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# Top-down impact through a bottom-up mechanism. *In situ* effects of limpet grazing on growth, light requirements and survival of the eelgrass *Zostera marina*

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**ABSTRACT:** Temporal changes in abundance, size, productivity, resource allocation and light requirements of a subtidal eelgrass (*Zostera marina* L.) population were followed for 2 yr after the September 1993 appearance of a previously rare oval form of the commensal limpet *Tectura depicta* (Berry) in Monterey Bay, California, USA. By exclusively targeting the epidermis, limpet grazing impaired photosynthetic performance but left respiratory demand, meristematic growth and more than 90% of the leaf biomass intact. The resulting low *P:R* ratios of grazed plants raised the light requirements for the maintenance of positive carbon balance almost 2-fold relative to healthy ungrazed plants and prevented the summertime accumulation of internal carbon reserves. Shoot density in this once-continuously vegetated 30 ha meadow declined from more than 50 shoots m<sup>-2</sup> (2230 g fresh wt [FW] m<sup>-2</sup>) to sparse patches supporting an average of 16 shoots m<sup>-2</sup> (380 g FW m<sup>-2</sup>). More than 50% of the continuously vegetated meadow was converted to bare sand despite ambient light availability and water temperatures that were favorable for growth of healthy, ungrazed plants. Plant size declined by 50% and internal sugar reserves declined more than 4-fold within 6 mo after the appearance of *T. depicta*. Plant losses were most extensive during winter, when internal carbon reserves were minimal. The dramatic decline in eelgrass vigor and abundance reported here, despite a physical environment that was favorable for healthy eelgrass survival, illustrates the amplification of top-down control by this relatively inconspicuous limpet through a feeding mechanism that specifically impairs photosynthesis, a bottom-up process.

**KEY WORDS:** Seagrass · Grazing · *Zostera marina* · *Tectura depicta* · Light requirements · Carbon balance · Photosynthesis

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## INTRODUCTION

Dramatic regional declines in seagrass populations are frequently attributed to anthropogenic modification of coastal water quality through sediment loading and eutrophication-stimulated blooms of nuisance algae (Orth & Moore 1983, Dennison 1987, Duarte 1991, Zim-

merman et al. 1991, Dennison et al. 1993, Morris & Tomasko 1993, Dunton 1994, Short & Wyllie-Echeverria 1996). Seagrass vulnerability to light limitation is caused by fundamentally high light requirements that can be traced to inefficient carbon-concentrating mechanisms for photosynthesis (Duarte 1991, Durako 1993, Zimmerman et al. 1995b, 1997, Beer & Rehnberg 1997). In contrast to the extensive literature on bottom-up controls, grazer-mediated regulation of seagrass productivity has received considerably less attention.

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Large grazers can impact seagrass productivity significantly if released from predation control, but co-exist with healthy seagrasses when grazer population checks remain intact (Valentine & Heck 1991, Heck & Valentine 1995, Stoner et al. 1995). Herbivory by small invertebrate grazers generally has minimal negative impacts on seagrass growth and biomass in otherwise healthy populations, and may have important positive functions by controlling epiphyte growth and mobilizing seagrass detritus (Howard & Short 1986, Klumpp et al. 1992, Mazzella et al. 1992, Neckles et al. 1993, 1994, Tunberg et al. 1994, Thom et al. 1995, Nelson & Waaland 1997, Fong et al. 2000).

Several species of cryptic limpets live commensally on seagrass leaves, and a few graze directly on the leaf epidermis (Barbour & Radosevich 1979). At low densities, these limpets have negligible effects on seagrass productivity, but extensive grazing of the leaf epidermis can significantly impact productivity, resource allocation and survival of eelgrass (Zimmerman et al.

1996). The previously rare oval form of the commensal acmeid limpet *Tectura depicta* (Berry) appeared suddenly in high abundance within a subtidal eelgrass (*Zostera marina* L.) meadow in Monterey Bay, California, USA in September 1993. Prior to our discovery, this oval form was known from fewer than 10 preserved specimens and a few fossil shells collected more than 600 km to the south near San Pedro, California (Lindberg 1980).

The common laterally compressed 'Zostera form' of *Tectura depicta* can be found on intertidal populations of eelgrass throughout the Californian biogeographic province south of Pt. Conception, California (see Fig. 1). The laterally compressed form has not, however, been reported from the Oregonian biogeographic province north of Pt. Conception (which includes Monterey Bay) since a warm-water period in the mid 19th century (Lindberg 1980). The rare oval form reported here has never been found north of the Pt. Conception boundary, and its persistence in Monterey Bay may constitute a significant new structuring element in seagrass meadows of northern and central California.

