

# Seagrass responses to long-term light reduction by brown tide in upper Laguna Madre, Texas: distribution and biomass patterns

Christopher P. Onuf\*

National Biological Service, Southern Science Center, 6300 Ocean Drive, Corpus Christi, Texas 78412, USA

**ABSTRACT:** A brown tide caused by a very dense bloom of an as yet undescribed species of the new class Pelagophyceae was first reported in upper Laguna Madre, Texas, USA, in June 1990 and has been there continuously through December 1995. No change in response to reduced light was evident in the distribution of the seagrass *Halodule wrightii* along transects sampled before the brown tide in 1988 and resampled after initiation of the brown tide in 1991 and 1992; however, in winter 1993–94 losses were documented over 2.6 km<sup>2</sup> of bottom and by winter 1994–95 the area of vegetation lost had more than tripled to 9.4 km<sup>2</sup>. Changes in biomass presaged the changes in distribution. Decreases in biomass at depths >1.4 m were evident 2 yr before bare areas were detected. Reductions in biomass were more pronounced toward the south, in keeping with a gradient of increasing light attenuation from north to south. Support of a diminishing number of new shoots by reclamation of nutrients and stored reserves from senescing shoots and rhizomes may allow *H. wrightii* to persist under conditions of insufficient light for periods greatly in excess of the life span of any one shoot. This postulated capability would account for the pattern of diminishing biomass over time where the seagrass persists in deeper areas and the long lag between light reduction and change in distribution where the seagrass succumbed.

**KEY WORDS:** Distribution · Biomass · Seagrass · *Halodule wrightii* · Light · Irradiance · PAR · Brown tide · Subtropical Texas

## INTRODUCTION

Clear water is increasingly recognized as a key requisite for the development and maintenance of healthy seagrass meadows, and conversely, reductions in water clarity have been implicated in large-scale losses of seagrass (Kenworthy & Haunert 1991). The causes of reduced water clarity range from nutrient enrichment (Costa 1988, Lewis 1989, Pulich & White 1991, Batiuk et al. 1992, Dennison et al. 1993), to increased suspended loads resulting from hydrological alteration (Giesen et al. 1990) and frequent resuspension of dredge deposits (Onuf 1994). In most cases, the process of water clarity loss and seagrass decline has been the result of anthropogenic inputs and modifica-

tions, has occurred gradually over an extended period, has been accompanied by many structural and hydrologic changes of the coastal environment, and has occurred with little or no documentation of conditions before losses were noticed. Consequently, the connection between seagrass loss and water clarity can be difficult to document.

In contrast to a gradual, anthropogenically driven change, the advent of a brown tide in upper Laguna Madre, Texas, USA, in June 1990 resulted in almost instantaneous light reduction that has persisted to December 1995. Also, unlike many locations suffering diminished water clarity and seagrass loss, antecedent conditions were well documented. Seagrass distribution and biomass had been assessed in 1988 (Quammen & Onuf 1993), and a multidisciplinary study of the upper lagoon had been under way for a year when the brown tide began, and was continued for 3 yr after (Stockwell et al. 1993, Dunton 1994). These unusual

\*Present address: National Biological Service, Midwest Science Center, 6300 Ocean Drive, Corpus Christi, Texas 78412, USA. E-mail: chris\_onuf@nbs.gov

circumstances lend themselves to a particularly strong assessment of effects of reduced light on seagrass meadows. The abrupt and persistent reduction in light by the phytoplankton bloom is more akin to the manipulative field experiments of Backman & Barilotti (1976) and Dennison & Alberte (1982) than to the inferred reconstructions necessary in most trend analyses. However, the change of the light regime is on the scale of the whole ecosystem, not a tiny fragment.

The effect of the brown tide on the light regime of Laguna Madre was abrupt and large and of unprecedented persistence (Stockwell et al. 1993). Prior to the initiation of the brown tide, upper Laguna Madre was renowned for the clarity of its waters (Pulich 1980). In the 13 mo leading up to the beginning of the brown tide in June 1990, chlorophyll concentrations never reached as high as  $20 \mu\text{g l}^{-1}$ . In the next 11 mo, chlorophyll concentrations reached  $90 \mu\text{g l}^{-1}$  and seldom fell as low as  $20 \mu\text{g l}^{-1}$  (Stockwell et al. 1993, their Fig. 2). The brown tide alga, an undescribed species in the newly recognized class Pelagophyceae (DeYoe & Suttle 1994) was not seen before June 1990 but exceeded  $10^6$  cells  $\text{ml}^{-1}$  thereafter. Light transmission through the top 1 m of the water column dropped from a mean of 47 % the year before the brown tide to 19 % the first year of the brown tide (calculated from Stockwell et al. 1993, their Fig. 2). Continued sampling at one site documents that the influence of the brown tide persists. Annual total irradiance reaching the seagrass canopy in the 5 yr since the start of the brown tide has ranged from 33 to 54 % of what it had been the year before the brown tide began (Dunton 1994, pers. comm.). That the brown tide is largely responsible for the light reduction is indicated by a highly significant ( $p < 0.001$ ,  $r^2 = 0.60$ ) relationship between monthly measures of diffuse attenuation coefficient and chlorophyll concentration (Dunton 1994).

Here, I report an assessment of the spatial pattern and time course of effects of light attenuation by the brown tide on seagrass distribution and biomass afforded by resampling seagrasses in 1991, 1992, 1993 and 1994 at the same time of year along the same transects as were sampled in 1988. In addition, I predict the ultimate extent of seagrass loss owing to light reduction by brown tide by integrating reports of minimum light requirements for *Halodule wrightii* (Kenworthy et al. 1991, Onuf 1991, Dunton 1994, this study) with measurements of the underwater light regime and depth in different parts of the lagoon.

## METHODS

**Distribution.** Observations to detect effects of light attenuation by brown tide on a seagrass meadow dominated by *Halodule wrightii* were made in the upper

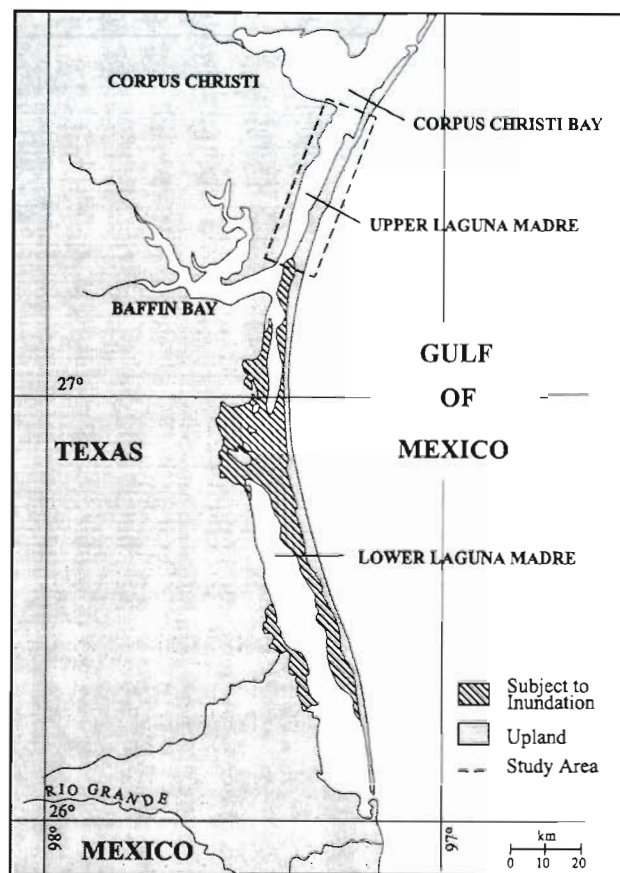


Fig. 1 Map of south Texas coastal region showing location of study area in the northern part of upper Laguna Madre (USA)

Laguna Madre of Texas north of Baffin Bay (Fig. 1), the part of the lagoon in which the brown tide was most prevalent. A survey used to determine the status of seagrasses in Laguna Madre in 1988 (Quammen & Onuf 1993, Onuf 1996) provided an assessment of seagrass distribution and biomass-depth relations before the brown tide. Sampling transects generally ran perpendicular from shore either west or east to the Gulf Intracoastal Waterway (Fig. 2). Dredge deposits on one side of the waterway or the other prevented continuous transects across the whole lagoon. Intervals between transects averaged 5 km. Sampling stations were 100 to 400 m apart, depending on location and proximity to a boundary, along 17 transects. Positions were determined by LORAN C or by dead reckoning in 1988, by LORAN C in 1991 and by Global Positioning System (GPS) in 1992, 1993, and 1994. Two transects were added to the sampling array in 1991 to provide more detailed coverage of deeper parts of the lagoon, where effects of light reduction by brown tide were expected to be most strongly expressed. All sampling was carried out in October and November, except that the 1992 sampling was not completed until 8 January 1993.

