water temperature data for the Waquoit Bay system between November 1997 and 1998. Irradiance data from R. Payne, Woods Hole Oceanographic Institution. Temperature data from the Waquoit Bay National Estuarine Research Reserve Baywatchers Program (mean ± S.E.).

Shoot density peaked between 280 and 428 shoots m^{-2} between mid May and late June in all estuaries except in Hamblin Pond, where density remained low and fluctuated slightly over the year (Fig. 2). Density in Jehu Pond exhibited an early peak and rapidly decreased in June and July when irradiance was highest. During winter minima, these perennial populations maintained ~40–100 shoots m^{-2} .

Peaks in shoot biomass occurred between mid May and late July, with maxima ranging from 250 to 530 mg dry weight shoot⁻¹ (Fig. 3, top). Differences observed in shoot biomass among estuaries were primarily a result of differences in leaf length, with average shoot heights approximately 1.4–2.1 times longer in Sage Lot Pond and Jehu Pond compared to those in Timms Pond and Hamblin Pond (Table 1). Number of leaves per shoot, leaf length, and leaf width contributed to the

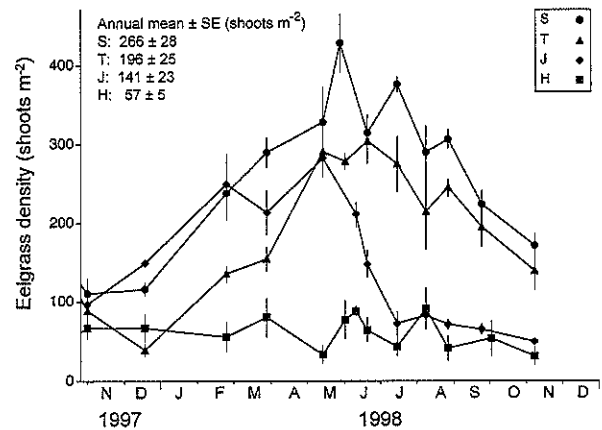


Fig. 2. Annual cycles of eelgrass (*Zostera marina*) shoot density (means ± S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Annual mean densities ± propagated S.E. are summarized at top of figure.

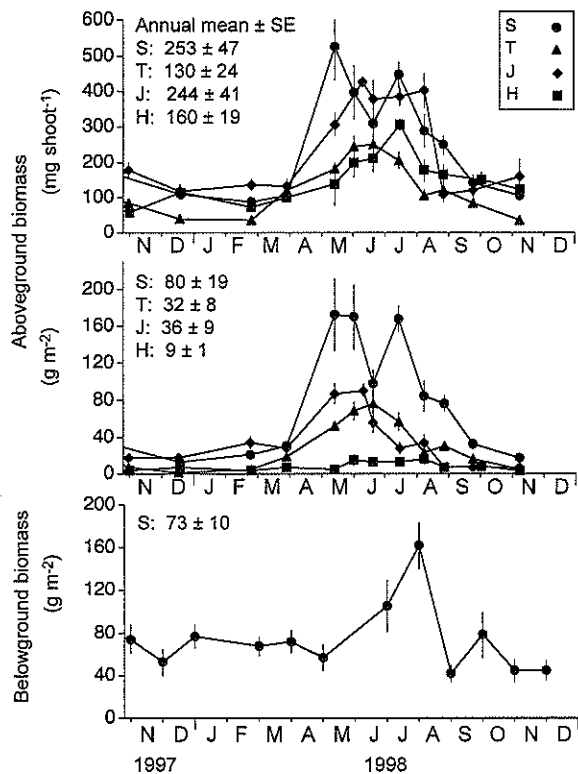


Fig. 3. Annual cycles of eelgrass (*Zostera marina*) aboveground shoot biomass (top), aboveground areal biomass (middle), and belowground areal biomass (bottom) (means \pm S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Annual means \pm propagated S.E. are summarized at top of panels.

seasonality observed in shoot biomass, with minimum values of all occurring in winter and maximum values occurring during summer. Leaf-specific weight ranged from 1.5 to 3.8 mg dry weight cm⁻² but with no apparent seasonal pattern.

