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## Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance

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**Abstract** Continuous year-round measurements of photosynthetically active radiation (PAR) were collected in relation to leaf elongation and plant biomass in the shoal-grass, *Halodule wrightii* Aschers., within three different estuarine systems on the south Texas coast (Laguna Madre: May 1989 to September 1993; Corpus Christi Bay: February 1990 to September 1993; San Antonio Bay: May 1990 to April 1991). Large differences in water transparency at all three sites masked seasonal variations in surface insolation as reflected in average diffuse attenuation coefficient ( $k$ ) values ranging from 0.7 to 2.9 and differences in the maximum depth penetration of *H. wrightii*, which varied from 0.6 to about 1.3 m. The continuous presence of a chrysophyte (brown tide) algal bloom in Laguna Madre since 1990 led to significant decreases in spring leaf elongation rates and a nearly 50% decline in below-ground biomass, which was reflected in root:shoot ratio (RSR) values that declined from 5.4 in 1989 to 2.3 in 1992. Increased turbidity and lower light levels in San Antonio Bay also corresponded with diminished plant biomass and the subsequent loss of plants; at both locations, the annual quantum flux ranged from 2200 to 2400 mol m<sup>-2</sup> yr<sup>-1</sup>, or about 18% of surface irradiance (SI). In contrast, *H. wrightii* populations growing at ca. 1.2 m depths and characterized by high RSR values ( $\geq 4.0$ ) were exposed to 5100 to 5700 mol m<sup>-2</sup> yr<sup>-1</sup>, or about 41 to 46% SI. Under these conditions, plants were exposed to daily saturating levels of PAR ( $H_{\text{sat}}$ ) of 3 to 8 h during the spring/summer period of maximum growth, compared to an average of 2 h in Laguna Madre (after 1990) and San Antonio Bay based on field-derived measurements of photosynthetic parameters. Leaf elongation in *H. wrightii* exhibited a clear circannual rhythm at all sites, regardless of underwater light levels

and therefore was not a sensitive indicator of light stress. Instead, chronic long-term reductions in underwater PAR were most strongly reflected in total plant biomass. The higher light demand (18% SI) for *H. wrightii* in relation to many other seagrasses (11% SI; Duarte 1991) may be related to its higher photosynthetic light requirement, but may also reflect the different methods used to evaluate the minimum light requirements of seagrasses. In estuarine and coastal waters, which are characterized by large and unpredictable variations in water transparency, continuous measurements of in situ PAR are invaluable in assessing the growth and photosynthetic responses of seagrasses to variations in underwater irradiance.

### Introduction

The distribution and primary productivity of submerged aquatic vegetation is largely regulated by variations in light attenuation within the water column. In coastal regions, declines in water quality from human encroachment has caused worldwide losses in the distribution of seagrasses (for review, see Dennison et al. 1993). In Texas, the documented loss of over 140 km<sup>2</sup> of seagrasses in the lower Laguna Madre since the 1960's is attributed to decreased water transparency from maintenance dredging (Quammen and Onuf 1993; Onuf 1994); the nearly complete loss of seagrass beds in Galveston Bay (over 20 km<sup>2</sup>) is also attributed to decreased water transparency and eutrophic conditions that resulted from wastewater discharges, subsidence and dredging activities (Pulich and White 1991). The growing perception of an association between deteriorating water quality and seagrass loss has prompted efforts to establish minimum water quality standards for submerged aquatic vegetation (Kenworthy and Haunert 1991).

Light energy has long been recognized as one of the most important forcing functions in seagrass habitats (Zieman and Wetzel 1980), but there are few long-term measurements of in situ irradiance. The light requirements for growth and survival of several species of marine algae are

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well-known (Lüning and Dring 1979; Chapman and Lindley 1980; Dean 1985; Dunton 1990 a; Markager and Sand-Jensen 1992) and are largely based on in situ light measurements of photosynthetically active radiation (PAR). The photosynthetic characteristics of several seagrasses have been determined (Drew 1979; Libes 1986; Marsh et al. 1986; Fouquerean and Zieman 1991; Pérez and Romero 1992), but photosynthetic data have not been applied to in situ measurements of irradiance, which have been lacking. Instead, most estimates of the minimum light requirements of seagrasses are based on surveys of plant distributions and Secchi disc readings (Orth and Moore 1988; Duarte 1991; Dennison et al. 1993).

The applicability of a Secchi disk in evaluating the light requirements of submerged aquatic vegetation is limited and not easily related to underwater irradiance levels (Preisendorfer 1986); therefore, the information is difficult to apply to current estimates of the lower depth limits of seagrasses [8 to 25% surface irradiance (SI); Duarte 1991; Dennison et al. 1993], determinations of  $H_{\text{sat}}$  (duration of daily light saturated photosynthesis) and plant carbon budgets (Dennison and Alberte 1982, 1985; Zimmerman et al. 1989, 1991; Fourqurean and Zieman 1991). More importantly, Secchi disk measurements are instantaneous rather than integrative measurements; since seagrasses are light integrators (Dennison et al. 1993), continuous measurements of PAR would be extremely valuable in providing quantitative data on water transparency and in the modeling of plant carbon budgets. Such data would be extremely useful in establishing water quality standards and in the development of predictive models of plant production.

The present study presents the first long-term measurements of underwater PAR for seagrass communities dominated by *Halodule wrightii*. The in situ photosynthetic requirements of *H. wrightii* (Dunton and Tomasko 1994) were used, in conjunction with PAR data from three different locations, to determine the minimum light requirements of *H. wrightii* and to explain site differences in maximum depth penetration, plant biomass and rates of leaf elongation. This analysis demonstrates how in situ measurements of PAR, which can be remotely collected with relatively inexpensive instruments, can be utilized to establish minimum water transparency standards for seagrasses.

## Materials and methods

### Study sites

Field studies were conducted at three sites in three estuarine systems along the south Texas coast (Fig. 1). From north to south, these included Blackjack Peninsula (GBP) in San Antonio Bay (Guadalupe estuary), East Flats (NEF) in Corpus Christi Bay (Nueces estuary) and site LM-151 in the upper Laguna Madre estuary. Sediment characteristics at GBP and NEF have been reported previously (Dunton 1990 b) and did not differ substantially from sediments at LM-151, which were composed of about 86% sand and shell, 9% clay and 5% silt. At all three sites, we sampled within monotypic stands of *Halodule wrightii* Aschers. At site NEF, *H. wrightii* was also found mixed with two other seagrasses, *Thalassia testudinum* and *Syringodium*

*filiforme*, at various depths. The maximum depth of *H. wrightii* distribution varied among locations. At GBP, the maximum depth penetration of *H. wrightii* was about 0.6 m, compared to 1.2 m at NEF. In Laguna Madre, *H. wrightii* extended to depths of 1.6 to 1.8 m (Onuf personal communication).

All three sites were relatively protected from waves and adverse sea conditions by barrier islands or shoals that reduced fetch from prevailing southeasterly winds to 0.5 km or less. Salinities varied from 5 to 30‰ at GBP, compared to 27 to 32‰ at NEF (Dunton 1990 b) and were generally above 35‰ at LM-151 in Laguna Madre (Dunton and Tomasko 1994). The seasonal range in water temperatures at these sites ranged between 10 and 30°C (Dunton 1990 b; Dunton and Tomasko 1994). Lunar tides seldom exceed 15 cm in this area of the Texas coast (Hedgpeth 1947).