Four 80 cm<sup>2</sup> by 15 cm deep cores with plants were collected at each station 2.5 m apart along the port side of the boat. The time and depth were recorded at each, and depths for 1991, 1992, 1993 and 1994 surveys were standardized by adjusting measured depth by the deviation from mean sea level (MSL) at sampling time for the Texas Coastal Ocean Observation Network tide gauge at Bird Island, located near the

middle of the study area (Fig. 3). The difference between the mean depth of all stations on a transect in 1988, before installation of the tide gauge, and the mean of the depths corrected to MSL for the same LORAN coordinates in 1991 were used to refer 1988 depths to MSL.

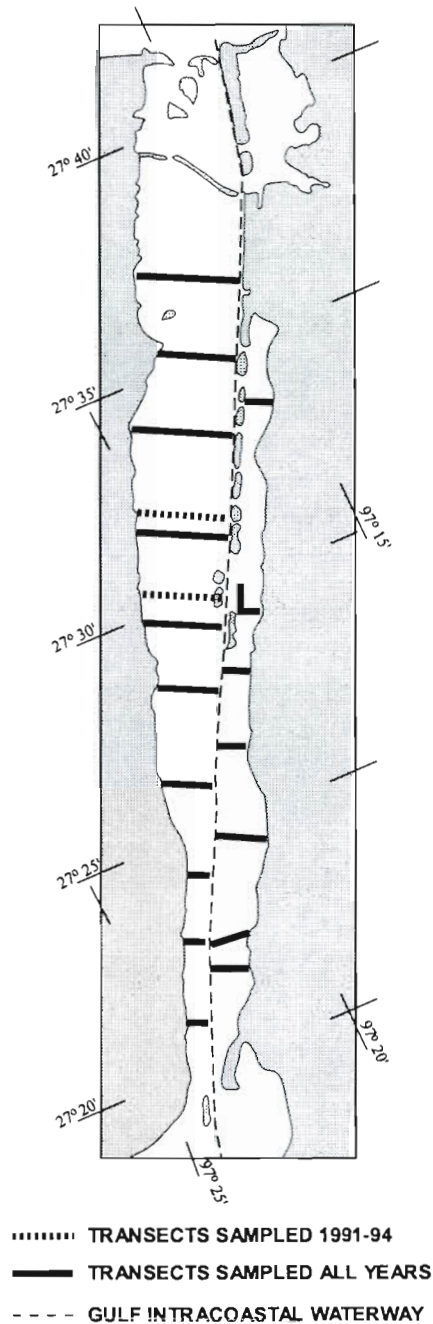


Fig. 2 Map of study area showing location of transects sampled in different years

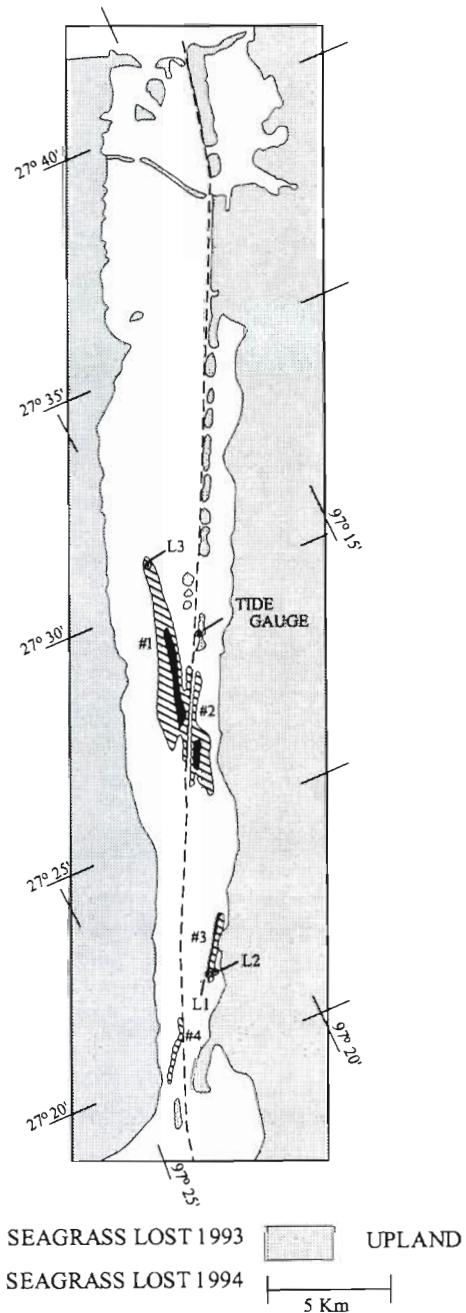


Fig. 3. Map showing location of light monitors, tide gauge and areas of seagrass cover lost during the brown tide. Light monitors are designated as in the text and in Table 1. Areas are numbered (#1–#4) as in the text and in Table 1. Dashed line indicates the course of the Gulf Intracoastal Waterway.



Cores were washed on 1 mm screens, the retained plant material identified, and the dominant and other contributors to cover recorded. Occurrence data were plotted on maps to depict the distribution of seagrasses.

In 1993 and 1994, the edges of bare areas were defined to  $<0.01'$  of longitude or latitude by repeatedly halving the interval between the last station where seagrass was encountered and the first station along the same transect that was bare (4 bare core samples and no seagrass rooted material pulled up on the anchor at that location). When vegetated and bare samples were  $0.01'$  or less apart, a stake was driven at the outermost vegetated station. These locations were also marked with a plastic line-float attached by a stainless steel cable secured to a screw-in anchor in some cases, because stakes sometimes disappeared between visits. Similar sampling was conducted between the regularly sampled transects and along the long axis of the bare areas to delineate the bare areas more closely. Differences in the location of the outer boundary between observations were determined by plotting on maps or were measured with a fiberglass tape. In January and February 1995, the locations of all surviving boundary markers were determined using differential GPS. In most cases, there was no ambiguity as to what was meadow and what was not. All samples at a station were either vegetated or bare. Patchy stations were mostly limited to a 20 m band at the outer edge.

**Biomass.** The retained material from 2 of the 4 cores from each station, randomly chosen by coin toss, was placed in plastic bags and returned to the laboratory on ice, where the samples were frozen until processed. Processing consisted of thawing and separating into live (turgid green and white to beige structures) and dead (flaccid brown to washed-out maroon) fractions. The live fraction was sorted further according to species and into aboveground (green portions of shoots) and belowground (root, rhizome, and unpigmented portions of shoots) fractions. The sample fractions were dried to constant weight at  $60^{\circ}\text{C}$  (72 h), weighed, ashed at  $530^{\circ}\text{C}$  for 3 h, and weighed again. Dry weight and ash-free dry weight were calculated for all plant parts and dead material and expressed on a  $\text{per m}^2$  basis.

Biomass samples were separated into depth classes to determine whether light attenuation resulting from the brown tide affected biomass. Depth classes were defined to yield a sample size of at least 10 in any year for statistical comparisons between years:  $<85$ ,  $85\text{--}115$ ,  $115\text{--}130$ ,  $130\text{--}140$ , and  $\geq 140$  cm depths. Variances were not equal between years regardless of transformation. Consequently, Mann-Whitney  $U$  tests were performed on pair-wise comparisons for 1988 vs 1993,

1991 vs 1993 and 1992 vs 1993 for each depth class to determine whether there was a cumulative effect over the whole period of the brown tide and whether effects could be discriminated over shorter periods, up to the last year for which biomass determinations were available. The expectation was that if light attenuation resulting from brown tide is affecting biomass, it will be manifested in reduced biomass in later years in the deeper depth classes. Other differences might suggest other causes.