Aboveground areal biomass peaked between May and July in all estuaries (76–173 g dry weight m⁻²) except Hamblin Pond (Fig. 3, middle). In Hamblin Pond, summer values of aboveground areal biomass (ca. 15 g dry weight m⁻²) were only slightly higher than values for the rest of the year (<10 g dry weight m⁻²). Sage Lot Pond had the greatest mean aboveground areal eelgrass biomass, 2.3–2.7 times higher than

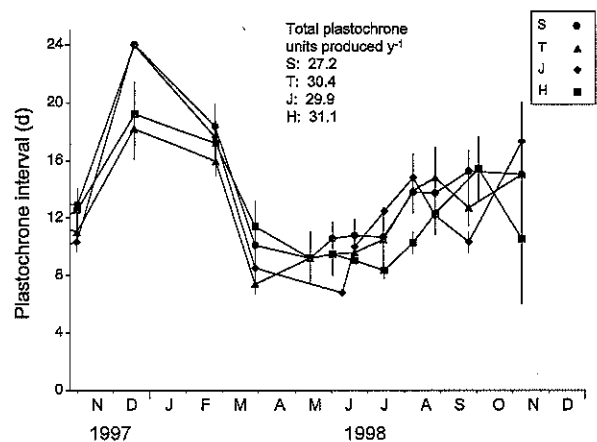


Fig. 4. Annual cycles of eelgrass (*Zostera marina*) plastochrone interval (number of days between appearance of consecutive new leaves on a shoot) (means \pm S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Annual total number of plastochrone units produced per shoot \pm propagated S.E. is summarized at top of figure.

that of Jehu or Timms Ponds, and 9 times higher than that in Hamblin Pond.

In Sage Lot Pond, belowground areal biomass peaked in early August at 162 g dry weight m⁻² and maintained approximately 40–75 g dry weight m⁻² throughout the remainder of the year (Fig. 3, bottom). During the spring and summer, aboveground areal biomass:belowground areal biomass ranged from 1.1 to 3.1 (Fig. 3, middle, bottom). During the fall and winter, this ratio dropped to \sim 0.4.

Plastochrone intervals were shortest during spring months, when shoots produced \sim 1 leaf per week (Fig. 4). Plastochrone intervals steadily increased throughout summer and fall and were longest in winter when they ranged from 17 to 24 days. Annually, shoots from all estuaries produced approximately 30 plastochrone units. Consequently, differences in leaf, rhizome, and root growth rates among estuaries were result of different rates of elongation, not differences in the rate of appearance of new plastochrone units.

Leaf growth rates peaked between late May and mid July at \sim 5.1–8.2 mg dry weight shoot⁻¹ day⁻¹ (Fig. 5, top). Significant leaf growth occurred during winter, when water temperatures approached 2 °C, and ranged from 0.3 to 1.1 mg

Table 1

Morphological features of eelgrass (*Zostera marina*) from four estuaries of Waquoit Bay, including mean (\pm S.E.) and maximum shoot height, ranges of mean leaf width and density, and mean number of leaves per shoot. Shoot height was based on the length of the longest leaf on a shoot. Minimum values for all measurements except leaf density consistently occurred during winter, and maximum values occurred during summer

Morphological feature	Estuary			
	Sage Lot Pond	Timms Pond	Hamblin Pond	Jehu Pond
Mean shoot height (cm)	50 \pm 5	31 \pm 3	36 \pm 2	66 \pm 9
Maximum shoot height (cm)	106	84	79	140
Leaf width (cm)	0.37–0.52	0.25–0.46	0.28–0.51	0.32–0.56
Leaf-specific weight (mg cm ⁻²)	2.2–3.8	2.1–3.8	1.5–3.6	2.1–3.7
Number of leaves shoot ⁻¹	4.5	4.7	4.7	4.3