### Quantum-irradiance measurements

Measurements of photosynthetically active radiation (PAR = ca. 400 to 700 nm wavelength) on the seabed were collected continuously at each of the three stations using a LI-193SA spherical (4π) quantum sensor that provided input to a LI-1000 datalogger (LI-COR Inc., Lincoln, Nebraska, USA). The datalogger was placed in a weighted clear polycarbonate housing (Ikelite Model 5910, Indianapolis, IN) and wired to the sensor cable through a molded underwater connector (Crouse-Hinds Series 41 Penetrator, La Grange, NC). Sacrificial zinc anodes were attached to the stainless steel bands that secured the lid and the housing was placed within a plastic bag and buried in the seabed to reduce corrosion and likelihood of discovery by fishermen. The sensor was mounted on a 3-cm PVC pipe at canopy level (usually 15 to 20 cm above the bottom) to minimize fouling by drift algae and seagrass leaves. The sensors were cleaned at 1- to 3-wk intervals depending on season and location. Fouling was least during winter and virtually non-existent throughout the year in Laguna Madre; it was pronounced at sites NEF and GBP and the sensors at these sites were cleaned frequently.

Instantaneous PAR was measured at 1-min intervals and integrated hourly. Coincident measurements of incident PAR were made at The University of Texas Marine Science Institute (UTMSI) in Port Aransas (Fig. 1), using a LI-190SA quantum sensor and datalogger. The sensor was mounted on the roof of the highest building to minimize the effects of shading. The UTMSI site is located within 8 km of NEF and is centrally located with respect to sites GBP and LM-151 (about 50 km). Unfortunately, it was not practical for us to collect incident measurements of PAR at GBP and LM-151. However, for the purposes of the present study, the integrated daily quantum fluxes collected at UTMSI are probably reflective of the overall daily conditions at all three sites on most days. The sensors used in this study are accurate to ±5% (traceable to National Bureau of Standards), stability is ±2% over any 1-yr period, and data are recorded with a precision of ±0.01 μmol m<sup>-2</sup> s<sup>-1</sup>.

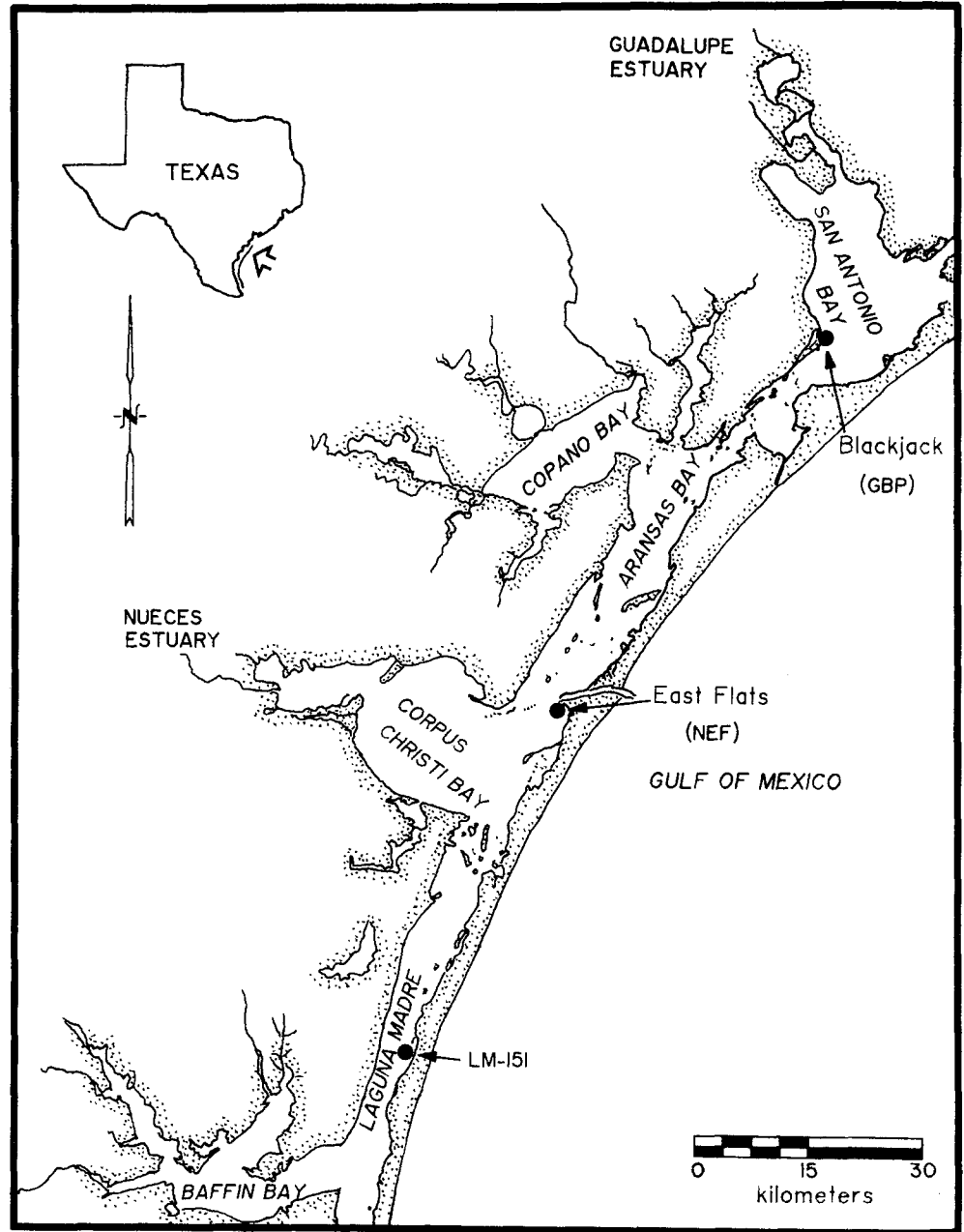
A continuous record of underwater PAR was collected for LM-151 from May 1989 to September 1993, for NEF, from February 1990 to September 1993, and for GBP, from May 1990 through April 1991. Dataloggers were serviced at 2- to 3-mo intervals during periods of deployment. Since tidal ranges are minimal, depth was measured on every visit to the study sites and the mean of all observations were used in the calculation of light attenuation coefficients ( $k$ ) for each site. The Bouguer-Lambert Law was used to describe the attenuation of light with depth, as used by McPherson and Miller (1987):

$$k = \frac{\ln(I_0/I_z)}{z} \quad (1)$$

where  $I_0$  is the incident (surface) light intensity (as measured at UTM-SI),  $I_z$  is the light intensity at depth  $z$  (the average depth at the site from which measurements were made in meters), and  $k$  is the light attenuation coefficient (m<sup>-1</sup>).