**Light.** Underwater photosynthetically active radiation (PAR, 400 to 700 nm) was measured at 3 locations (Fig. 3): Stn L1, just inside the outer boundary of a meadow toward the south end of the study area ( $1.66$  m MSL,  $27^{\circ} 21.80' \text{ N}$ ,  $97^{\circ} 22.10' \text{ W}$ ); Stn L2, 200 m shoreward of the boundary location ( $1.52$  m MSL,  $27^{\circ} 21.80' \text{ N}$ ,  $97^{\circ} 21.96' \text{ W}$ ); and Stn L3, in a deep, continuously vegetated area near the middle of the study area ( $1.91$  m MSL,  $27^{\circ} 30.93' \text{ N}$ ,  $97^{\circ} 19.53' \text{ W}$ ). Underwater PAR measurements were made at 1 min intervals and integrated every hour on a continuous basis using an LI-193SA spherical quantum sensor inputting to an LI-1000 datalogger (LI-COR, Lincoln, NE, USA). The sensor was positioned at canopy level, the top of the sensor 25 cm above the bottom. The sensor was wrapped in transparent plastic wrap that was replaced at 1 or 4 wk intervals, depending on season, to minimize fouling. The periods of record were May 1993 to August 1994 for Stns L1 and L2 and October 1993 to August 1994 for Stn L3. Daily total fluxes of underwater PAR were referred to daily total fluxes of incident PAR as measured with a LI-190SA  $2\pi$  sensor mounted on top of a building at Port Aransas, Texas ( $27^{\circ} 52' \text{ N}$ ,  $97^{\circ} 03' \text{ W}$ ) by K. Dunton, University of Texas.

The spatial pattern of light attenuation in the lagoon was evaluated at approximately monthly intervals from March 1992 to November 1994 with a 20 cm diameter Secchi disc. Measurements were made and depth recorded at stations  $\sim 100$  m from the eastern and western shores of the lagoon and at the midpoint on east-west transects at  $27^{\circ} 20'$ ,  $22'$ ,  $26'$ ,  $30'$ ,  $34'$ ,  $38'$ , and  $40'$ . All Secchi depth determinations were made by the same observer outside the shadow of the boat and were the means of the depths of disappearance of the disk on descent and reappearance on ascent. Secchi depths were related to PAR at depth by simultaneously measuring Secchi depths and determining the percent of surface irradiance (SI) reaching Secchi depth with an LI-193SA spherical quantum sensor mounted on a lowering frame inputting to an LI-1000 datalogger on 22 June, 12, 13, 31 October, and 2, 3, 4, 7, 8 November 1994. Hourly wind data were obtained from Blucher Institute, Texas A&M University, Corpus Christi, Texas, for the Bird Island station of the Texas Coastal Ocean Observation Network (Fig. 3) to interpret

large differences in light attenuation for small Secchi depths. Conditions were classified as calm for winds  $<24 \text{ km h}^{-1}$  (15 miles  $\text{h}^{-1}$ ) at the time of light and Secchi measurements and for protected locations (within 200 m of shore on the lee side with respect to prevailing wind) regardless of wind speed. Conditions were classified as rough at exposed locations when wind speed was  $>24 \text{ km h}^{-1}$ .

The frequency of hourly observations of winds  $>24 \text{ km h}^{-1}$  from 1 October 1993 to 17 October 1995 was assessed to determine whether high light attenuation associated with rough water was likely to differ between the November to April period of frequent frontal passage and the May to October period of prevailing southeasterly breezes. Winds  $>24 \text{ km h}^{-1}$  were further categorized by direction according to  $90^\circ$  sectors centered on the long axis of upper Laguna Madre or at right angles to the long axis. The fetch of the winds aligned with the long axis was greater than for winds oriented cross-wise and presumably promoted the development of rougher seas.

These relations of % SI reaching Secchi depth were then used to compute diffuse attenuation coefficients corresponding with Secchi depths. The attenuation coefficients were applied to bathymetric profiles at intervals of 0.1' longitude along transects at intervals of 1' latitude to generate estimates of the proportion of surface light reaching the bottom according to the Beer's law relation:

$$I_z/I_0 = e^{-kz}$$

where  $I_z$  is photon flux density ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) at depth  $z$ ,  $I_0$  is photon flux density at the surface,  $k$  is diffuse attenuation coefficient ( $\ln \text{ m}^{-1}$ ), and  $z$  is depth (m). The mean of these values for all dates that Secchi

depths were measured was then computed as the long-term measure of available light at different depths in different parts of the lagoon. An estimate of 15% of surface light reaching canopy level, near the midpoint of the published range for the minimum light requirement of *Halodule wrightii* (Kenworthy et al. 1991, Onuf 1991, Dunton 1994), was then used to predict the ultimate extent of loss of seagrass likely to result from the prolonged occurrence of the brown tide.

## RESULTS

### Distribution

No change in seagrass distribution was evident between surveys of 1988 and 1991 or 1992, despite large reductions in light reaching the bottom in upper Laguna Madre after initiation of the brown tide in June 1990 (Stockwell et al. 1993). These conditions have persisted at least through December 1995 (Dunton 1994, pers. comm.). The first evidence of distributional change came from installation of a light monitor just inside the boundary of the seagrass meadow near the south end of the study area in May 1993. In November 1993, the outer boundary was 30 m landward of the monitor (Fig. 3: Area #3). Elsewhere, bare areas were encountered in November 1993 on 3 transects at stations that had been vegetated in 1992 (Fig. 3: Areas #1 and #2). In aggregate, 2.6  $\text{km}^2$  of seagrass meadow had been lost between observations (Table 1).

Boundary locations marked in November and December 1993 were reexamined in December 1994 and January-February 1995. Boundaries had receded from 50 to 800 m. In January 1995, Area #1 in the middle of the lagoon was 8 km long and on average 0.8 km wide (Fig. 3). On the other side of the Gulf Intracoastal Waterway, Area #2 extended 5 km, constricted by dredge disposal areas. The outer boundaries for Areas #3 and #4 in the south had retreated 140 m on average (Fig. 3). Over the whole period, 9.4  $\text{km}^2$  of seagrass has been lost, more than a 3-fold increase since winter 1993 (Table 1).

### Biomass

Trends in biomass over time differed according to depth (Fig. 4, Table 2). In the 2 shallowest depth classes, there was no change over time. In the 115–

Table 1. Statistics on extent of loss of seagrass cover in upper Laguna Madre (Texas, USA) since the advent of the brown tide. Area numbers (#1–#4) are as in the text and Fig. 3

Area	Width of meadow lost (m)			Length (m)	Area (km <sup>2</sup> )	Number of determinations of outer boundary
	Mean	Minimum	Maximum			
November 1992 or May 1993 to November 1993						
#1	330	260	550	5100	1.7	11
#2	560	—	—	1450	0.8	1
#3	30	30	30	3000	0.1	2
#4 not surveyed						
Total					2.6	
November 1993 to January 1995						
#1	770	220	1340	8100	6.2	20
#2	430	220	800	5400	2.3	15
#3	180	150	210	2700	0.5	4
#4	140	80	220	2900	0.4	4
Total					9.4	

130 cm depth class, the main difference was that biomass was >30% higher in 1991 than other years. The significant reduction in biomass between 1992 and 1993 is consistent with a brown tide effect; however, the lack of a significant difference between the pre-brown tide year and 1993 argues against this interpretation.

In the 130–140 cm depth class, biomass was elevated in 1991 also (Fig. 4). However, in this case, there was a significant reduction in biomass between the pre-brown tide year and 1993, the last year for which biomass data are available. The reduction from 1992 to 1993 was not significant (Table 2).

The strongest indication of a cumulative effect of brown-tide-caused light attenuation on seagrass biomass is the monotonic decrease of biomass over time in the  $\geq 140$  cm depth class (Fig. 4). Over the whole period, biomass diminished by >60%. The reductions were significant from 1988 to 1993 and from 1991 to 1993 but not from 1992 to 1993 (Table 2).

For the  $\geq 140$  cm depth class, spatial differentiation also was evident (Fig. 5). Biomass in the southern half of the study area was less than in the north in 1991 and 1992 but not in 1993 (Table 3).