The capacity of ecologically relevant densities of *Tectura depicta* to impact eelgrass light requirements, productivity and survival has been demonstrated experimentally (Zimmerman et al. 1996). Here we describe the temporal changes in abundance, light requirements, productivity and chemical composition of a subtidal eelgrass population following the appearance of *T. depicta* in Monterey Bay. The dramatic decline in eelgrass vigor and abundance reported here, despite a physical environment that was favorable for eelgrass growth, exemplifies the sometimes subtle mechanisms by which introductions or changes in the abundance of apparently innocuous species can rapidly alter the function of subtidal ecosystems.

## MATERIALS AND METHODS

**Study site.** Prior to our first observation of *Tectura depicta* (Berry) in September 1993, eelgrass (*Zostera marina*) was distributed as a continuous 30 ha meadow along Del Monte Beach at the southern end of Monterey Bay, California, USA (Fig. 1). The shallow limit roughly followed the 3 m depth contour, and was probably controlled by wave action on this partially exposed coastline. The deep edge was most probably determined by light availability. The meadow was bounded on the west by the Monterey Harbor and on the east by a shale reef that supports a rocky substrate community dominated by the giant kelp *Macrocystis pyrifera* (L.) C. Agardh.

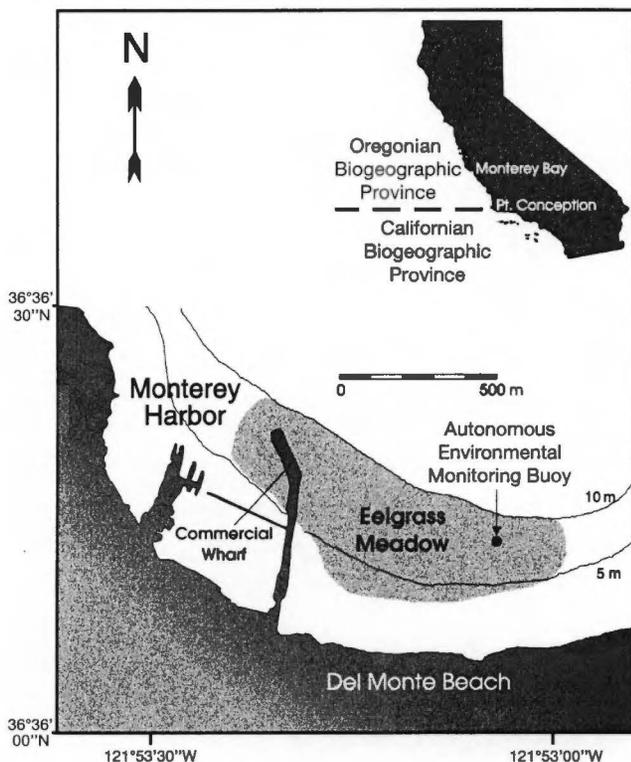


Fig. 1. Marine biogeographic boundary separating Monterey Bay and the Oregonian biogeographic province north of Pt. Conception from the Californian biogeographic province in the south, and the Del Monte Beach study site located in Monterey Bay, California. *Zostera marina* meadow was located between 3 and 10 m depth contours just east of Monterey Harbor. Ambient light availability and water temperature were measured continuously by the autonomous environmental monitoring buoy located at the site marked on the map

The Del Monte Beach eelgrass meadow was separated from the nearest eelgrass population to the north in Elkhorn Slough by 30 km of wave-swept sandy coast. Genetic analysis revealed restricted gene flow between these eelgrass populations (Alberte et al. 1994). The nearest eelgrass population to the south exists in Morro Bay, which is separated from Del Monte Beach by 180 km of open rocky coast. No *Tectura depicta* or grazing scars were found on eelgrass growing in Elkhorn Slough (30 km north), San Francisco Bay (150 km north) Tomales Bay (200 km north) or Morro Bay (180 km south) throughout 1994 and 1995. Prior to the initiation of this study, the eelgrass distribution at Del Monte Beach had been temporally stable and dense (mean shoot density = 50 shoots  $m^{-2}$ , mean leaf area index, LAI,  $\approx 2$ ) for more than 10 yr (Zimmerman pers. obs.).