Calculations of  $H_{\text{sat}}$ , the number of hours of irradiance-saturated photosynthesis on a daily basis, and  $H_{\text{comp}}$ , hours of irradiance above compensation irradiance (Dennison and Alberte 1982), were performed using values of saturation ( $I_k$ ) and whole-plant compensation irradiance ( $I_{\text{cp}}$ ) obtained for *Halodule wrightii* by Dunton and

**Fig. 1** Location of study sites on the south Texas coast (GBP Blackjack Peninsula; NEF East Flats; LM-151 upper Laguna Madre)



Tomasko (1994). Estimates of  $H_{\text{sat}}$  were derived using two values of saturation irradiance:  $I_{k(\text{field})}$ , measured for entire plants in situ ( $315 \mu\text{mol m}^{-2} \text{s}^{-1}$ ); and  $I_{k(\text{lab})}$ , measured on leaf segments incubated under laboratory conditions ( $101 \mu\text{mol m}^{-2} \text{s}^{-1}$ );  $H_{\text{comp}}$  was calculated based on an  $I_{\text{cp}}$  of  $80 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $I_k$  and  $I_{\text{cp}}$  values were derived from Dunton and Tomasko 1994).

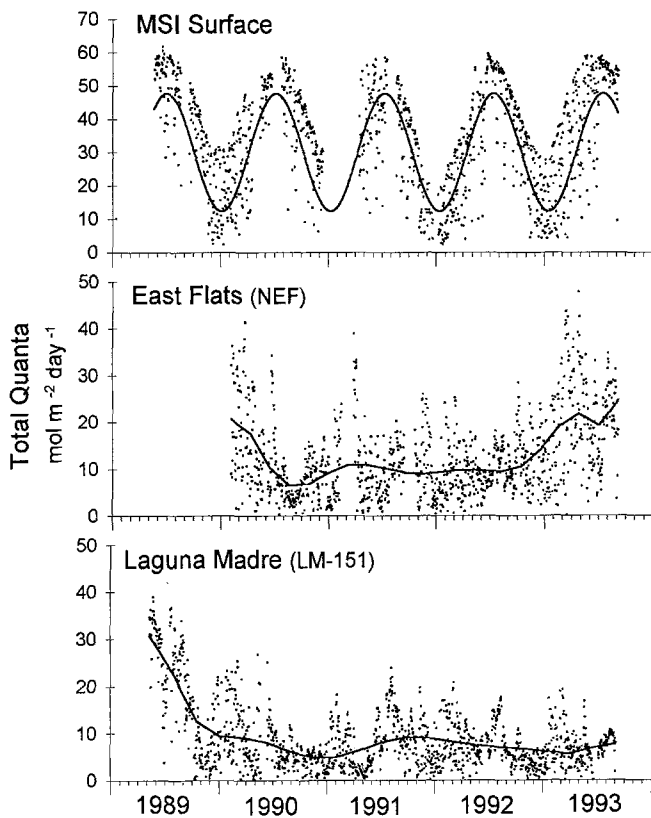
#### Seasonal growth and biomass measurements

Estimates of leaf growth and total plant biomass were made at LM-151, NEF and GBP adjacent to the light sensor at each site following the procedures outlined by Dunton (1990b). Measurements of total plant biomass were made at 2- to 3-mo intervals from four replicate samples collected with a 9-cm diameter coring device at each site. Samples were thoroughly cleaned of any epiphyte material in the laboratory, separated into above-ground and below-ground live biomass [to calculate root:shoot ratios (RSR)] and dried at  $60^\circ\text{C}$  to a constant weight. Results are expressed as total biomass

( $\text{g dry wt m}^{-2}$ ) of all shoot, rhizome and root material collected in each core. Measurements of leaf elongation rate and shoot production were collected using the leaf-clipping technique described by Virnstein (1982) for *Halodule wrightii* (the leaves of *H. wrightii* are too thin for leaf-tagging techniques). Shoots were clipped about 2 cm above the basal sheath to permit regrowth, and cores were collected from each clipped area to measure net growth at 3- to 6-wk intervals. In the laboratory, the length of the newly formed blades was recorded for individual shoots and all new blade material was pooled from each of four replicate cores for determination of shoot production on a dry weight basis. The mean leaf elongation rate for each replicate core sample was based on the measurement of 20 to 30 blades.

#### Statistics

Statistical analyses were performed on a 486 PC using a general linear model procedure (SAS Institute 1987). Significant differences in photon-flux density (PFD,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) among years and sites was



**Fig. 2** Daily total quantum flux measurements collected underwater (sites LM-151 and NEF) and at the surface (*MSI* Marine Science Institute) in Port Aransas from May 1989 to September 1993 based on continuous 1-h integrations. Surface data were explained by a simple cosine wave function. A tenth-order polynomial equation was used to fit a line to the underwater measurements

tested using a two-way block analysis of variance (ANOVA), where year and site are the two main treatment effects, and sampling time is the block, since light measurements were collected simultaneously at each site. In this case, "time" is the date and time recorded with each integrated light measurement. A one-way ANOVA was used to test significant differences in PFD between years at site LM-151.

A two-way ANOVA was used to test for significant differences in leaf elongation and plant biomass among years and sites. When a significant difference for a main effect ( $P < 0.05$ ) was observed, the means were analyzed by a Tukey multiple-comparison test to determine significant differences. Data were transformed when necessary to meet the assumptions of parametric statistics. Correlation coefficients were calculated using a least-squares fit between the various growth parameters and/or light.

## Results

### In situ PAR

The distinct seasonal variations in surface measurements of PFD collected between May 1989 and September 1993 were not reflected in underwater measurements of PAR collected over the same period at LM-151 or NEF (Fig. 2). Surface light ( $PAR_{surf}$ ) measurements followed a distinct

seasonal pattern that was explained well by a simple cosine (cos) wave function:

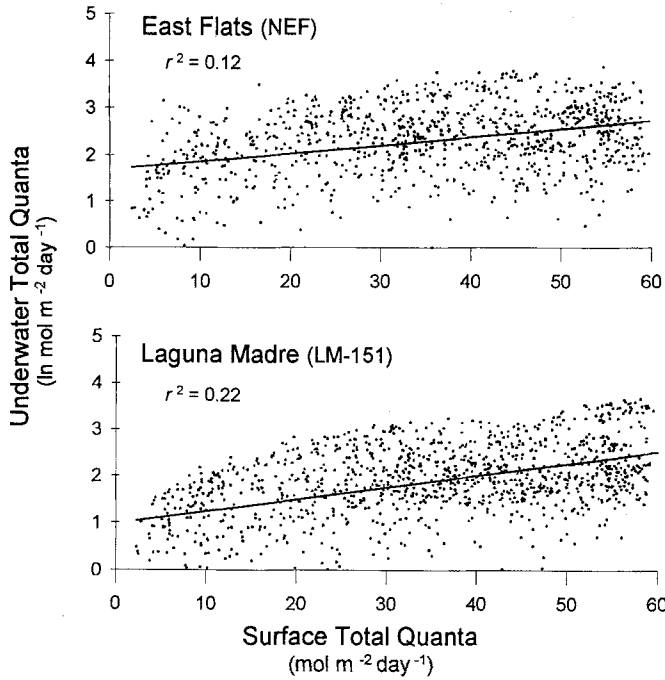
$$PAR_{surf} = A \cos \frac{2\pi t}{T} + c, \quad (2)$$

where  $A$  (amplitude) is one-half of the average annual variation in total quanta,  $t$  is time,  $T$  is the wavelength period, and  $c$  is a constant that is the sum of the amplitude and the average annual minimum quantum flux. On cloudless days, maximum winter midday values of PFD averaged about  $1250 \mu\text{mol m}^{-2} \text{s}^{-1}$ , compared to near  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  in summer; corresponding values of total daily quantum flux ranged from  $30 \text{ mol m}^{-2} \text{d}^{-1}$  (winter) to  $58 \text{ mol m}^{-2} \text{d}^{-1}$  (summer).