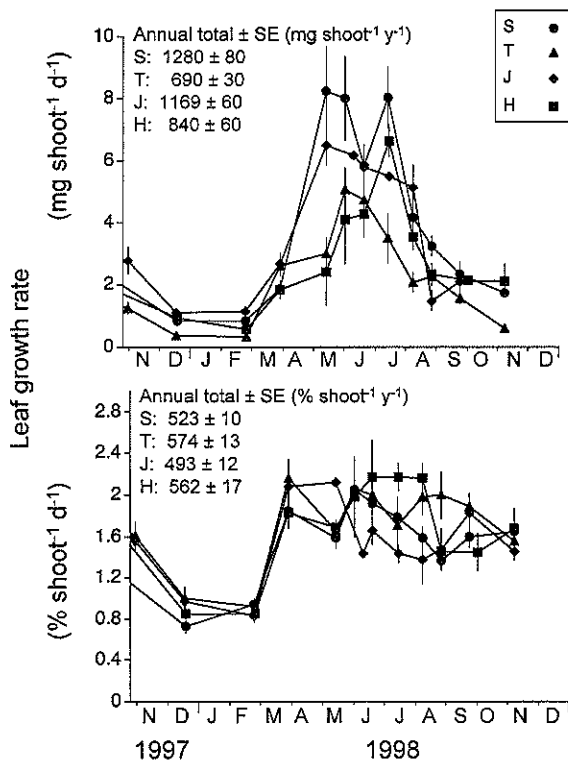


Fig. 5. Annual cycles of eelgrass (*Zostera marina*) absolute leaf growth rate (top) and growth rate relative to aboveground shoot biomass ((g growth/g biomass) × 100) (bottom) (means ± S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Annual total growth per shoot ± propagated S.E. is summarized at top of panels.

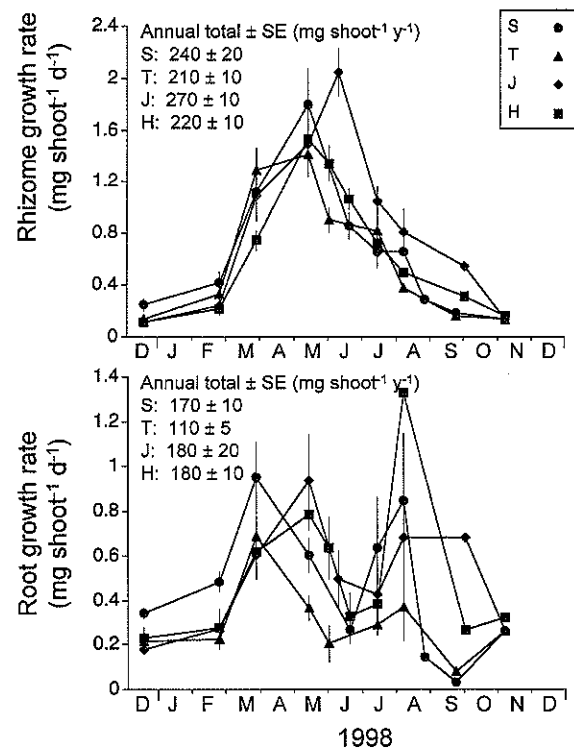


Fig. 6. Annual cycles of eelgrass (*Zostera marina*) absolute rhizome (top) and root (bottom) growth rates (means ± S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Estimates of root growth were based on standing biomass and represent minimum rates. Annual total growth per shoot ± propagated S.E. is summarized at top of panels.

dry weight shoot⁻¹ day⁻¹. On an annual basis, a shoot from Sage Lot Pond produced on average 1280 mg dry weight of leaf material compared to the minimum of 690 mg dry weight in Timms Pond. Weight-specific leaf growth rates were ~1.4–2.2% day⁻¹ during spring, summer, and fall and ~0.9% day⁻¹ during winter (Fig. 5, bottom). On an annual basis, shoots from all estuaries replaced aboveground standing biomass 5–6 times (Fig. 5, bottom).