**Environmental conditions.** Water temperature and light availability were monitored continuously from September 1993 through August 1995 at the Del Monte Beach study site using a moored autonomous buoy (Fig. 1). Temperature and irradiance sensors were deployed from the buoy through the water column and along the sea floor. Submarine scalar irradiance,  $E_o(\text{sub})$ , was measured at the sediment surface (8 m depth) and 0.5 m above the bottom with LiCor spherical ( $4\pi$ ) quantum sensors calibrated for photosynthetically active radiation (PAR = 400 to 700 nm). The attenuation coefficient of scalar irradiance ( $K_o$ ) was calculated from the difference in  $E_o(\text{sub})$  readings of the 2 submarine sensors according to Beer's law, using only *in situ* readings taken between 10:00 and 15:00 h each day to minimize the effect of sun angle (Miller & McPherson 1995). Downwelling plane irradiance at the sea surface,  $E_d(\text{air})$ , was measured using a Li-Cor cosine ( $2\pi$ ) PAR sensor mounted on the top of the buoy. Water temperature was measured by YSI precision thermistors located at the water surface, 4 m below the surface, and on the sea floor (8 m depth, mean lower low water). All sensors were interrogated every 15 min. Data were stored by an on-board logger and transmitted to a laboratory-based computer via packet radio transceivers every day. The system was powered by batteries charged from a solar panel on the buoy. Submarine irradiance sensors were cleaned manually of fouling and accumulated debris every 2 wk. Fouling of the sensors was minimal throughout the course of the study, and had no effects on measured submarine irradiance as determined by comparison of data recorded immediately before and after the sensors were cleaned. (Temporal gaps in the time series of environmental data resulting from occasional sensor failure are indicated by breaks in the time series plots in Figs 2 & 12B.)

**Eelgrass population density.** Eelgrass density was determined periodically along a 30 m transect at 8 m depth in the center of what was initially a dense continuous meadow (50 shoots  $m^{-2}$ , LAI  $\approx 2$ ). A meter tape was deployed roughly parallel to the 8 m isobath by SCUBA divers using a compass heading of  $270^\circ$  magnetic beginning near the bottom-mounted sensor array. Shoot densities within  $0.20 m^2$  quadrats were determined every 2 m along the transect. The meter tape was retrieved at the end of each survey to prevent mechanical damage of the eelgrass population that might result from a permanently installed line. Successive shoot-density quadrats did not re-sample the same plot as deployment of the transect was not identical each time.

Size of surviving eelgrass patches was assessed by SCUBA divers in April 1995 after extensive fragmentation of the meadow. Ten 100 m long transects running in a north-south direction parallel to the depth gradient were laid 50 m apart between the Municipal Wharf and the moored autonomous buoy (range = 3 to 8 m) (Fig. 1). Presence or absence of eelgrass was assessed at stations every 10 m along each transect. Percent cover was calculated from the fraction of the 110 stations (11 per transect) containing eelgrass. Shoot density was determined by counting all shoots within 2 haphazardly placed  $0.38 m^2$  quadrats within each patch. For stations containing eelgrass, elliptical patch areas were calculated from measures of the longest axis across each patch and the axis normal to it.

**Eelgrass and limpet morphometrics.** Each month, 20 shoots were haphazardly selected for determination of (1) growth rates, (2) biomass allocation among shoots, roots and rhizomes, (3) carbon reserves, (4) metabolic performance and (5) light requirements. The leaf sheath of each shoot was punched with a 20 gauge hypodermic needle. A length of surveyors' flagging tape buoyed by a plastic vial was tied around the rhizome. Tagged plants were harvested by hand after growing undisturbed for 10 to 14 d. Care was taken to collect each plant in its entirety, including all attached rhizomes and roots. A few plants consisted of 2 or at most 3 shoots during the spring period of vegetative proliferation; most plants, however, consisted of a single shoot with its attached rhizome and roots, which is the typical growth form for eelgrass. Collected plants were transported to the laboratory in seawater-filled coolers.

In the laboratory, plants were divided into shoots, roots, and rhizomes, and rinsed in clean seawater to remove sediment, particularly from the roots. All limpets were removed from each shoot, enumerated and measured (longest shell axis) to the nearest 0.01 mm using a digital caliper. The divided sections

were blotted dry and weighed to the nearest mg. Growth rates were determined by measuring (1) the total length of each leaf on each shoot and (2) the distance from the original punch mark on the outer sheath to the existing hole on each leaf (Zieman & Wetzel 1980). All leaf material below each punch mark, plus young leaves without punch marks, were considered new growth. Daily growth rates were calculated by dividing the length of new leaf tissue by total leaf length of each shoot and by the number of days since marking (Zimmerman et al. 1995b).