Table 2. Mann-Whitney  $U$  tests for reductions in biomass in different depth classes for 3 time periods: 1988 vs 1993, 1991 vs 1993 and 1992 vs 1993.  $U$ : test statistic;  $z$ : standardized normal deviate;  $N$ : sample size earlier year, later year;  $p$ : probability

Depth class	Time period	$U$	$z$	$N$	$p$
<85	1988 vs 1993	164	-0.18	20, 17	0.43
	1991 vs 1993	148	-0.43	19, 17	0.33
	1992 vs 1993	209	-0.68	28, 17	0.25
85–115	1988 vs 1993	776	0.83	22, 63	0.20
	1991 vs 1993	1945	-0.91	68, 63	0.18
	1992 vs 1993	1685	0.45	51, 63	0.33
115–130	1988 vs 1993	133	-1.06	14, 24	0.14
	1991 vs 1993	338	2.69	19, 24	0.004
	1992 vs 1993	320	-1.69	36, 24	0.046
130–140	1988 vs 1993	124	-1.88	16, 24	0.03
	1991 vs 1993	71	-3.34	16, 24	<0.001
	1992 vs 1993	183	-0.84	18, 24	0.20
>140	1988 vs 1993	44	-3.69	10, 46	<0.001
	1991 vs 1993	512	-4.68	50, 46	<0.001
	1992 vs 1993	1086	-0.63	51, 46	0.20

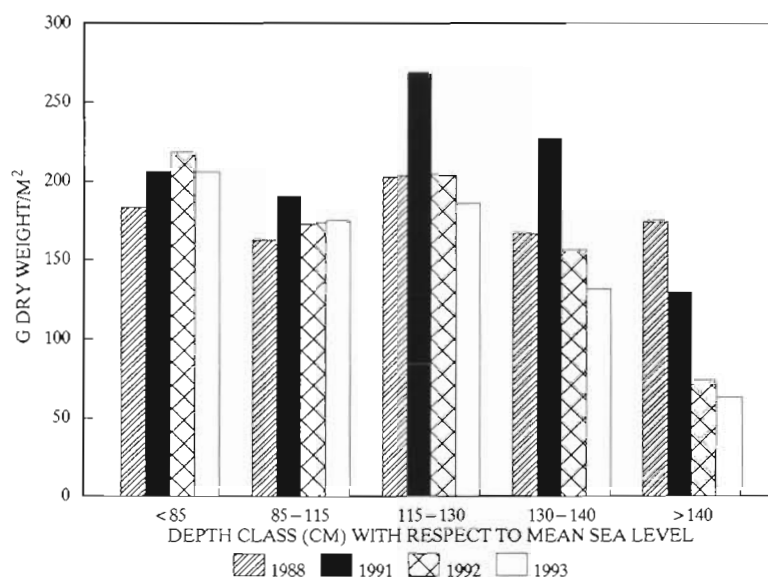


Fig. 4. Mean biomass in 5 depth classes over 4 yr: 1988, before the advent of the brown tide; and 1991, 1992, 1993, under the influence of the brown tide. See Table 2 for statistical comparisons

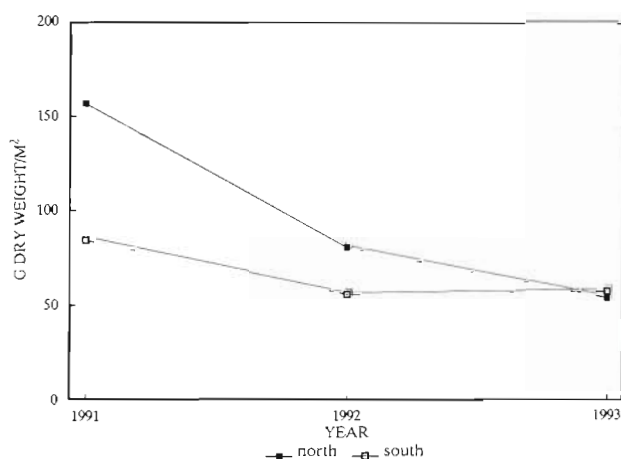


Fig. 5. Biomass in the >140 cm depth class in northern vs southern parts of the study area from 1991 to 1993. See Table 3 for statistical comparisons

Table 3. Mann-Whitney  $U$  tests for differences in biomass in the >140 cm depth class in the northern (less affected by brown tide) and southern (more affected by brown tide) parts of the study area in different years.  $U$ : test statistic;  $z$ : standardized normal deviate;  $N$ : sample size north, sample size south;  $p$ : probability

Year	$U$	$z$	$N$	$p$
1991	177	-3.7	28, 29	<0.001
1992	252	-2.1	30, 25	0.02
1993	358	0.45	29, 23	0.33



## Light

In May 1993, continuously recording underwater light monitors were installed at canopy height at the outer boundary of a seagrass meadow (Stn L1) and 200 m into the meadow (Stn L2) to document with precision minimum and sufficient levels of PAR to sustain established seagrass meadows. In October 1993 a third monitor was installed 17 km to the north in a deep site with continuous seagrass cover (Stn L3), with the intent of documenting the light environment at a clearer location. By December 1993, the outer boundary had receded 30 m landward from Stn L1 (Fig. 3). By January 1995, the outer boundary was within 30 m of Stn L2 and had receded past Stn L3 (Fig. 3). Over the period with records from all 3 stations (10 October 1993 to 21 August 1994), 9% of incident PAR reached canopy level at Stn L1, 14% at Stn L2, and 16% at Stn L3; however, the temporal distribution of percent of surface PAR reaching seagrass canopy level was highly variable and differed between locations (Fig. 6). A higher percentage of incident PAR reached the seagrasses in winter (November 1993 to March 1994) than in the spring-summer period of active growth (April to August 1994) at all stations. Much more light penetrated to canopy level at Stn L3 than at Stn L2 in winter

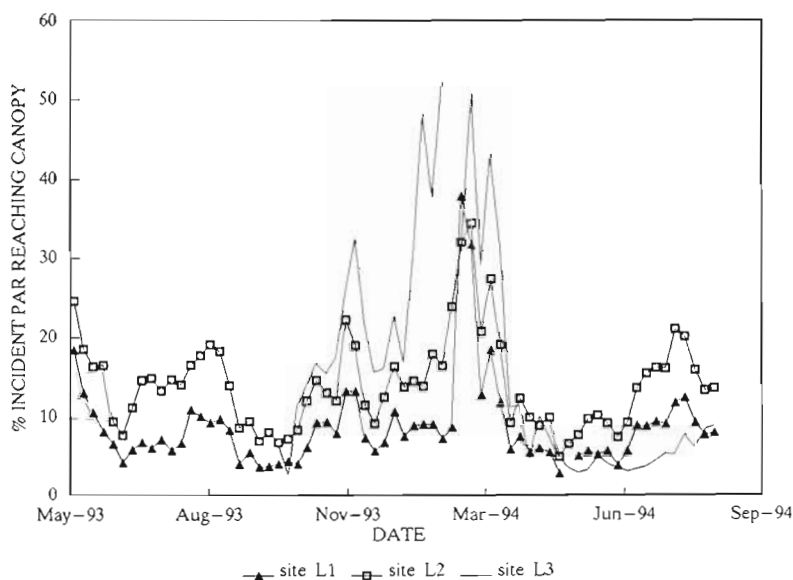


Fig. 6. Weekly mean percentage incident PAR reaching canopy level at 3 stations in upper Laguna Madre. See Fig. 2 for locations of monitors in relation to shifts in seagrass boundaries

(28 vs 18%), but the relationship was reversed the following spring and summer (6% of incident PAR reaching canopy level at Stn L3 vs 12% at Stn L2). By November 1995, seagrass had disappeared at Stn L2 as well.

Periodic Secchi disk measurements at stations throughout the study area revealed a north-south gradient in light attenuation (Fig. 7). Based on pooled data for 20 sampling dates and 1 to 3 stations on a latitude transect of sufficient depth to measure Secchi depths, the percent frequency of Secchi depths <60 cm (relatively high light attenuation) increased from 15 to 55 from the north end of the study area to the south, while the percent frequency of Secchi readings >100 cm (relatively clear water) decreased from 50 to 15. This increase in light attenuation from north to south is consistent with the higher biomass seen in the  $\geq 140$  cm depth range in the northern half of the study area than in the southern half in 1991 and 1992 (Fig. 5).