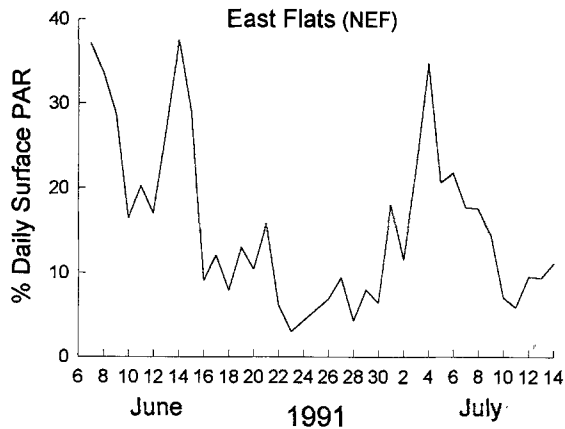
Underwater measurements of PFD were considerably more variable and showed no predictable pattern. A tenth order polynomial regression fit to the points showed that there was little seasonal variability in underwater PAR in contrast to the clear cyclic pattern in surface insolation. In Laguna Madre, quantum flux measurements averaged over  $30 \text{ mol m}^{-2} \text{d}^{-1}$  between May and October 1989, reflecting the exceptionally clear waters of this hypersaline lagoon (Fig. 2). However, with the onset of the brown tide chrysophyte bloom in late spring 1990 (Stockwell et al. 1993), light levels decreased to less than  $10 \text{ mol m}^{-2} \text{d}^{-1}$ , and dropped to only 2 to  $3 \text{ mol m}^{-2} \text{d}^{-1}$  in April 1991. The brown tide has persisted in Laguna Madre through summer 1993, and this is reflected in very low water visibility ( $< 30 \text{ cm}$ ) and low levels of underwater irradiance.

In contrast, quantum flux measurements at site NEF in Corpus Christi Bay have remained consistently above  $10 \text{ mol m}^{-2} \text{d}^{-1}$  with the exception of summer 1990, when the brown tide spread into this area from Laguna Madre (Fig. 2). Measurements of total PAR were highest during early spring 1990 and 1993 in conjunction with noticeable increases in water transparency (water visibility  $> 5 \text{ m}$ ). However, large day-to-day fluctuations in daily underwater irradiance, which are not related to surface PFD, are also apparent at NEF. The large variations in water transparency at both sites is reflected by the absence of a clear relationship between daily integrated surface and underwater light at LM-151 or NEF (Fig. 3). At both sites, values of  $r^2$  indicated that only 12 (NEF) to 22% (LM-151) of the variance could be explained by the linear model. The incidental nature of these variations is reflected in Fig. 4, which shows the changes in the percentage of surface PFD at NEF on a daily basis during June and July 1991. Measurements of total daily irradiance at GBP (not shown) collected between May 1990 and April 1991 were also characterized by day-to-day variations of similar magnitude. Quantum fluxes at GBP averaged about  $10 \text{ mol m}^{-2} \text{d}^{-1}$  through September 1991 but then dropped to less than  $5 \text{ mol m}^{-2} \text{d}^{-1}$  from October through early May 1991, when *Halodule wrightii* disappeared from the deeper (ca. 0.6 m) areas of this site.

The total annual quanta received by *Halodule wrightii* at sites LM-151, NEF, and GBP are shown in Table 1. Since the onset of new growth in *H. wrightii* begins in May, annual budgets are based on the period 1 May through 30



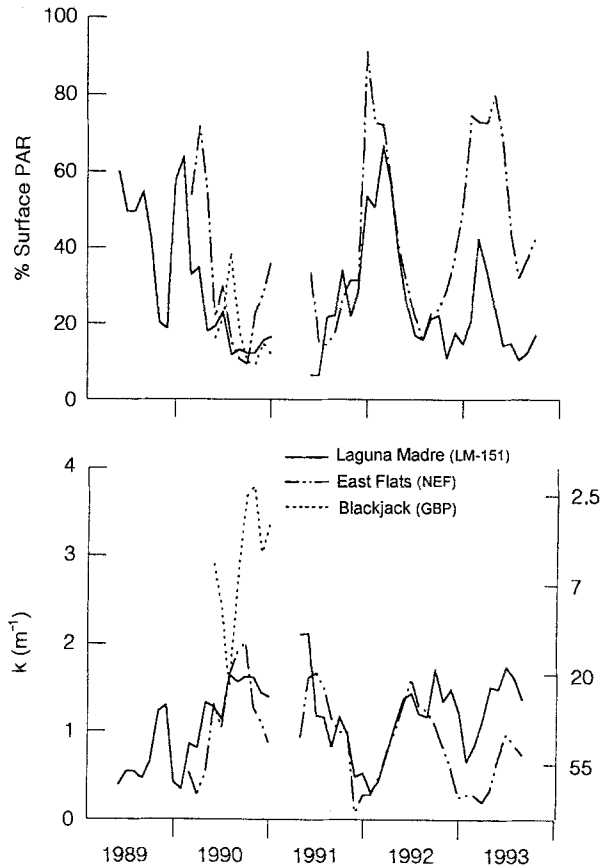
**Fig. 3** Relationship between coincident measurements of surface and underwater daily total quantum flux at sites LM-151 and NEF



**Fig. 4** Daily variations in percent surface irradiance (%SI) at site NEF in Corpus Christi Bay during June and July 1991. The short term changes in %SI shown here are normally associated with the effects of storm and related wind events on water turbidity. (PAR photosynthetically active radiation)

April. Values range from a maximum of 5672 mol m<sup>-2</sup> yr<sup>-1</sup> in growth year (GWYR) 1989 at LM-151 to a low of 2162 mol m<sup>-2</sup> yr<sup>-1</sup> at LM-151 in GWYR 1990.