**Eelgrass metabolism and chemical composition.** Leaf photosynthesis ( $P$ ) versus irradiance ( $E$ ) responses were measured polarographically each month in well-stirred, temperature-controlled incubation chambers (5 ml vol.) using sections cut 10 cm below the tip of the mature leaf #3 (youngest = #1) from 10 of the harvested plants. By selecting a fixed distance below the tip of this mature but non-senescent leaf, tissue samples were not biased by arbitrary selection of samples based on the degree of leaf grazing. Ten irradiances between 3 and 500  $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$  were provided by slide projectors and neutral-density filters. A circulating water bath held the incubation chambers at the mean temperature recorded *in situ* over the previous 30 d.  $P$  versus  $E$  data were fit to the exponential function of Webb et al. (1974) using a non-linear direct-fit procedure and error-estimation routine (Zimmerman et al. 1987). Respiration ( $R$ ) of each leaf section was measured in the dark in 100% air-saturated seawater. Root  $R$  was measured at an initial  $[\text{O}_2]$  of 200% air saturation to maximize aerobic metabolism (Zimmerman et al. 1989). Leaves were homogenized on ice in 90% (v/v) acetone to extract chlorophylls  $a$  and  $b$  after measuring  $P$  and  $R$ . Homogenates were centrifuged and pigment content of each supernatant was quantified spectrophotometrically using the extinction coefficients of Jeffrey & Humphrey (1975). Sugar content of leaves, roots and rhizomes was measured on 80% ethanol extracts using a resorcinol assay standardized against sucrose (Zimmerman et al. 1995a).

**Whole-plant carbon budgets.** *In situ* periods of irradiance-saturated photosynthesis ( $H_{\text{sat}}$ ) were determined by numerical integration of daily  $E_{\text{o(sub)}}$  time-series using the irradiance saturation parameter  $E_k$  calculated from the  $P$  versus  $E$  response curves measured each month (Zimmerman et al. 1994). Daily carbon demand and  $H_{\text{sat}}$  requirements were calculated according to Zimmerman et al. (1996, 1997). Physiological rate parameters ( $P_m$ ,  $R_{\text{leaf}}$ ,  $R_{\text{root}}$ ,  $E_k$ ) and biomass distribution among shoots, rhizomes and roots necessary to calculate  $H_{\text{sat}}$  requirements were taken from the monthly determinations described above. All error terms are reported as standard errors throughout.

**Statistical analyses.** Regression analysis was employed to evaluate the statistical significance of linear trends in the time series observations and relationships between measured variables. For those variables showing no significant temporal trend by regression, the statistical significance of temporal variations was evaluated using 1-way ANOVA, followed by LSD multiple-comparison tests providing ANOVA  $p \leq 0.05$ . Solid lines at equivalent  $y$ -axis elevations on the corresponding figures were used to indicate statistically identical monthly observations determined by LSD analysis.

## RESULTS

### Environmental conditions

Daily mean temperature within the *Zostera marina* meadow at 8 m depth fluctuated seasonally from a low of 10.5°C in mid-summer to a high of 15.5°C in early October (solid line in Fig. 2A). The water column was essentially isothermal from December to March, but showed evidence of stratification and surface warming from June to September. The maximum temperature difference between surface water and the eelgrass meadow (8 m depth) was about 5°C in July and August. Semi-diurnal thermal oscillations were observed in the 15 min time-series of temperature at 4 and 8 m during stratified periods (not shown), and were consistent with tidally-driven internal waves propagated along the thermocline boundary (Zimmerman & Kremer 1984).

Daily-integrated  $E_{\text{d(air)}}$  varied approximately 3-fold seasonally between solstices. Cloud-free irradiances ranged from a winter minimum of 15 mol quanta  $\text{m}^{-2} \text{d}^{-1}$  to a summer peak of 45 mol quanta  $\text{m}^{-2} \text{d}^{-1}$  (open circles in Fig. 2B). Clouds and fog produced variations in daily  $E_{\text{d(air)}}$  that were often greater than the seasonal range for cloud-free conditions. Daily  $E_{\text{o(sub)}}$  at the depth of the eelgrass meadow (8 m) ranged seasonally from 0 to 15 mol quanta  $\text{m}^{-2} \text{d}^{-1}$  (black symbols in Fig. 2B). Variation in water-column optical properties affected the transmission of  $E_{\text{d(sub)}}$  to the seagrass canopy, resulting in a poor but statistically significant relationship between  $E_{\text{d(air)}}$  and  $E_{\text{o(sub)}}$  (Fig. 2B inset, see also Table 2). The scalar attenuation coefficient ( $K_0$ ) was highly variable from day to day, ranging from a low of 0.1 to a high of 2.8  $\text{m}^{-1}$  (Fig. 2C). Periods of maximum  $K_0$  were often associated with runoff and high wave energy generated by storms during the winter and early spring rainy season. Even in summer, however,  $K_0$  frequently exceeded 0.5  $\text{m}^{-1}$  and changed by a factor of 2 or 3 within 24 h.