In order to apply this north-south gradient in Secchi depths to predictions of the area of seagrass likely to be lost in different parts of the study area as a result of brown tide shading, a correspondence had to be established between Secchi depth and light attenuation. The % SI reaching Secchi depth proved to be extremely variable, ranging from 15 to 40 (Fig. 8). For Secchi depths

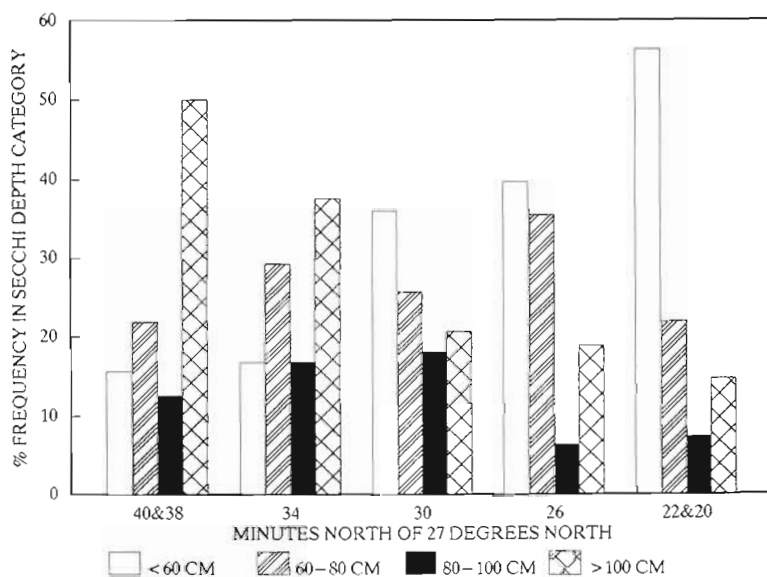


Fig. 7. Percentage frequency of observations in different Secchi depth categories along a latitudinal gradient in upper Laguna Madre, April 1992 to September 1994

>60, % SI reaching Secchi depth tended to decrease as Secchi depth increased. For Secchi depths <60 cm, % SI tended to be lower when winds exceeded  $24 \text{ km h}^{-1}$  at exposed locations ( $\bar{x} = 24$ ,  $\text{SE} = 2.1$ ) than for all locations when winds were  $<24 \text{ km h}^{-1}$  ( $\bar{x} = 30$ ,  $\text{SE} = 1.3$ ) and for protected locations when winds exceeded  $24 \text{ km h}^{-1}$  ( $\bar{x} = 31$ ,  $\text{SE} = 1.8$ ).

The difference in % SI for Secchi depths <60 cm between rough water conditions (stiff breeze, exposed locations) and calm (moderate breeze or protected location) was significant ( $t = 3.14$ ,  $\text{df} = 22$ ). Therefore, the mean of the 9 observations for exposed locations with winds  $>24 \text{ km h}^{-1}$  was taken as representative for rough conditions (24% SI reaching Secchi depth). For calm conditions, estimates of % SI were generated from the linear regression equation for all other points in Fig. 8:  $\% \text{ SI}_{\text{SD}} = 35.1 - 0.0698 \text{ SD}$  ( $r^2 = 0.37$ ,  $\text{df} = 39$ ), where SD is Secchi depth.

Winds exceeded  $24 \text{ km h}^{-1}$  39% of the time in the November to April period of frequent frontal passage compared to 15% of the time in May to October, based on the 2 yr of records analyzed for the monitoring station near Bird Island (Fig. 3). The difference was more pronounced for winds with long fetch, oriented along the long axis of the lagoon. They prevailed 17% of the time in November to April compared to 3% of the time in May to October.

The geographic survey of light attenuation by Secchi depth, the light versus Secchi depth relations and a bathymetric survey (Fig. 9) were then integrated to depict % SI at canopy height over the study area.

Because of the low frequency of winds  $>24 \text{ km h}^{-1}$  from May to October, especially oriented along the long axis of the lagoon, estimates of light at depth for that period were derived from the linear regression

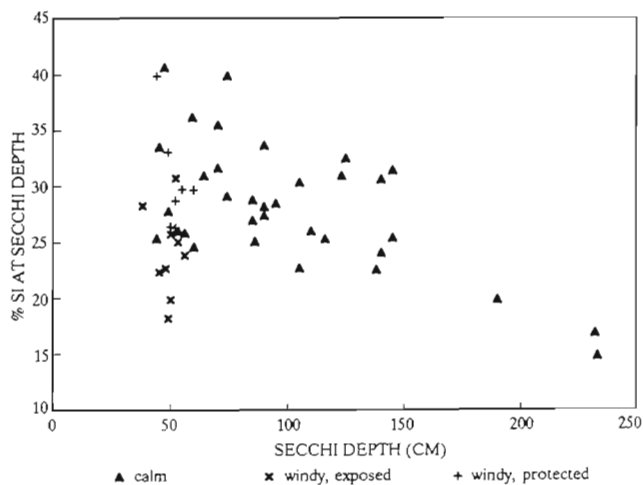


Fig. 8. Relationship between Secchi depth and percentage of incident PAR reaching Secchi depth under calm and rough conditions

equation for the 'calm' array of points in Fig. 8 ( $\Delta$  and + symbols). Short Secchi depths in November to March were assumed to be the result of episodes of sediment resuspension associated with winter storms. Consequently, the mean % SI for the 'rough' array in Fig. 8 was used for Secchi values <60 cm in November to April. The relationship for the calm array was used for Secchi depths >60 cm.

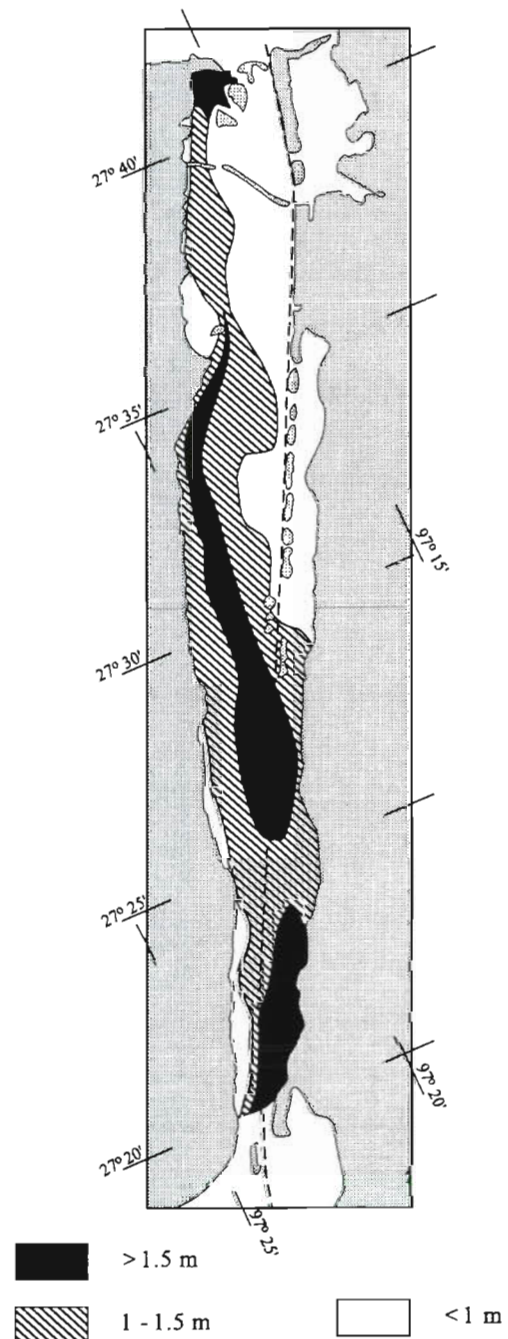


Fig. 9. Bathymetric map of study area. Dashed line marks the course of the Gulf Intracoastal Waterway. Small channels and emergent or shoal areas are not depicted.