Rhizome growth rates peaked between mid May to mid June at 1.4–2.0 mg dry weight shoot⁻¹ day⁻¹ (Fig. 6, top). Winter growth rates were reduced to <0.25 mg dry weight shoot⁻¹ day⁻¹. On an annual basis, a shoot produced 210–270 mg dry weight of rhizome material (range for the four estuaries). Our conservative estimates of root growth rate exhibited two peaks throughout the annual cycle, the first in spring, and the second in late summer/early fall (Fig. 6, bottom). Peak root growth rates were ~0.7–1.3 mg dry weight shoot⁻¹ and minimum growth rates were 0.1–0.2 mg dry weight shoot⁻¹. Annually, a single shoot produced at least 110–180 mg dry weight of root material (range for the four estuaries).

Areal production was highest between late spring to early summer, with peaks ranging from 360 to 3080 mg dry weight m⁻² day⁻¹ for leaves, 90–680 mg dry weight m⁻² day⁻¹ for rhizomes, and 90–280 mg dry weight m⁻² day⁻¹ for roots

(Fig. 7). Areal production was sizeable during winter months, when occasional ice cover was observed; production during winter months accounted for ~22% of annual leaf production, ~20% of annual rhizome production, and ~26% of annual root production in all estuaries.

To quantify the coupling between eelgrass growth and surface irradiance in the four estuaries examined, we plotted the eelgrass variables measured versus irradiance for each estuary and adjusted the best-fit to the pattern observed using least-square regression analysis (Figs. 8 and 9). In all estuaries, shoot biomass and leaf and rhizome growth rates increased exponentially, and plastochrone interval decreased exponentially, with higher irradiance (Fig. 8). Weight-specific leaf growth rates also increased exponentially with higher irradiance in all estuaries except in Jehu Pond (Fig. 8). Root growth rates, on the contrary, were not associated with irradiance in any of the estuaries (Fig. 8) as a result of the consistent midsummer trough (Fig. 6, bottom). Shoot density increased linearly with higher surface irradiance in Sage Lot Pond and Timms Pond, but was independent of irradiance in Jehu Pond and Hamblin Pond (Fig. 9). Aboveground areal biomass increased exponentially with higher irradiance in all estuaries (Fig. 9). Belowground areal biomass, however, was not associated with irradiance in the only estuary where we measured it (Sage Lot Pond, not shown in figure; $r^2 = 0.23$,

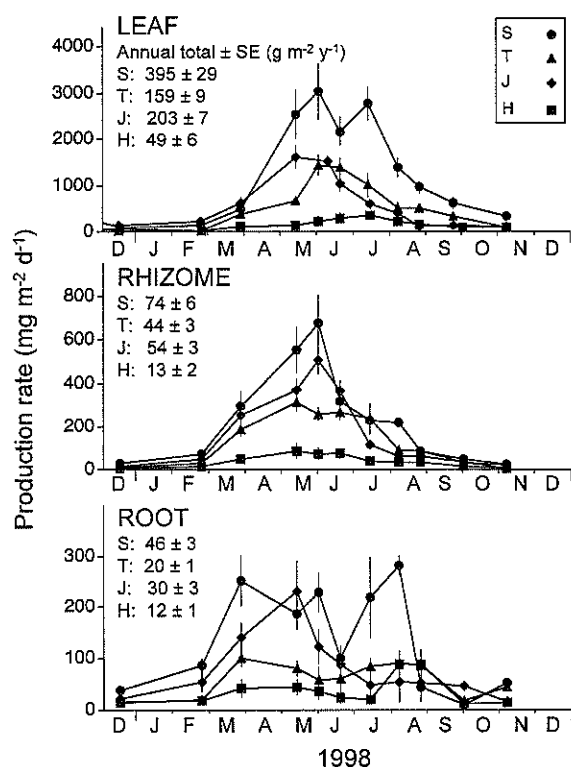


Fig. 7. Annual cycles of eelgrass (*Zostera marina*) areal leaf (top), rhizome (middle), and minimum root (bottom) production (means \pm S.E.) in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Annual total growth per shoot \pm propagated S.E. is summarized at top of panels.