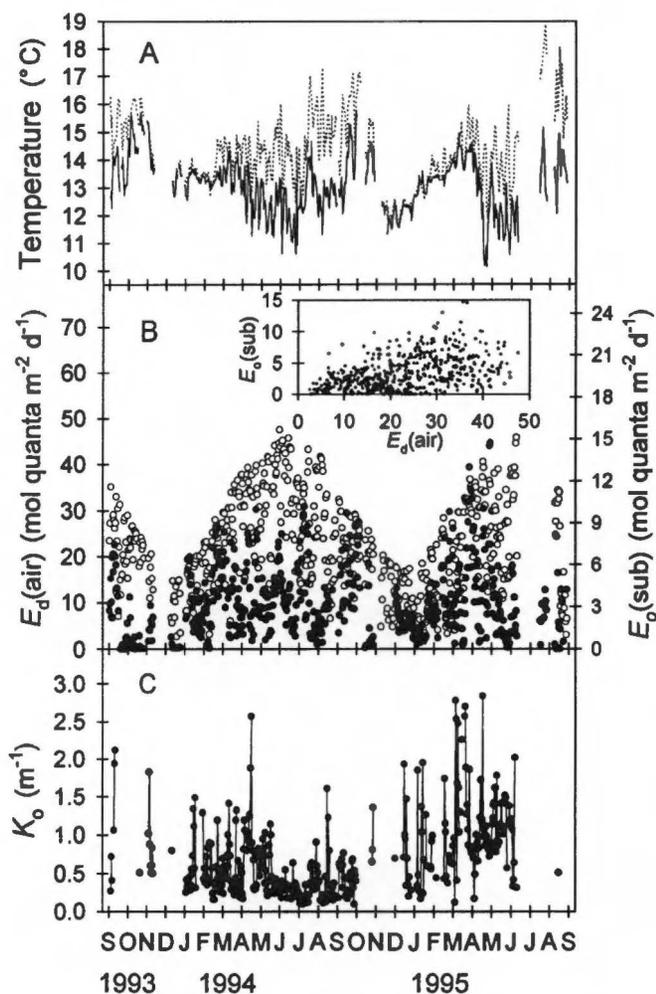


Fig. 2. (A) Time series recordings of mean daily temperature at the surface (····) and within *Zostera marina* meadow at 8 m (—). (B) Daily integrated irradiance incident on the sea surface,  $E_d(\text{air})$  (○, left vertical axis), and at the top of the eelgrass canopy,  $E_0(\text{sub})$  (●, right vertical axis); B inset: scatterplot of  $E_0(\text{sub})$  versus  $E_d(\text{air})$ . (C) Mean daily diffuse attenuation coefficient ( $K_d$ )

#### Eelgrass population density and standing crop

Eelgrass density declined from 50 shoots m<sup>-2</sup> (2230 g FW m<sup>-2</sup>) in September 1993 to near-extinction by the end of 1994 (Fig. 3A) as the once-continuous and densely vegetated meadow was fragmented into a series of small patches, mostly less than 5 m<sup>2</sup> in size (Fig. 3B). More than 36% of the surviving meadow was reduced to extremely small patches (<2 m<sup>2</sup>). In total, 56% of the original meadow was converted to bare sand by 1995. Eelgrass density averaged 16 ± 1 shoots m<sup>-2</sup> (380 g FW m<sup>-2</sup>) within the surviving patches in April 1995, representing a 70% reduction in shoot den-

sity and an 80% reduction in area-specific standing crop within the surviving vegetated patches relative to the continuously vegetated meadow in September 1993.

#### Limpet density and size

*Tectura depicta* were first noticed on eelgrass in September 1993, but their density and size were not measured until February 1994. Prior to the appearance of limpets, ungrazed eelgrass leaves were fully green and buoyant (Fig. 4A). Leaves collected beginning in October 1993, however, showed increasing visual evidence of grazing each month, including distinctive grazing scars, pale brown leaves and a lack of leaf buoyancy (Fig. 4B,C). Limpet density averaged more than 5 individuals shoot<sup>-1</sup> throughout the first half of 1994, but had declined to about 2 individuals shoot<sup>-1</sup> by August