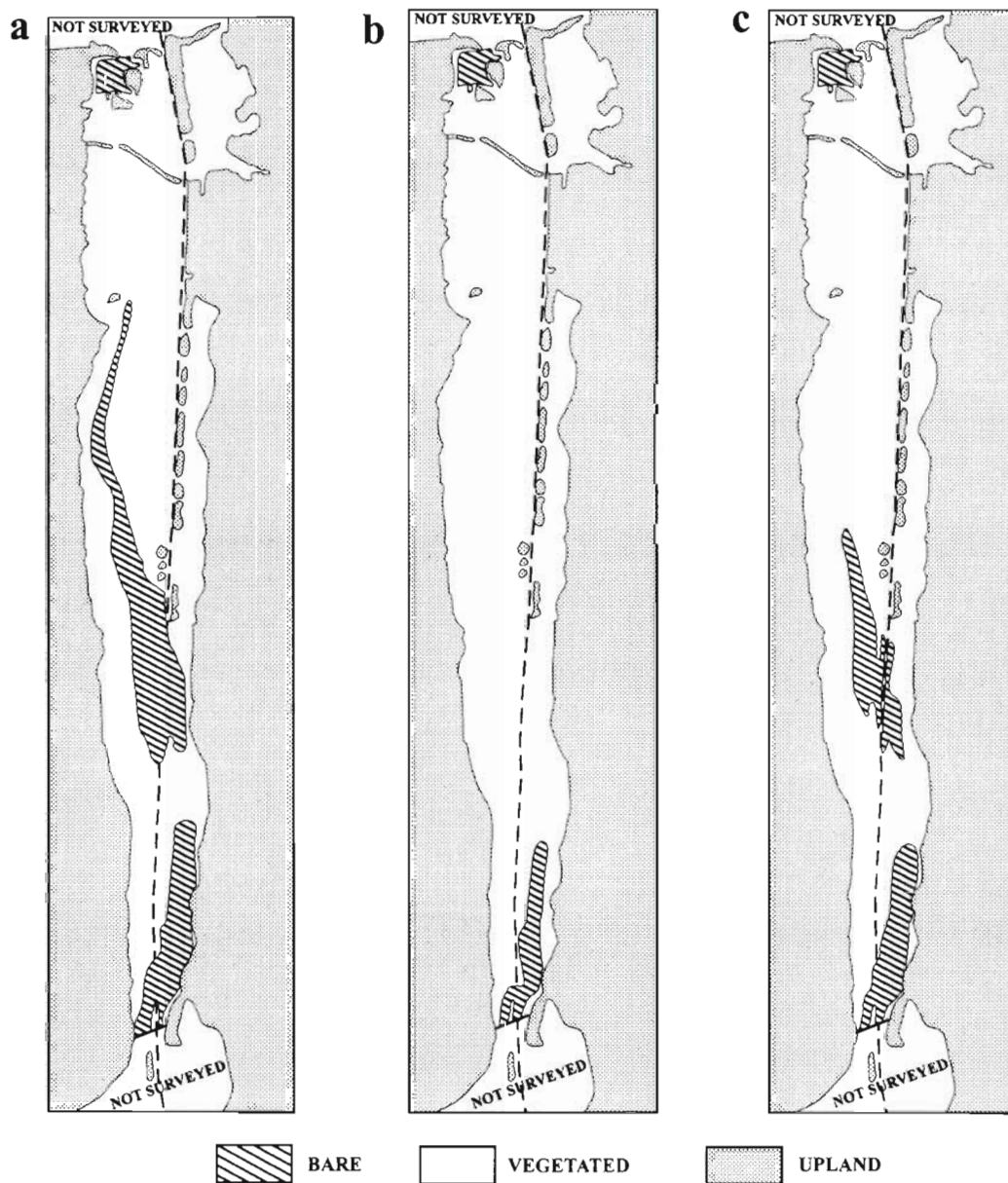


Fig. 10. Bare areas in upper Laguna Madre (a) predicted based on measured light attenuation, depth and assumption that <15% of incident PAR reaching canopy level is limiting to meadow development. (b) determined by survey October-November 1988, before advent of the brown tide; (c) determined by survey October-November 1994, after 4 growing seasons of brown tide. Dashed line indicates the course of the Gulf Intracoastal Waterway.

Applying the criterion that long-term mean light reaching canopy level must exceed 15% of incident PAR to sustain *Halodule wrightii* meadows (Kenworthy et al. 1991, Onuf 1991, this study) to the Secchi depth and light data of this study, the predicted maximum depth of seagrasses varied from 180 cm at 27° 38–41' N to 170 cm at 27° 34–37' N, 160 cm at 27° 30–33' N, 150 cm at 27° 26–29' N, and 140 cm at 27° 20–25' N. The northern part of the lagoon is mostly shallow (82% <1 m deep north of 27° 37' N compared to 22% <1 m deep south of 27° 30' N; Fig. 9). Therefore, if availabil-

ity of light is governing distribution in this system, a seagrass meadow should survive there, regardless of how long the brown tide persists. To the south, increasing light attenuation and deeper water yield predictions of larger expanses of bare bottom (Fig. 10a). In all, on the basis of measured light attenuation, 24% of the study area is predicted to be too deep to support seagrass meadow. In contrast, only 6% of the study site was bare before the advent of the brown tide (Fig. 10b). The greatest change in cover between pre-brown tide conditions and that predicted based on

Table 4. Final % of study area predicted to go bare if brown tide persists long enough for distribution of seagrasses to reach steady state with the light regime for different assumptions about minimum light requirements and relations between light attenuation and Secchi depth

% SI at Secchi depth	Minimum light requirement for <i>Halodule wrightii</i>	
	15% SI	18% SI
Varies with season and wind	18	24
Does not vary systematically (use mean for all conditions)	20	27

available light with brown tide is in the middle of the study area (Fig. 10a, b). Documented losses also are concentrated in the middle of the study area (Fig. 10c); however, as yet, the area predicted to go bare from measurements of the underwater light regime is considerably larger than what is bare (Fig. 10a, c).

Because the assumptions about the seasonality of light attenuation versus Secchi depth and the minimum light requirement for *Halodule wrightii* are subject to question, losses were estimated for 2 other assumptions. In one case, no systematic variation of % SI with respect to Secchi depth was assumed, and the mean for all 50 observations (27.8% SI reaching Secchi depth) was used to estimate % SI reaching canopy level (25 cm above bottom) under all conditions. In the other case, 18% SI was assumed to be the minimum necessary to support a seagrass meadow as reported by Dunton (1994), rather than the 15% suggested in this study. Both alternative assumptions lead to somewhat higher estimates of bare bottom at steady state with the brown-tide-influenced light regime than as described above (Table 4).

## DISCUSSION

The depth limit of seagrass meadows is commonly assumed to be set by light attenuation underwater (Bulthuis 1983, Orth & Moore 1983, Iverson & Bittaker 1986, Dennison 1987, Duarte 1991, Dennison et al. 1993). In this study, >50% reduction of light caused by a dense phytoplankton bloom compared to pre-bloom conditions had no discernible effect on distribution until after the fourth growing season under reduced light. However, an effect on biomass was seen sooner. Biomass at depths >140 cm was less in the first sampling after the initiation of the brown tide, after 2 growing seasons of reduced light, than before.

Four factors contribute to the apparent discordance between the magnitude of the environmental change and the expression of an effect on seagrass distribu-

tion. First, much of the lagoon is so shallow that even drastic light reduction would have no effect on distribution or biomass over much of the area. Almost 50% of the study area is <1.0 m deep, while the *Halodule wrightii* meadow extended at least to 1.8 m before the brown tide began. Second, there was a distinct gradient in light attenuation increasing from north to south. Since the long-term light record for the upper lagoon (Dunton 1994) is from the south, much of the lagoon was not subject to such severe light deprivation as measured there. Third, the resolution of the initial sampling program in 1988 was so coarse that substantial changes in distribution could have occurred without being detected. The original sampling design was patterned after an earlier survey of the lagoon (Merkord 1978) to maximize the power of the analysis for trends between studies (Quammen & Onuf 1993). This meant that relatively little effort was expended in the most critical areas for detecting possible effects of light limitation: deep areas with vegetation and the zone where vegetation terminated in deep water. Fourth, the morphology of the lagoon is such that the middle region is relatively flat, while the slope is relatively steep toward the edge. In the one part of the lagoon where the seagrass meadow terminated in deep, bare bottom, the outer boundary lay in this region of steeper slope. Therefore, any lateral shift in outer boundary corresponding to a decrease in the compensation depth for the seagrasses was relatively small.

