Contribution of green macroalgal mats (*Enteromorpha* spp.) to seasonal production in an estuary

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ABSTRACT: Benthic green macroalgal mats, composed primarily of *Enteromorpha* spp., were studied on a mudflat in the Coos Bay estuary (Oregon, USA) during 1981 and 1982. Monthly field collections indicated highest biomass during August of both years. From April to September, maximum algal abundance progressed from low- to mid-intertidal elevations until storms physically removed algae from the mudflat. Annual production was estimated at 1100 g C m^{-2} by integration of (1) field measurements of standing crop, light, salinity, and temperature; (2) laboratory measurements of carbon fixation rates under varying conditions of desiccation, light, salinity, and algal density; (3) computer-generated estimates of tidal emersion and submergence for the Coos Bay estuary. Submerged photosynthesis accounted for an average of 95 % of total production despite light attenuation by the water column at the lowest intertidal elevations sampled. Emersed production was restricted by desiccation, light attenuation within the compressed algal mat, inorganic carbon limitation, and decreasing time of daylight emergence through the growing season. *Enteromorpha* contributes to the estuarine production chiefly through release of dissolved organic carbon, burial of algae in sediments, herbivore-enhanced fragmentation, and whole-plant loss.

INTRODUCTION

Benthic macrophytes are major contributors to the total primary productivity of temperate estuaries (Correll 1978). While salt marshes are often the macrophyte communities of greatest importance, the Coos Bay estuary (Oregon, USA) presently retains only 10 % of its historically known marshes (Hoffnagle & Olson 1974). As in many other Pacific coast estuaries, what little marsh remains is confined to the uppermost intertidal zone, where infrequent tidal submergence restricts exchange of materials with the rest of the estuary. Coos Bay does possess many extensive beds of eelgrass (*Zostera marina* L.), but from 10 to 70 % of the macrophyte biomass in these beds consists of associated green macroalgae (Gonor et al. 1979). Such algae, primarily species of *Enteromorpha* and *Ulva*, also form seasonally abundant mats that cover many intertidal mudflats. Although ephemeral, such algal mats are highly productive in other Oregon and Washington estuaries (Price & Hylleberg 1982, Davis & McIntire 1983, Thom 1984).

Environmental factors in the estuarine intertidal habitat exploited by these algal populations fluctuate greatly over varying time scales. Photosynthesis and growth of submerged algae are affected by temperature, salinity, and light intensity (King & Schramm 1976, Fitzgerald 1978, Arnold & Murray 1980, Gordon et al. 1980, Shellum & Josselyn 1982). Photosynthesis of emersed algae may be restricted by desiccation (Wiltens et al. 1978, Quadir et al. 1979, Beer & Eshel 1983a, Pregnall 1983). Light penetration through a compressed algal mat may be insufficient to permit high rates of photosynthesis by the lowermost algal filaments (Bach & Josselyn 1978, Gordon et al. 1980). Densely matted algae left by the receding tide in shallow, water-filled depressions on the mudflat may become carbon limited. The interaction between the mixed semidiurnal tides experienced by the Coos Bay estuary and seasonal changes in daylength creates a large gradient of daylight emergence *versus* submergence over the vertical range of the *Enteromorpha* mats. Thus, effects of submergence and exposure upon algal photosynthetic performance will differentially affect

and control algal mat production at different intertidal elevations.

Our objective was to determine how estuarine fluctuations in salinity, light attenuation, and tidal exposure would affect algal distribution and production in order to estimate the seasonal production of an *Enteromorpha* mat and how the algal production entered the Coos Bay estuarine system. We approached this by (1) monitoring distribution, abundance, and species composition of macroalgae on a mudflat for 2 yr; (2) determining in the laboratory the ability of the algae to fix carbon under the range of conditions of temperature, salinity, light, and desiccation observed in the estuary; (3) computing the amount of time available for algal photosynthesis under emersed and submerged conditions.

MATERIALS AND METHODS

Study site. A study site (Fig. 1) was chosen in the South Slough arm of the Coos Bay estuary (43° 20' 15" N, 124° 19' 30" W). Surveys of the estuary in 1979 and 1980 indicated numerous locations with large seasonal populations of *Enteromorpha* spp., but the South Slough site provided the simplest and most rapid access from shore or by boat. The mudflat is bounded at the upper edge (1.9 m above Mean Lower Low Water, MLLW = 0.0 m) by a marsh dominated by *Salicornia virginica* L. and at the lower edge (MLLW) by an eelgrass (*Zostera marina*) bed. The mudflat is approximately 140 m wide between MLLW and +1.6 m and has a nearly constant slope of about 1 %.