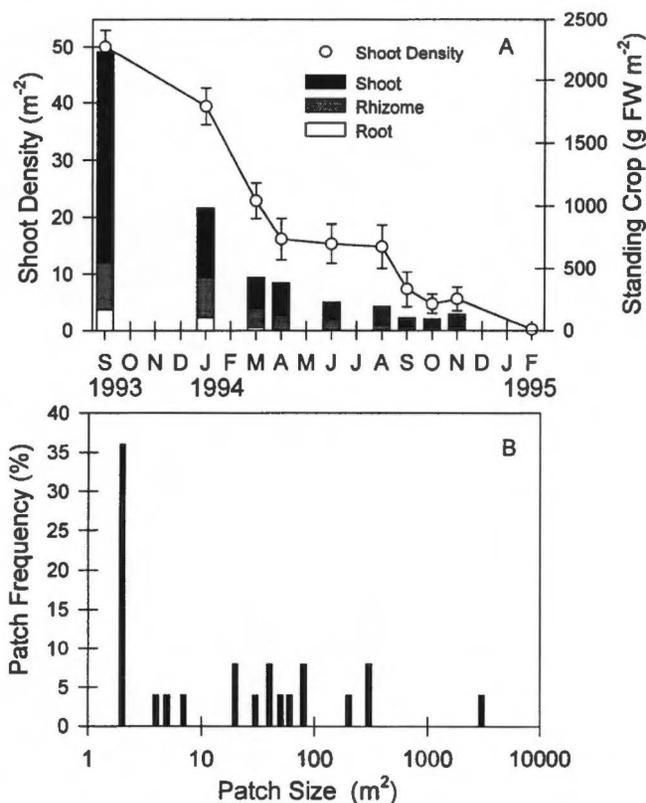


Fig. 3. *Zostera marina*. (A) Time series of shoot density (○, left vertical axis) and standing crop (vertical bars, right vertical axis) from September 1993 until the disappearance of all plants along the permanent transect in February 1995, error bars: ± 1 SE of the mean for each monthly observation of shoot density. (B) Size-frequency distribution of surviving eelgrass patches measured in spring 1995; shoot density within the surviving patches averaged 16 ± 1 shoots m<sup>-2</sup>. FW: fresh weight