Regardless of the characteristics of the sampling program diminishing its sensitivity to detect change resulting from light reduction, the area of bottom experiencing light reduction below that required to sustain a seagrass meadow was far in excess of the detection limits of the sampling program. One possible explanation for the persistence of an established seagrass meadow under conditions of limiting light is that surviving shoots cannibalize the resources of adjacent shoots as they succumb to light limitation. According to this conceptual model, an established meadow might be able to survive much longer under insufficient light than the life span of individual shoots would suggest by translocation of reserves from dying parts to rhizomes, analogous to the process of reclamation of nutrients and presumably other materials from senescent leaves to support new growth in *Zostera marina* (Pederson & Borum 1993). These resources might then subsidize survival of existing shoots and even development of new shoots. This progressive pooling of resources from a formerly larger population to support new growth in a progressively smaller population operating at a deficit would seem necessary to account for the persistence over years of a species in which the mean life span of individual shoots is 110 d (Gallegos et

al. 1994). Alternatively, the life span of individual shoots may be longer under conditions of light limitation than under the conditions assessed by Gallegos et al. (1994).

No data are available to evaluate the responses of populations of shoots; however, the gradual decrease in biomass in deep areas where *Halodule wrightii* persists is consistent with this proposed mechanism. If reclamation of nutrients and stored reserves is responsible for the persistence of seagrasses in Laguna Madre under conditions of light limitation caused by the brown tide, then a reduction in seagrass biomass over time should be evident in deeper parts of the lagoon where light is now limiting, compared to shallower areas where light remains sufficient. This trend was apparent. While there was no downward trend over time in seagrass biomass in depths up to 115 cm and equivocal changes between 115 and 140 cm, biomass diminished by >60% in the  $\geq 140$  cm depth range by the end of the 1993 growing season (Fig. 4). The fact that the reduction from 1992 to 1993 was not significant may signal that shoot density in deep areas has equilibrated with the low light conditions of the brown tide and that no more losses will occur. An alternative explanation is that the process of biomass loss continues, but the mean for the depth class has not changed, because some of the lowest biomass sites of 1992 had gone bare by 1993 and are not represented in the 1993 determination of mean biomass for vegetated samples.

Detailed observations by Dunton (1996) at one site where he had also collected continuous data on light reaching the bottom are consistent with this interpretation of persistence accomplished by reclamation of nutrients and other resources from dying parts. Peak biomass of rhizomes and roots based on quarterly determinations had diminished every year since the beginning of the brown tide, from  $>500 \text{ g m}^{-2}$  in 1989 to  $<200 \text{ g m}^{-2}$  in 1993.

The difference in biomass in deep water in 1991 and 1992 between the northern and southern parts of the study area (Fig. 5) is consistent with the gradient seen in water clarity (Fig. 7). If, as hypothesized, the light regime of the Laguna Madre is driving the changes in biomass and distribution observed over the last 6 yr, then the diminution of the north-south contrast in biomass in 1993 suggests that the latitudinal gradient in light has broken down. This is suggested by the continuous monitoring records for light at Stns L1 and L2 near the south end of the study area and Stn L3 near the middle of the study area (Fig. 6). The probable cause for the deterioration of water clarity at Stn L3 is that the bottom has gone bare around it (Fig. 3). Without an intact seagrass meadow to buffer the action of waves and the fabric of rhizomes and roots to bind the sediments, resuspension of bottom sediments is likely

to occur under calmer conditions than previously (Ward et al. 1984) and more frequently. An indirect effect may be the efflux of nutrients from the sediments as the recently dead seagrasses are remineralized, enhancing the growth of the brown tide organism.

Obviously, there is a limit to how long this holding action by seagrasses can go on, if indeed light has been reduced below the ecological compensation point (sensu Kenworthy et al. 1991). That limit was surpassed in some parts of the lagoon in 1993. Approximately  $3 \text{ km}^2$  of seagrass meadow went bare between distributional surveys made in fall 1992 and fall 1993, and the process of loss of seagrass cover has accelerated through fall 1994 (Fig. 3).

Predictions of how much further the losses might proceed are difficult to make because the light regime of the lagoon is not uniform and no determination of minimum light requirements was made before the advent of the brown tide. Therefore, it is necessary to use determinations made elsewhere of minimum light requirements to support development of continuous meadows of *Halodule wrightii* and evaluate them in terms of the measurements made in this study, when the outer boundaries were not fixed. Kenworthy et al. (1991), working in Hobe Sound, Florida, USA, and Onuf (1991), in lower Laguna Madre, calculated from long-term monitoring of light along transects crossing the outer boundary of meadows at many locations that the ecological compensation point for the species was where 12 to 20% of surface light reached canopy level. In this study, sites where 9 and 16% of incident PAR reached to the depth of the seagrass canopy over the 10 mo period of record had gone bare by December 1994. The remaining site where 14% of surface light reached canopy level had gone bare by November 1995. Two other studies from Texas closely bracket the minimum light requirement for *H. wrightii*. In a shading experiment in eastern Corpus Christi Bay, Texas, *H. wrightii* was eliminated within 9 mo when receiving 16% SI (Czerny & Dunton 1995). In upper Laguna Madre, *H. wrightii* persists at a site receiving an average of 18% SI since the advent of the brown tide (Dunton 1994). These results indicate that there is a region of uncertainty in the determination of minimum transmission of light required to sustain a seagrass meadow, but that 15% of incident PAR reaching canopy level is in the middle of that range. The difference in the seasonal patterns of light availability between Stns L2 and L3 (Fig. 6) may explain the anomaly of longer persistence of seagrass at the site with less light. Performance of the seagrasses is likely to be governed more strongly by light availability in the growing season than by availability over the whole year. Between April and August 1994, half as much light reached canopy



level at Stn L3 as at Stn L2, even though more light got to canopy level at Stn L3 over the whole period of record from October 1993 to August 1994.

These findings generally validate the estimate of minimum light necessary to maintain the seagrass meadow that was used in this study to project the ultimate extent of seagrass loss caused by the persistent brown tide. Therefore, the difference between the extent of bare bottom measured so far (Fig. 10c) and that expected on the basis of where light at canopy level drops below 15% of what reaches the surface of the water (Fig. 10a) suggests that considerably more seagrass will be lost before seagrass meadows of upper Laguna Madre come to equilibrium with the brown-tide-influenced light regime. This interpretation is least reliable for the northern part of the study area, where continuous records of underwater light are not available and where incursions of the brown tide are shorter and more sporadic than to the south. Here, the 1 to 2 mo intervals between sampling in the Secchi disc survey may not have been sufficient to represent the light regime, or there may have been episodes of clear water during the growing season sufficient to sustain seagrasses, despite low light for the year as a whole.

The weakest assumptions used in predicting the ultimate extent of seagrass cover to be lost as a result of brown tide shading are the choice of 15% of incident PAR reaching canopy level as the minimum light required by *Halodule wrightii* and the attribution of different Secchi depth versus PAR attenuation relationships (Fig. 8) to winter and summer periods based on their different wind regimes. Results using Dunton's (1994) estimate of 18% SI as the minimum requirement of *H. wrightii* and attenuation based on the mean of all observations of % SI yielded somewhat higher estimates of area of seagrass lost (Table 4). Since *H. wrightii* still survives at Dunton's (1994) site and has succumbed at the 3 stations with continuous light monitoring records in this study, the actual limit may lie between. I have no independent evidence to evaluate the relative merits of the alternative approaches for estimating light at canopy level from Secchi measurements.