Consistently lower levels of PAR (2200 to 3000 mol m<sup>-2</sup> yr<sup>-1</sup>) have been recorded at LM-151 since the onset of the brown tide algal bloom in late spring 1990. In GWYR 1989, prior to the brown tide, total annual PAR was significantly higher ( $P < 0.05$ ) than in all subsequent years at this site. Light levels at NEF between 1990 and 1992 ranged from 3300 to 5100 mol m<sup>-2</sup> yr<sup>-1</sup>, similar to LM-151 in GWYR

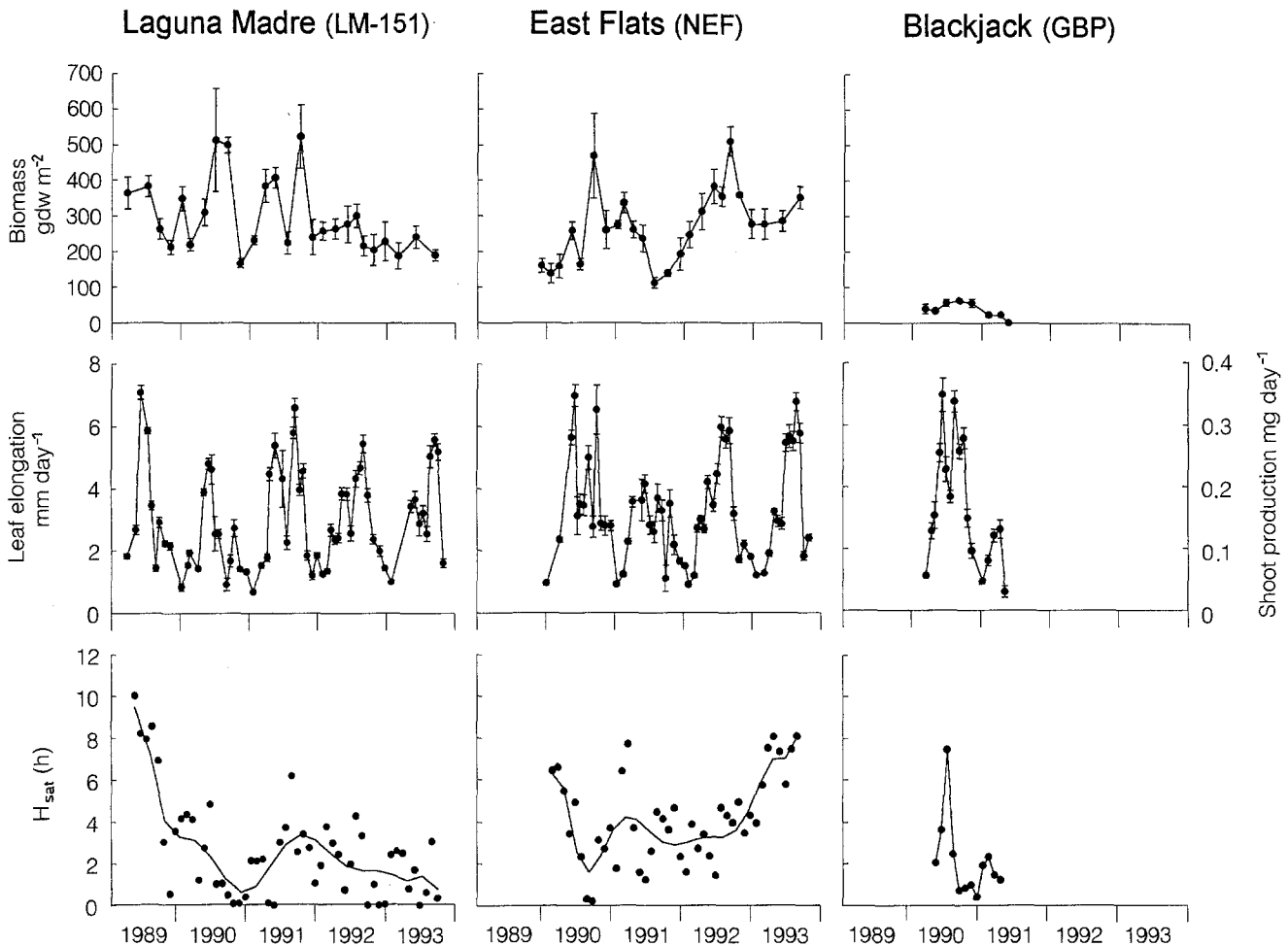


**Fig. 5** Measurements of water transparency at three estuarine sea-grass beds in south Texas over a 4-yr period. Top panel: percentage of surface irradiance (% SI); bottom panel: diffuse attenuation coefficient expressed as  $k$ -values (left axis) and as % m<sup>-1</sup> (right axis). Underwater measurements were made at canopy levels at the deep edges of *Halodule wrightii* beds at LM-151 (1.3 m), NEF (1.2 m), and GBP (0.6 m)

**Table 1** *Halodule wrightii*. Total annual quanta received by sea-grass plants in three estuarine systems in south Texas in 1989, 1990, 1991 and 1992, based on 12-mo periods that begin on 1 May. (LM-151 Laguna Madre; NEF East Flats; GBP Blackjack Peninsula; nd no data)

Growth year	Total irradiance (mol m <sup>-2</sup> yr <sup>-1</sup> )			
	Surface	LM-151	NEF	GBP
1989	12555	5672	nd	nd
1990	14417	2162	3343	2276
1991	10528	3042	3300	nd
1992	12526	2441	5122	nd

1989 but generally much higher than recorded in all other years at LM-151 and at GBP. In GWYR 1990, PFD was significantly higher ( $P < 0.05$ ) at NEF than at LM-151 or GBP, which were not significantly different ( $P > 0.05$ ) from each other. Comparison of coincident measurements of irradiance at LM-151 and NEF over the entire period of study showed that PAR was significantly greater ( $P = 0.0001$ ) at NEF than at LM-151.



**Fig. 6** *Halodule wrightii*. Total plant biomass (top panel), leaf elongation (center panel) and levels of  $H_{sat}$  (bottom panel) within three seagrass beds located in Laguna Madre (*LM-151*), Corpus Christi Bay (*NEF*) and San Antonio Bay (*GBP*). Values are  $\bar{x} \pm SE$  for biomass ( $n=4$ ) and leaf growth ( $n=80$  to 120 blade measurements). Corresponding values for shoot production based on linear regression analysis are shown on the right axis. Estimates of  $H_{sat}$  are based on an  $I_k$  value of  $315 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Dunton and Tomasko 1994). Plants at GBP died in spring 1991 following an 8-mo period in which most  $H_{sat}$  values remained less than 2 h. A tenth-order polynomial equation was used to fit a line to the  $H_{sat}$ -values from LM-151 and NEF

est at GBP despite its shallower depth, generally ranging from 9 to 22% SI, compared to either NEF or LM-151, in which most values ranged from 15 to 60% SI. No distinct seasonal trends were apparent, although water transparency appeared slightly higher during the winter months based on lower values for  $k$  and higher values of % SI at NEF (all years) and LM-151 (all years but 1990/1991). The highest diffuse attenuation coefficients at LM-151 ( $k=2.1$ ) occurred in April and May 1991 and corresponded to low levels of PAR (Fig. 2) and to record high chlorophyll *a* concentrations in the water column (Stockwell et al. 1993). Average  $k$ -values were 0.7 and 1.2 at LM-151 (before and after the start of the brown tide, respectively), 0.9 (NEF) and 2.9 (GBP).

#### In situ water transparency

The percentage of surface irradiance reaching the bottom at each site (% SI) and corresponding values for the diffuse attenuation coefficient  $k$ , were based on integrated monthly measurements of total surface and underwater PAR and average water depth at the sensor location for each site (Fig. 5). Water depths ranged from 0.6 m at GBP (SD=0.15,  $n=20$ ) to 1.2 m at NEF (SD=0.15,  $n=46$ ) and 1.3 m at LM-151 (SD=0.12,  $n=53$ ).