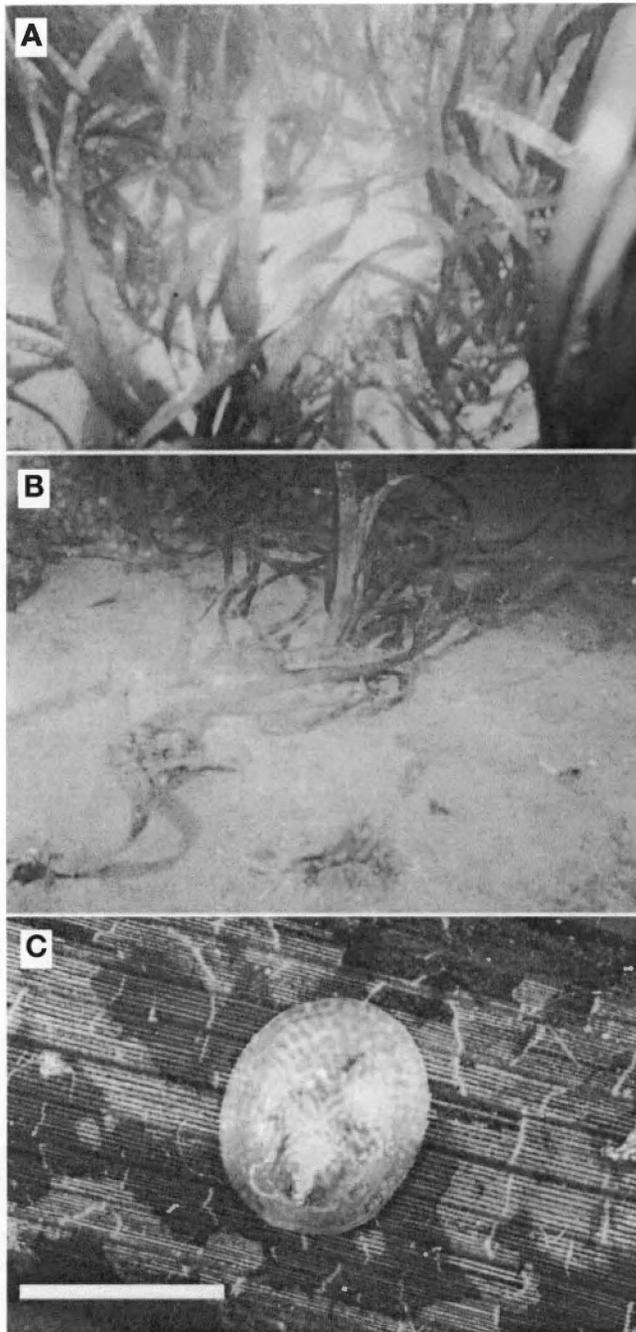


Fig. 4. *Zostera marina*. (A) Dense eelgrass vegetation in an ungrazed region of the meadow; white spots evident on the older leaves are epiphytes, mostly encrusting bryozoans. (B) An impacted region of the meadow showing a few heavily grazed but surviving eelgrass shoots; brown colored leaves were stripped of chlorophyll by the limpets and lost the buoyancy normally derived from lacunae filled with photosynthetically produced  $O_2$ . (C) *Tectura depicta* on an eelgrass leaf illustrating the ungrazed (bright green) and freshly grazed (yellow) regions; lacunae (vein-like striations) and all sub-cuticular cells in the grazed areas remained intact (see Zimmerman et al. 1996) for photomicrograph of a grazed eelgrass leaf in cross-section). White scale bar = 5 mm

1995 (Fig. 5A). Statistically significant peaks in limpet density occurred in spring 1994 and winter 1995 (Table 1, Fig. 5A). Limpet density was lowest during summer months in both 1994 and 1995. In contrast, limpets were larger in summer months than in winter (Table 1, Fig. 5B). The negative relationship between limpet density and size (Table 2) probably resulted from the pulsed settlement of new individuals followed by summer growth and mortality.

#### Eelgrass growth, biomass allocation and area-specific productivity

Eelgrass growth rate and size declined dramatically during the fall of 1993, as shoot density declined and limpet grazing became increasingly evident (Table 1, Fig. 6). Size-specific growth rates (Fig. 6A) were consistently higher in summer than winter. Mean plant size decreased significantly from 45 g FW in September 1993 to about 20 g FW in January 1994 and remained around 20 g FW for the rest of the study (Fig. 6B). The fraction of biomass allocated to below-ground tissue varied seasonally from a summertime low of about 0.2 to a winter high of about 0.4 (Table 1, Fig. 6C). Although the repeating cycle of size-specific growth rate appeared insensitive to limpet grazing, the combined reductions in plant size and

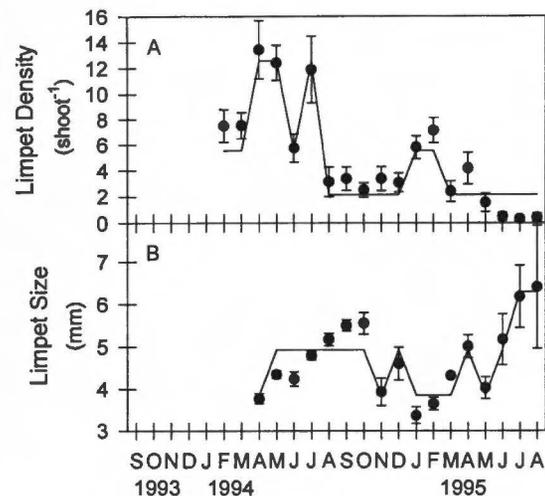


Fig. 5. *Tectura depicta*. (A) Time series of limpet density on *Zostera marina* shoots; (B) Limpet size (longest shell axis). Error bars:  $\pm 1$  SE of the mean for each monthly observation. Significant temporal differences among monthly means determined by LSD post-hoc analysis are indicated by different heights of the line running through the data on each plot

Table 1. *Tectura depicta* and *Zostera marina*. ANOVA results for temporal variations in limpet and plant parameters not exhibiting significant monotonic trends. Post-hoc analyses were employed to evaluate specific differences among individual observations when ANOVA revealed statistically significant temporal variation ( $p \leq 0.05$ )

	Effect		Error		F	p
	df	MS	df	MS		
<b><i>T. depicta</i></b>						
Density	18	221.07	224	16.28	13.58	<0.001
Limpet size	16	19.72	694	1.39	14.15	<0.001
<b><i>Z. marina</i></b>						
Specific growth rate	21	2.59	174	0.11	23.02	<0.001
Size	23	673.48	203	67.78	9.94	<0.001
Arcsine (below-ground biomass fraction)	23	463718.84	201	442200.63	1.05	0.04
Leaf respiration	22	0.01	202	0.00	4.34	<0.001
Root respiration	22	0.00	143	0.00	1.08	0.38
Chlorophyll a:b	22	0.59	198	0.06	9.63	<0.001
Rhizome internode #1 sugar	23	13379.92	199	1541.31	8.68	<0.001
Rhizome internode #3 sugar	12	26525.14	115	2121.50	12.50	<0.001

shoot density lowered area-specific productivity (= shoot density  $\times$  plant size  $\times$  specific growth) of this meadow by 95%: from 44 g FW  $m^{-2} d^{-1}$  in September 1993 to 2 g FW  $m^{-2} d^{-1}$  in September 1994. Continued plant losses through August 1995 reduced seagrass production to virtually zero at this site.