Whether losses extend to 18 or 27% of the study area, they are of considerable concern, because they follow major losses of seagrass cover and displacement of *Halodule wrightii* by other species in lower Laguna Madre (Quammen & Onuf 1993). In aggregate, the area of *H. wrightii* in the Laguna Madre has diminished >30% between the mid 1960s and 1994. Laguna Madre is the primary wintering area of redhead ducks *Aythya americana*, and, while in residence, the redheads feed almost exclusively on *H. wrightii* (Cornelius 1977). Degradation of the forage stock in the lagoon is a particular concern, because some other tra-

ditional North American wintering areas such as Chesapeake Bay, Pamlico Sound and Galveston Bay have been abandoned already (midwinter waterfowl survey compilations, Office of Migratory Bird Management Files, U.S. Fish and Wildlife Service, Laurel, MD) and major modifications are proposed for the Laguna Madre de Tamaulipas, just across the delta of the Rio Grande in Mexico, the second most important redhead wintering area.

This study sheds no light on the critical question of how long the brown tide may last. Stockwell et al. (1993) reasonably speculated that regional drought and hypersalinity established conditions that favored the brown tide organism. Then a freeze-caused fish kill conceivably provided the limiting organic or inorganic compounds necessary to promote rapid growth. Limited water exchange and reduced grazing pressure undoubtedly contribute to unprecedented persistence of the brown tide (Stockwell et al. 1993); however, some additional source of nutrients also seems necessary (T. Whitledge pers. comm.), and ammonium is the most likely candidate, since the brown tide alga is not able to use nitrate (DeYoe & Suttle 1994). One possible source could be ammonium regenerated from dying seagrasses. If this is the case, the brown tide might be expected to persist as long as the seagrass meadows continue to recede. However, possible contributions from watershed sources cannot be discounted.

**Acknowledgements.** J. J. Ingold assisted in all phases of the study. L. J. Hyde assisted in the laboratory. K. H. Dunton kindly supplied data on incident PAR. Data on water level and wind speed and direction were kindly supplied by the Texas Coastal Ocean Observation Network, operated by the Conrad Blucher Institute for Surveying and Science at Texas A&M University, Corpus Christi. D. W. Hicks and B. B. Hardegree prepared final versions of maps. The manuscript has benefited from the comments of E. J. Buskey, K. H. Dunton, J. J. Ingold and 2 anonymous reviewers.

#### LITERATURE CITED

- Backman TW, Barilotti DC (1976) Irradiance reduction: effects on standing crop of the eelgrass *Zostera marina* in a coastal lagoon. *Mar Biol* 34:33–40
- Batiuk RA, Orth RJ, Moore KA, Dennison WC, Stevenson JC, Staver LW, Carter V, Rybicki NB, Hickman RE, Kollar S, Bieber S, Heasley P (1992) Chesapeake Bay submerged aquatic vegetation habitat requirements and restoration targets: a technical synthesis. US Environmental Protection Agency, Chesapeake Bay Program, Report CBP/TRS 83/92
- Bulthuis DA (1983) Effects of in situ light reduction on density and growth of the seagrass *Heterozostera tasmanica*, (Martens ex Ascher.) in Western Port, Victoria, Australia. *J Exp Mar Biol Ecol* 67:91–103
- Cornelius SE (1977) Food resource utilization by wintering redheads on lower Laguna Madre. *J Wildl Mgmt* 41:374–385
- Costa JE (1988) Eelgrass in Buzzards Bay: distribution, pro-

- duction, and historical changes in abundance. US Environmental Protection Agency, Office of Marine and Estuarine Protection Report No. EPA 503/4-88-002
- Czerny AB, Dunton KH (1995) The effects of in situ light reduction on the growth of two subtropical seagrasses, *Thalassia testudinum* and *Halodule wrightii*. *Estuaries* 18: 418–427
- Dennison WC (1987) Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquat Bot* 27:3–14
- Dennison WC, Alberte RS (1982) Photosynthetic response of *Zostera marina* L. (eelgrass) to in situ manipulations of light intensity. *Oecologia* 55:137–144
- Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA (1993) Assessing water quality with submersed aquatic vegetation: habitat requirements as barometers of Chesapeake Bay health. *BioSci* 43:86–94
- DeYoe HR, Suttle CA (1994) The inability of the Texas 'brown tide' alga to use nitrate and the role of nitrogen in the initiation of a persistent bloom of this organism. *J Phycol* 30: 800–806
- Duarte CM (1991) Seagrass depth limits. *Aquat Bot* 40: 363–377
- Dunton KH (1994) Seasonal growth and biomass of the subtropical seagrass *Halodule wrightii* in relation to continuous measurements of underwater irradiance. *Mar Biol* 120:479–489
- Dunton KH (1996) Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries* 19:436–447
- Gallegos ME, Merino M, Rodriguez A, Marba N, Duarte CM (1994) Growth patterns and demography of pioneer Caribbean seagrasses *Halodule wrightii* and *Syringodium filiforme*. *Mar Ecol Prog Ser* 109:99–104
- Giesen WBJT, van Katwijk MM, den Hartog C (1990) Eelgrass condition and turbidity in the Dutch Wadden Sea. *Aquat Bot* 37:71–85
- Iverson RL, Bittaker HF (1986) Seagrass distribution and abundance in eastern Gulf of Mexico waters. *Estuar Coast Shelf Sci* 22:577–602
- Kenworthy WJ, Fonseca MS, DiPiero SJ (1991) Defining the ecological light compensation point for seagrasses *Halodule wrightii* and *Syringodium filiforme* from long-term submarine light regime monitoring in the southern Indian River. In: Kenworthy WJ, Haunert DE (eds) The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. NOAA Tech Mem NMFS-SEFC-287, NOAA, p 106–113
- Kenworthy WJ, Haunert DE (1991) The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. NOAA Tech Mem NMFS-SEFC-287, NOAA
- Lewis RR III (1989) Biology and eutrophication of Tampa Bay. In: Estevez ED (ed) Tampa and Sarasota Bays: issues, resources, status, and management. National Oceanic and Atmospheric Administration, Estuarine Programs Office, NOAA Estuary-of-the-Month Seminar Series No. 11, Washington, p 89–112
- Merkord GW (1978) The distribution and abundance of seagrasses in Laguna Madre of Texas. MS thesis, Texas A&I University, Kingsville
- Onuf CP (1991) Light requirements of *Halodule wrightii*, *Syringodium filiforme*, and *Halophila engelmanni* in a heterogeneous and variable environment inferred from long-term monitoring. In: Kenworthy WJ, Haunert D (eds) The light requirements of seagrasses: proceedings of a workshop to examine the capability of water quality criteria, standards and monitoring programs to protect seagrasses. US Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, NOAA Tech Mem NMFS-SEFC-287, p 95–105
- Onuf CP (1994) Seagrasses, dredging, and light in Laguna Madre, Texas, USA. *Estuar Coast Shelf Sci* 39:75–91
- Onuf CP (1996) Biomass patterns in seagrass meadows of the Laguna Madre, Texas. *Bull Mar Sci* 58:404–420
- Orth RJ, Moore KA (1983) Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. *Science* 222:51–53
- Pedersen MF, Borum J (1993) An annual nitrogen budget for a seagrass *Zostera marina* population. *Mar Ecol Prog Ser* 101:169–177
- Pulich W Jr (1980) The ecology of a hypersaline lagoon: the Laguna Madre. In: Fore PL, Peterson RD (eds) Proceedings of the Gulf of Mexico coastal ecosystems workshop. US Fish and Wildlife Service Biological Report FWS/OBS-80/30, Albuquerque, NM
- Pulich WM, White WA (1991) Decline of submerged vegetation in the Galveston Bay system: chronology and relationships to physical processes. *J Coast Res* 7:909–926
- Quammen ML, Onuf CP (1993) Laguna Madre: seagrass changes continue decades after salinity reduction. *Estuaries* 16:303–311
- Stockwell DA, Buskey EJ, Whitledge TE (1993) Studies on conditions conducive to the development and maintenance of a persistent 'brown tide' in Laguna Madre, Texas. In: Smayda TJ, Shimizu Y (eds) Toxic phytoplankton blooms in the sea. Elsevier Science Publishers, New York, p 693–698
- Ward LG, Kemp WM, Boynton WR (1984) The influence of waves and seagrass communities on suspended particulates in an estuarine embayment. *Mar Geol* 59:85–103

This article was presented by G. W. Thayer (Senior Editorial Advisor), Beaufort, North Carolina, USA

Manuscript first received: April 25, 1995  
Revised version accepted: January 24, 1996