Of the three sites, GBP was the most turbid, with most  $k$ -values ranging from 2.5 to 3.8, compared to much lower values at NEF and LM-151 ( $k=0.2$  to 2.1). The percentage of surface irradiance-reaching the bottom was also low-

#### Variations in seasonal growth and biomass

Vegetative biomass of *Halodule wrightii* showed large seasonal changes at all three sites (Fig. 6). At site LM-151, total biomass between March 1989 and September 1991 ranged from ca. 200 to over  $500 \text{ g dry wt m}^{-2}$ , with higher values recorded during summer. Since fall 1991 however, biomass had not exceeded  $300 \text{ g dry wt m}^{-2}$  and declined in 1993 to less than  $200 \text{ g dry wt m}^{-2}$ . The decline in total biomass was at the expense of below-ground tissues, as re-

flected in a two-fold drop in RSR, which declined from their annual winter maximum of 5.4 in 1989 to 2.3 in winter 1993 (Table 2). This represents nearly a 50% decline in below-ground biomass over a 3-yr period. In December 1993, total biomass at LM-151 dropped to the lowest levels yet recorded over the entire study period ( $< 100$  g dry wt  $m^{-2}$ ; Dunton unpublished data). At NEF, biomass varied from ca. 150 to over 500 g dry wt  $m^{-2}$ , and peak RSR values ranged from 2.3 (1991) to 4.0 (1992). At GBP, biomass was significantly ( $P < 0.05$ ) lower than at LM-151 or NEF, dropping from a high of 62 g dry wt  $m^{-2}$  in September 1990 to 22 g dry wt  $m^{-2}$  in April 1991 (peak RSR was 3.5 in late 1990) before the plants completely disappeared at 0.6 m depths, although they continued to be widely distributed at shallower depths at this site.

Strong and consistent seasonal patterns in leaf elongation and shoot production were noted in *Halodule wrightii* plants among the three sites (Fig. 6). As reported previously for south Texas waters (Dunton 1990b), a significant ( $P = 0.0001$ ) positive correlation was found between leaf elongation rate and shoot production in *H. wrightii* ( $r^2 = 0.57$ ;  $P = 0.0001$ ). The linear relationship is given by the equation  $Y = 0.05x + 0.008$ , similar to the regression equation of  $Y = 0.04x + 0.003$  reported by Dunton (1990b) for *H. wrightii* from other locations in Texas.

Distinct seasonal patterns of leaf elongation at all three sites were apparent over the period of the present study.

On an annual basis, a peak period of growth in *Halodule wrightii* (4 to 7  $mm d^{-1}$ ) occurs between early May and mid-June; this period of high growth is usually followed by a second interval of elevated growth in late summer. Rates of leaf elongation drop rapidly during the autumn, reaching a minimum of less than 1  $mm d^{-1}$  by January. Comparison of peak spring elongation rates among sites and years showed that leaf elongation was significantly lowest in 1991 at GBP ( $P < 0.05$ ); by late May 1991 the plants at site GBP at 0.6 m had disappeared entirely following a rapid decrease in both leaf growth and plant biomass (Fig. 6).

In Laguna Madre, growth rates during the spring period of rapid growth were significantly highest ( $P < 0.05$ ) in 1989, before the onset of the brown tide (7.1  $mm d^{-1}$ ). Spring leaf elongation rates decreased 24% in 1990, and were 46% lower (3.6 to 3.8  $mm d^{-1}$ ) in 1992 and 1993. Since 1991, decreases in spring growth have been at least partially compensated by a distinct late summer/early autumn rise in leaf growth ( $> 5.4$   $mm d^{-1}$ ). This predictable pattern in leaf elongation is clearly not associated with variations in underwater PAR (as reflected by  $H_{sat}$ ), but is coincident with the constant decrease in plant RSR values that have occurred since 1990. At site NEF, most leaf growth occurred during summer, and the peak in spring leaf elongation was not as pronounced, although overall growth was greater at NEF than at LM-151 in all years but 1991.

**Table 2** *Halodule wrightii*. Annual values (means  $\pm$  SE,  $n = 4$ ) of maximum root:shoot ratios (RSR) recorded in winter at the study sites between 1989 and 1993. All measurements based on samples collected in winter, when values for RSR reach their annual peak. (LM-151 Laguna Madre; NEF East Flats; GBP Blackjack Peninsula; nd no data)

Growth year	RSR		
	LM-151	NEF	GBP
1989	5.4 $\pm$ 0.3	2.9 $\pm$ 0.5	nd
1990	4.3 $\pm$ 0.8	3.3 $\pm$ 0.4	3.6 $\pm$ 0.9
1991	3.5 $\pm$ 0.4	2.3 $\pm$ 0.5	nd
1992	2.3 $\pm$ 0.5	4.0 $\pm$ 0.6	nd

#### Estimates of $H_{sat}$ and $H_{comp}$

Values for  $H_{sat}$  and  $H_{comp}$  were calculated from estimates of saturation and compensation irradiance for *Halodule wrightii* reported by Dunton and Tomasko (1994). Measurements of saturation irradiance from both in situ incubations of whole plants [ $H_{sat(field)}$ ] and from laboratory experiments on leaf tissue [ $H_{sat(lab)}$ ] were used in calculating  $H_{sat}$  and are shown in Table 3 alongside values of  $H_{comp}$  for entire plants.

Annual daily averages of  $H_{sat(field)}$  for growth years 1989 to 1993 dropped about 50% in Laguna Madre (from 5.2 to less than 2.8 h) following the onset of the brown tide

**Table 3** *Halodule wrightii*. Average daily number of hours that photon-flux density fell above saturation irradiance ( $H_{sat}$ ) and compensation irradiance ( $H_{comp}$ ) at three sites in south Texas (LM-151, NEF, GBP) for growth years 1989 through 1992.  $H_{sat}$  values are based on both in situ estimates of saturation irradiance in entire plants

[ $H_{sat(field)}$ ] and on laboratory experiments using leaf segments [ $H_{sat(lab)}$ ] as reported by Dunton and Tomasko (1994). Data for  $H_{comp}$  are based on whole plant estimates of compensation irradiance. (nd no data)

Growth year	$H_{sat(field)}^a$ (h)			$H_{sat(lab)}^b$ (h)			$H_{comp}^c$ (h)		
	LM-151	NEF	GBP	LM-151	NEF	GBP	LM-151	NEF	GBP
1989	5.2	nd	nd	8.4	nd	nd	8.9	nd	nd
1990	1.4	3.3	2.1	5.7	7.2	5.3	6.5	7.8	6.0
1991	2.8	3.0	nd	6.9	7.2	nd	7.5	7.8	nd
1992	1.6	4.5	nd	6.5	8.6	nd	7.3	9.1	nd

<sup>a</sup>  $I_{k(field)} = 315 \mu mol m^{-2} s^{-1}$

<sup>b</sup>  $I_{k(lab)} = 101 \mu mol m^{-2} s^{-1}$

<sup>c</sup>  $I_{cp} = 80 \mu mol m^{-2} s^{-1}$

in June 1990. Estimates of  $H_{\text{comp}}$  and  $H_{\text{sat(lab)}}$ , which were greater than 8 h in GWYR 1989, also decreased, but to a lesser extent (to 6–7 h). At site NEF,  $H_{\text{sat(field)}}$ -values ranged from 3 to 4.5 h, compared to 2.1 at GBP; estimates of  $H_{\text{comp}}$  ranged from 8 to 9 h at NEF and were 6 h at GBP in GWYR 1990. The difference in values for  $H_{\text{sat(lab)}}$  and  $H_{\text{comp}}$  were generally less than 10%.