$P = 0.1$). Irradiance was significantly related to areal leaf, rhizome, and root production in the four estuaries (exponentially), with the exception of root production in Hamblin Pond (Fig. 9).

4. Discussion

Our results are consistent with previous reports of a close seasonal coupling between eelgrass growth and surface irradiance (Dennison and Alberte, 1982; Sand-Jensen and Borum, 1983; Dennison, 1987; Marbà et al., 1996). Contrary to our hypothesis, this coupling remains little altered across the gradient in anthropogenic eutrophication represented by the four estuaries we studied. Most of the eelgrass variables regressed with surface irradiance yielded significant associations in all four estuaries. Only 9 regressions were non-significant out of the 45 regressions presented in Figs. 8 and 9 (and belowground biomass in Sage Lot Pond). Six of the nine non-significant regressions occurred in the more eutrophic estuaries (Jehu Pond and Hamblin Pond), but, even in these estuaries, the temporal dynamics of eelgrass growth were generally well associated with the seasonality in surface irradiance. On aggregate, these results demonstrate a strong quantitative dependence of many eelgrass growth variables on

surface irradiance, with most of the significant relationships encountered (25 of 36) displaying a coefficient of determination (r^2) higher than 0.5. We found a strong coupling between shoot-based growth variables, such as shoot biomass and leaf and rhizome growth rates, and surface irradiance in all estuaries. Accordingly, areal biomass and leaf and rhizome production (i.e. expressed on a per m^2 basis), which result from the product between shoot density and shoot-based growth variables, were also associated with surface irradiance, emphasizing the importance of irradiance in regulating the timing of overall population productivity.

Despite generally tight associations between surface irradiance and most demographic variables, the temporal association between shoot density and surface irradiance contrasted notably between relatively pristine (Sage Lot and Timms Ponds) and more eutrophic estuaries (Jehu and Hamblin Ponds). Shoot density was strongly associated with irradiance in low nitrogen estuaries, but uncorrelated in higher nitrogen sites. This uncoupling suggests that light reduction between the air–water interface and eelgrass surfaces by planktonic, epiphytic, or benthic algae in these estuaries may be large. For young short shoots, light limitation by canopies of benthic macroalgae may be severe (Peckol and Rivers, 1996; Hauxwell et al., 2001, 2003). During the 1998 sampling period, Hamblin Pond sustained a relatively tall canopy of macroalgae (up to 15 cm) capable of attenuating 99% of incoming light for new shoots, and two blooms of macroalgae, similar in height to canopies in Hamblin Pond, occurred in Jehu Pond (Hauxwell et al., 2003). We, in fact, quantified the relationships between nitrogen loading rates, algal producers, and their potential effect on light supply to eelgrass in Hauxwell et al. (2003), and demonstrated potentially severe light limitation to newly recruiting shoots in these higher nitrogen estuaries. It is likely that macroalgal canopies contributed to diminished recruitment (and overall density) of eelgrass in the higher nitrogen estuaries (Hauxwell et al., 2001, 2003). These same estuaries have, in fact, also exhibited a 90% loss in areal coverage over the past decade. These data corroborate those of Nixon et al. (2001) in suggesting that a manner in which eelgrass decline occurs (in response to light limitation) is via decreased recruitment or increased mortality of established shoots.