#### Eelgrass metabolism and chemical composition

The rate of light-saturated gross photosynthesis ( $P_m$ ) fluctuated throughout the course of this study between 0.18 and 0.70  $\mu mol O_2 g^{-1} FW min^{-1}$ , and exhibited a statistically significant monotonic increase of 42% between September 1993 when the limpets were first

noticed and August 1995 when limpet density was at its lowest level (Fig. 7A, Table 2). The lowest value of  $P_m$  (0.18  $\mu mol O_2 g^{-1} FW min^{-1}$ ) was observed in December 1993, when leaves on all plants collected had been heavily grazed. The irradiance required to saturate photosynthesis ( $E_k$ ) did not show a statistically significant temporal trend, averaging  $29 \pm 3 \mu mol quanta m^{-2} s^{-1}$  throughout the course of this study (regression ANOVA  $F[1,21] = 1.26$ ,  $p = 0.27$ ,  $r^2 = 0.06$ ). Student's *t*-tests adjusted for multiple comparisons using the Bonferonni correction identified no statistically significant differences between any of the monthly estimates of  $E_k$  (Bonferonni adjusted  $t_{0.05} = 5.69$  for 253 comparisons, 18 df). Although leaf respiration ( $R_{leaf}$ ) varied from  $-0.06 \mu mol O_2 g^{-1} FW min^{-1}$  in late summer

Table 2. *Tectura depicta* and *Zostera marina*. Linear regression parameters and ANOVA statistics quantifying significant interactions between specific pairs of variables (Ind.: independent; Dep.: dependent). Plots of regressed data can be found in indicated figures (nf = no figure). Numbers in parentheses: standard errors of slopes and intercepts; \* $p \leq 0.05$ , \*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ .  $E_d$ (air): downwelling plane irradiance at the sea surface;  $E_o$ (sub): submarine scalar irradiance;  $P_m$ : light-saturated gross photo-synthe-

Fig.	Ind. variable	Dep. variable	Slope	Intercept	Regression ANOVA statistics			
					$r^2$	F	df	p
2B (inset)	$E_d$ (air)	$E_o$ (sub)	0.1 (0.01)	1.01 (0.25)	0.17	111.03	1,536	<0.001**
nf	Limpet density	Limpet size	-0.10 (0.05)	5.18 (0.29)	0.24	4.65	1,15	0.047*
7A	Time	$P_m$	0.008 (0.003)	0.36 (0.04)	0.26	7.26	1,21	0.04*
8A	Time	Chlorophyll [a+b]	0.09 (0.01)	1.12 (0.19)	0.70	48.27	1,21	<0.001***
9	Limpet density	Chlorophyll [a+b]	-0.09 (0.03)	3.04 (0.19)	0.36	9.29	1,14	0.009**
10A	Time	Leaf [sugar]	2.36 (0.35)	12.63 (5.27)	0.18	46.32	1,206	<0.001***
10B	Leaf [sugar]	Absolute growth	0.0003 (0.0003)	0.29 (0.02)	0.30	80.28	1,188	<0.001***
nf	Leaf [sugar]	Specific growth	0.002 (0.0008)	1.71 (0.06)	0.04	7.74	1,185	0.006**
11A	Time	Root [sugar]	0.57 (0.11)	4.19 (1.61)	0.12	28.59	1,205	<0.001***
nf	Leaf [sugar]	Root [sugar]	0.04 (0.01)	10.11 (1.02)	0.03	6.77	1,213	0.01**
nf	Leaf [sugar]	Rhizome #1 [sugar]	0.27 (0.07)	93.43 (5.13)	0.06	14.3	1,217	0.002**
11B	Leaf [sugar]	Rhizome #3 [sugar]	0.87 (0.15)	92.32 (9.46)	0.72	34.62	1,124	<0.001***
13A	Specific growth	$H_{eat}$	0.16 (0.04)	0.53 (0.31)	0.48	18.56	1,20	0.003**
13B	Limpet density	$H_{eat}$ requirement	0.42 (0.13)	4.10 (0.65)	0.48	10.15	1,11	0.009**