Variations in monthly averages for  $H_{\text{sat(field)}}$  varied from nearly zero at all sites to 6–10 h. In Laguna Madre,  $H_{\text{sat}}$ -values rarely exceeded 4 h after June 1990 when plant biomass began to slowly decline but were frequently greater than this at NEF; at GBP, spring 1990 leaf elongation in *Halodule wrightii* decreased and the plants subsequently died following an 8-mo period in which all but one monthly  $H_{\text{sat(field)}}$ -value was less than 2 h (Fig. 6).

Generally,  $H_{\text{sat}}$ -values for the period 1 April to 30 September, the most active period of growth for *Halodule wrightii* at all sites, were nearly the same as the 12-mo annual averages listed in Table 2. At LM-151, the average  $H_{\text{sat}}$  in 1989 for the 6-mo period ending 30 September was 8.2 h but then dropped precipitously in subsequent years to 1.7 h (1990), 2.6 h (1991) and 2.1 h (1992). Despite the four-fold drop in  $H_{\text{sat}}$  in response to the brown tide since 1990, maximum rates of spring/summer leaf elongation have remained close to  $6 \text{ mm d}^{-1}$  (Fig. 6), although total biomass and RSR values have declined during the same period. At NEF,  $H_{\text{sat}}$  for the spring/summer period averages 2.7 h (1990), 2.8 h (1991), and 3.4 h (1992); at GBP,  $H_{\text{sat}}$  was 2.4 in 1990. The trends of decreasing biomass at LM-151 and increasing biomass at NEF (Fig. 6) will likely continue into 1994 based on 1993 spring/summer  $H_{\text{sat}}$ -values, which dropped to a low of 1.2 h at LM-151 but rose to 7.1 h at NEF.

## Discussion

### In situ light requirements of *Halodule wrightii*

The continuous measurements of surface and underwater PFD collected in the present study provide the first estimates of the annual quantum flux received by seagrasses in their natural environment. For *Halodule wrightii* populations growing under ideal conditions at an average depth of 1.25 m, the annual light dose ranged from 5110 to  $5700 \text{ mol m}^{-2} \text{ yr}^{-1}$ , which corresponds to 41 to 46% SI based on an average surface irradiance of  $12506 \text{ mol m}^{-2} \text{ yr}^{-1}$ ; Table 1). Under these conditions, *H. wrightii* exhibited high rates of spring/summer leaf elongation ( $\geq 6 \text{ mm d}^{-1}$ ) and a high RSR ( $\geq 4.0$ ). In contrast, populations of *H. wrightii* exposed to quantum fluxes ranging from 2200 to  $2400 \text{ mol m}^{-2} \text{ yr}^{-1}$ , equivalent to 17 to 19% SI, showed signs of light stress as reflected in either significant decreases in spring leaf elongation with coincident drops in plant biomass and RSR values (site LM-151) or a decrease in biomass that led to the complete disappearance of the population (site GBP). It is noteworthy that plants at LM-151 and GBP were exposed to similar

light levels, although the average depth at both sites differed by more than two-fold (1.3 vs 0.6 m, respectively).

Based on the measurements presented in this paper, *Halodule wrightii* plants in Texas require at least 2200 to  $2400 \text{ mol m}^{-2} \text{ yr}^{-1}$  to achieve a positive net carbon balance in order to maintain a stable biomass. For comparison, the deepest growing kelps require 45 to  $71 \text{ mol m}^{-2} \text{ yr}^{-1}$ , which represents about 0.7% SI (Lüning and Dring 1979; Chapman and Lindley 1980; Dunton 1990 a). This annual total for kelp is equivalent to the amount of quanta received by *H. wrightii* plants over a 2- to 4-d period in late spring or early summer when daily fluxes are averaging 10 to  $30 \text{ mol m}^{-2} \text{ d}^{-1}$ .

To my knowledge, there are no published long-term measurements of underwater quantum flux in seagrass beds, although measurements of incident PAR have been reported. The seasonal pattern in daily photon flux reported at the surface in this study is similar to that predicted by models used to estimate oceanic primary production (Campbell and Aarup 1989) and for seagrass photosynthesis and growth (Wetzel and Neckes 1986). Large seasonal and daily differences in insolation were recorded by Wetzel and Penhale (1983) and Lindeboom and Sandee (1989) in studies that addressed photosynthetic production in seagrasses. However, Zimmerman et al. (1994) found that predicting seagrass production from surface insolation can result in large errors, especially if the daily in situ patterns of underwater PAR deviates from sinusoidal, as noted in the present study.

Although the spring-summer peak in leaf elongation corresponds with increased surface insolation as reflected in this study and others (Sand-Jensen 1975; Jacobs 1979; Kentula 1983), seasonal variations in insolation are poorly reflected in Texas estuarine waters (Fig. 3). Yet strong seasonal patterns of leaf elongation in *Halodule wrightii* occurred at all sites, including LM-151, where the brown tide has nearly eliminated any seasonal pattern in underwater irradiance (Fig. 2). Maintenance of seasonal patterns in shoot growth in Laguna Madre, despite a 50% drop in underwater light levels since 1990, may be partially attributed to the dependence of shoot growth on below-ground tissues, which have dropped nearly 50% at LM-151 since the start of the brown tide. The clear circannual rhythm of leaf elongation that occurs in *H. wrightii*, which is characterized by the onset of rapid leaf growth every May at all sites, regardless of underwater light conditions, has been noted before in seagrasses (Ott 1979). It is postulated that such rhythms are synchronized by an external Zeitgeber, such as daylength or temperature, which entrain circannual rhythms to a period of 12 mo or to shorter periods in the laboratory (Gwinner 1989; Lüning and Kadel 1993). Endogenous circannual rhythms have been found to control growth and/or reproduction in numerous animal species and a few higher plants (Spruyt et al. 1987; Gwinner 1989) and have become a promising and interesting topic of research in marine plants (Lüning 1991; Lüning and Kadel 1993).

Estimates of  $H_{\text{sat}}$  for *Halodule wrightii* were determined from underwater measurements of PAR and a knowledge



of photosynthetic performance in *H. wrightii*. In kelp, plant production is best correlated with  $H_{\text{sat}}$ , rather than total PAR (Dunton 1990 a), since  $H_{\text{sat}}$  incorporates information on the minimum light level required by a species to achieve maximum production. In *H. wrightii*,  $H_{\text{sat}}$ -values of about 2 h appear to be required for plant maintenance, but this is probably insufficient for net growth, based on our observations of plant biomass at LM-151 and GBP. For maintenance of above- and below-ground biomass and appreciable spring and summer growth,  $H_{\text{sat}}$ -values for this growth period ranged from about 3 to 8 h (NEF, all years; LM-151, 1989). These values agree well with estimates of  $H_{\text{sat}}$  predicted for *Zostera marina* by Zimmerman (1991) in San Francisco Bay (3 to 5 h), and those reported for *Z. marina* from Woods Hole (6 to 8 h) by Dennison and Alberte (1985). Values of  $H_{\text{sat(lab)}}$  based on laboratory measurements of photosynthesis were unreliable in predicting the response of *H. wrightii* to decreased PAR, and underscore the importance of accurate  $P$  vs  $I$  measurements in the modelling of plant production (Dunton and Tomasko 1994).