In the Waquoit Bay system, the temporal dynamics of eelgrass growth were closely associated with seasonality in surface irradiance, and increases in nitrogen loading and resulting declines in eelgrass cover and overall production did not significantly affect that association. The consistent correlation found between the many parameters of eelgrass growth measured here and irradiance just above the water's surface is surprising given the many factors that can attenuate light before it efficiently reaches the photosynthetic systems of eelgrass leaves, including water itself, phytoplankton and other inorganic and organic particles, epiphytes, benthic macroalgae (Hauxwell et al., 2001, 2003), and self-shading within the leaf canopy (Enriquez et al., 2002, 2004). The close relationship between eelgrass growth and surface irradiance found here likely results from the shallowness of the sites studied (depth in mean range for the for sites: 1.3–1.7 m). In fact, we might not

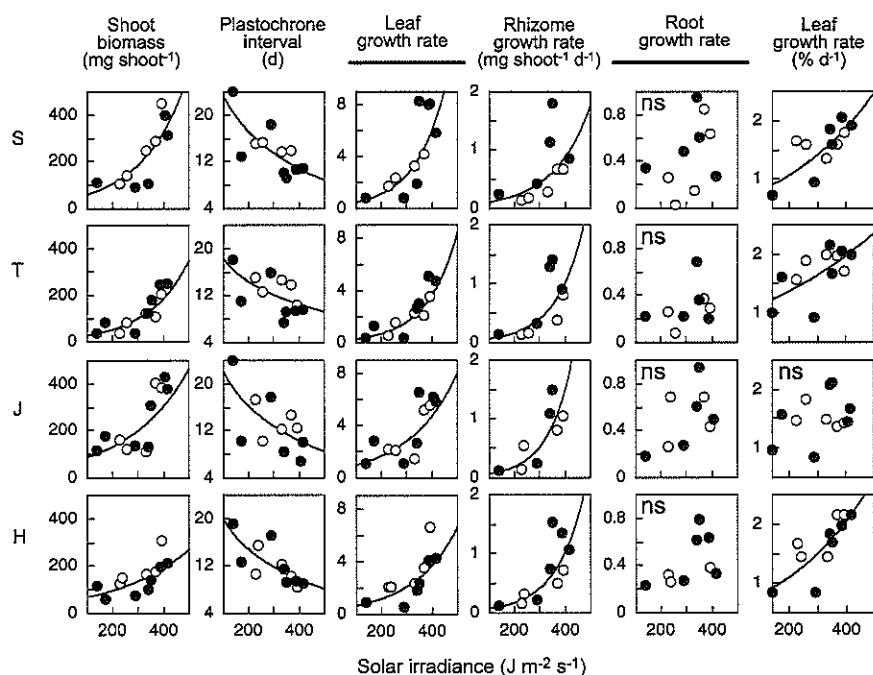


Fig. 8. Relationship between surface irradiance and eelgrass (*Zostera marina*) shoot biomass; plastochrone interval; leaf, rhizome, and root absolute growth rates; and weight-specific leaf growth rates over an annual cycle in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Filled symbols represent ascending values of the seasonal cycle in irradiance; open symbols represent descending values. Lines or curves represent significant relationships ($P < 0.05$); ns, non-significant relationships.