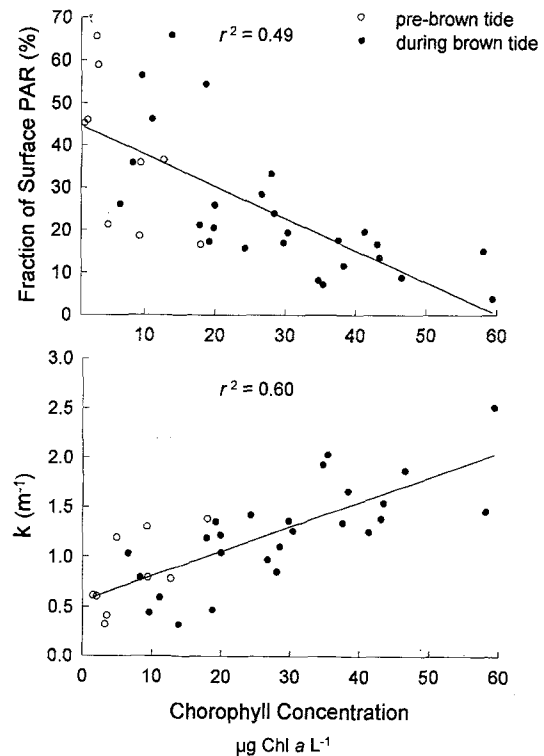
#### Maximum depth limits for *Halodule wrightii* in relation to water transparency

In a recent worldwide examination of the lower depth boundaries of seagrasses and their associated light attenuation coefficients, Duarte (1991) found that the average minimum light requirements for marine submergent vascular plants was about 11% SI. This value was later corroborated by Olesen and Sand-Jensen (1993), who found that the minimum light requirement for *Zostera marina* plants incubated under experimental conditions in the laboratory was equivalent to 8 to 11% SI. In the present study, the minimum light requirement for *Halodule wrightii* was much higher, averaging about 18% SI based on surface and underwater PFD measurements at three separate locations. Diffuse attenuation coefficients ( $k$ ) measured in this study were also much higher (commonly  $>1.0$ ) than those reported by Duarte (1991), all of which were nearly  $<1.0$ .

The large difference in the mean 11% SI estimate for the minimum light requirements for seagrasses predicted by Duarte (1991), compared to that found in this study (18% SI), is due to a number of important factors. The first is related to the higher photosynthetic light requirements of *Halodule wrightii* compared to other seagrasses (Dunton and Tomasko 1994). The use of spherical versus flat-plane cosine corrected sensors in the field and laboratory is another major consideration. In coastal and estuarine waters the underwater light field is considerably more diffuse due to the scattering of light by suspended particles, resulting in levels of scalar (diffuse) irradiance that may be 1.4 to 1.8 times the downward irradiance and 2.0 to 2.5 times greater in very turbid waters (Kirk 1983). Consequently, measurements of PFD using a cosine collector will underestimate the irradiance perceived by seagrass blades compared to a spherical quantum sensor, especially in coastal and estuarine waters of moderate turbidity.

Light attenuation coefficients calculated from Secchi disc measurements are also based on instantaneous measurements, and reflect downward irradiance. The uncertainty about the reliability of the Secchi disc in obtaining accurate optical information was recently resolved by Megard and Berman (1989), who now estimate Secchi depth at 22% SI, rather than the widely used value of 18% SI. The interpretation of surface irradiance, which reaches maximal values of about  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$  during summer at midday (Lindeboom and Sandee 1989; present study) has also been a source of confusion. Olesen and Sand-Jensen (1993), for example, mistakenly used a mid-day value of  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (B. Olesen personal communication) in predicting that the maximum irradiance experienced by eelgrass in situ was  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  (as opposed to  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). All of the factors listed above would contribute to a lower estimation of the minimum light requirements of seagrasses than that obtained here for *Halodule wrightii*.

In the present study, decreases in the maximum rates of leaf elongation in *Halodule wrightii* occurred at similar levels of annual quantum flux and  $H_{\text{sat}}$  at two distinct depths (1.3 and 0.6 m) owing to a large differences in water transparency. In both instances, the maximum depth of *H. wrightii* was about 18% SI, which is identical to the value obtained by Onuf (1994) for the maximum depth pen-



**Fig. 7** Relationship between water column chlorophyll *a* concentration and percentage of surface irradiance (top panel) and the diffuse attenuation coefficient,  $k$  (bottom panel). Data based on measurements of chlorophyll *a* (from Stockwell et al. 1993) and total diel photosynthetically active radiation (PAR) collected monthly over a 4-yr period at LM-151 in upper Laguna Madre

etration for *Syringodium filiforme* in the lower Laguna Madre. This value was based on underwater measurements of PFD using a spherical quantum sensor. In Florida, the minimal light requirements for *H. wrightii* and *S. filiforme* are estimated between 17 and 18% SI (W. J. Kenworthy personal communication as referenced by Dennison et al. 1993). In addition, preliminary results from shaded experimental plots containing *H. wrightii* suggest that light levels below  $2000 \text{ mol m}^{-2} \text{ yr}^{-1}$  (about 14% SI) are below the limits of survival for this species (Czerny 1994). The continued persistence of *H. wrightii* in Laguna Madre and the disappearance of this species at GBP, despite exposure to similar levels of irradiance, are attributed to the much larger size and longer establishment of the Laguna population and to the lower density of attached epiphytes on *H. wrightii* blades in Laguna Madre.

The large variation in  $k$ -values recorded in Texas estuarine waters reflect transient and unpredictable periods of high turbidity that make prediction of maximum depth limits difficult, even in Laguna Madre, where the relationship between chlorophyll  $a$  and water transparency (Fig. 7) is significant ( $P=0.001$ ). High chlorophyll  $a$  concentrations resulting from the brown tide chrysophyte bloom (Stockwell et al. 1993) increased values of  $k$  from an average of 0.7 (pre-brown tide) to 1.2 (brown tide). Chlorophyll  $a$  concentrations were  $< 15 \mu\text{g l}^{-1}$  before the brown tide but have since risen to concentrations that generally fluctuate between 20 and  $>80 \mu\text{g l}^{-1}$  (Stockwell et al. 1993), accounting for much of the variation in  $k$ -values that ranged from 0.3 to 2.1. Zimmerman et al. (1991) also noted that large variations in  $k$ , similar to those recorded in the present study, made it difficult to predict accurately the depth limit of eelgrass in San Francisco Bay. Evidence from this study, which is corroborated by recent work by Zimmerman et al. (1994), strongly suggest that in estuarine and coastal waters, continuous measurements of PAR are critical in developing the relationship between light availability and the depth distribution of seagrasses, and in establishing criteria for water transparency standards for maintenance of seagrass resources.

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