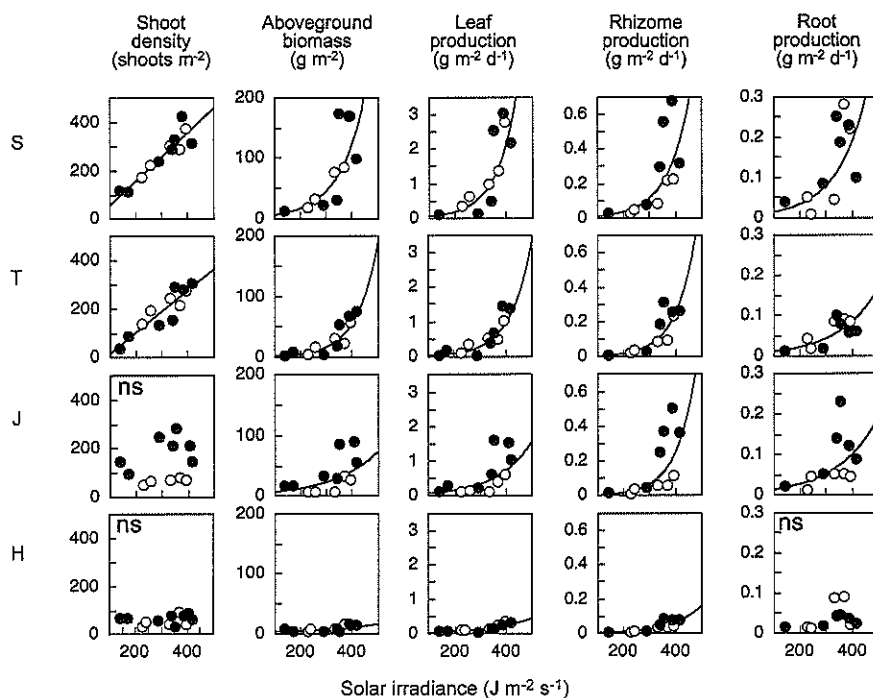


Fig. 9. Relationship between surface irradiance and eelgrass (*Zostera marina*) shoot density, aboveground areal biomass, and leaf, rhizome, and root areal production rates over an annual cycle in four estuaries of Waquoit Bay subject to different rates of land-derived nitrogen loading (S, Sage Lot Pond; T, Timms Pond; J, Jehu Pond; H, Hamblin Pond). Filled symbols represent ascending values of the seasonal cycle in irradiance; open symbols represent descending values. Lines or curves represent significant relationships ($P < 0.05$); ns, non-significant relationships.

have found such a consistent temporal coupling between eelgrass growth and surface irradiance in deeper systems with higher potential for attenuation through the water-column.

In most cases, the increase in eelgrass growth with higher surface irradiance observed in the Waquoit estuaries was exponential. Eelgrass biomass and growth, both on a per shoot or per m² basis, showed slow increases with increase in surface irradiance in late winter/early spring, but they showed disproportionately larger increases from mid spring to mid summer. This empirical pattern may reflect the disproportional effect of increasing light availability on plant biomass accrual, as photosynthesis becomes saturated with abundant light and new biomass photosynthesizes at maximum capacity (Zimmerman et al., 1994; Enriquez et al., 1994, 2004). Alternatively, the exponential pattern described here may reflect the synergetic effect between concomitant increases in light and temperature, as it has been observed in other temperate locations (van Lent and Verschuure, 1994; Olesen and Sand-Jensen, 1994; Marbà et al., 1996). Increasing temperature stimulates plant metabolic and photosynthetic rates, which, under saturating conditions due to abundant light availability, would result in disproportionately higher (i.e. exponential) biomass accrual.

In summary, our report provides further evidence of a tight coupling between surface irradiance and below- and above-ground eelgrass growth in shallow temperate estuaries. We quantify that coupling and show that growth variables generally increase as an exponential function of surface irradiance, and that seasonality in surface irradiance often explains a major fraction of the variability in eelgrass growth. We further show that the strong dependence of eelgrass growth on surface irradiance varies little across populations subject to contrasting levels of eutrophication, algal biomass, and light interception by algae. In the most eutrophic estuaries, enhanced algal shading on established shoots was not enough to uncouple their growth dynamics from light availability at the air–water interface. An important uncoupling occurred with plant density, indicating enhanced mortality of established shoots or diminished recruitment of new shoots as a manner in which eelgrass meadows decline. The levels of eutrophication encompassed (i.e. nitrogen loading rates) include most of the range within which eelgrass can survive, with higher values conducive to eelgrass disappearance via intense shading (or other deleterious effects) by algal producers (Valiela et al., 2000b; Valiela and Cole, 2002; Hauxwell et al., 2003). Hence, surface irradiance appears to, be a powerful predictor of above- and belowground eelgrass growth in shallow temperate estuaries despite eutrophication-induced differences in algal light sequestration.

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