Permanent sampling areas were fixed in the field site by placing stakes at 5 elevations between MLLW and +1.2 m (vertical interval between stakes was 0.3 m). Elevations were determined with a stadia rod and level and referenced against a tide gauge in the nearby Charleston boat basin at several slack tides. At each elevation, four 100 m long sampling regions were designated within a 500 m wide segment of the mudflat.

Field sampling. During the growing season, April through September, algae were collected on the better spring low tide series of each month. Fewer collections were made during winter. In each of the 20 sampling areas (5 elevations × 4 regions), 5 samples, with triplicate subsamples, were taken at predetermined random distances into each region. A subsample consisted of all algae covered by an inverted 100 × 15 mm Petri dish. Algae were washed free of sediments, separated to species as by Abbott & Hollenberg (1976), and weighed. Dry weights were measured after drying at 90 °C to constant weight.

Salinity and temperature of the water flowing off the mudflat were measured each month at the time of the field collections. Water retained at low tide in shallow
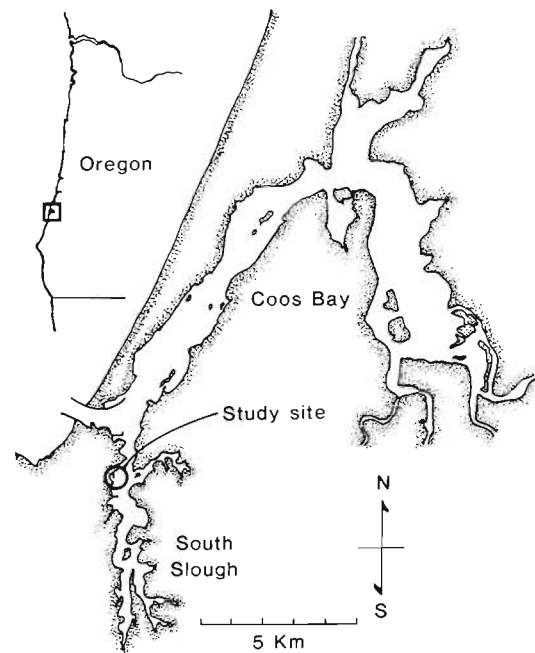

Fig. 1. Location of field-study site in the South Slough branch of the Coos Bay estuary, Oregon, USA

mudflat depressions was occasionally sampled for determination of salinity and of dissolved inorganic carbon content (by the method of Strickland & Parsons 1968). Ambient light was measured with a 2-cell light meter (Kahl Scientific, Model 269WA310); frequent readings were made between field collections during summer and fall. Light penetration through the water column was measured with a Secchi disk and with the 2-cell light meter.

Because the buoyant *Enteromorpha* filaments bend before tidal currents in all but extreme slack waters, the algal mat does not necessarily occupy the entire depth of the water column when submerged. To estimate the volume of water occupied by algae, locations of known standing crop within the field site were visited by wading or snorkeling, and the height to which algae floated above the mudflat surface was measured.

Emersed production should be a product of the duration of daylight emergence, the photosynthetic rate of exposed algae, and the biomass of photosynthesizing algae. Daylight emersion was estimated using the tidal simulations described below for the 5 elevations at which algal standing crop was measured. The degree of desiccation of *Enteromorpha* as a function of emersion time (0 to 5 h) and biomass (10 to 275 g dry wt m^{-2}) was determined as by Pregnall (1983). Carbon fixation by desiccated algae in air was determined from 20 min incubations in the presence of $^{14}CO_2$ using the procedure of Darley et al. (1976) as modified by Pregnall (1983).

Outgoing tides often left compacted mats of algae in shallow, water-filled depressions on the mudflat. While these algae were not truly 'exposed' and subject to desiccation, their potential production was considered as occurring during the period of tidal emersion. Since water from such depressions possessed very low inorganic carbon concentrations, carbon fixation by *Enteromorpha* was determined in incubations using artificial sea water (Rila Sea Salts) that had been flushed briefly with CO_2-free air to lower the dissolved inorganic carbon levels to 400 μM. Algal densities in the 1.5 l chambers ranged from 0.5 to 2.0 g dry wt l^{-1} for these measurements. Such densities were higher than those used for other photosynthetic incubations and higher than the densities recommended by Littler (1979), but lower than those observed in the field. The use of algal densities approaching those observed in the water-filled depressions would have prevented effective mixing within the chamber and caused severe self-shading (see below). The range of densities used did not reduce light levels below the saturation intensities reported by King & Schramm (1976).

Attenuation of light by an increasingly thick mat of freshly collected *Enteromorpha* was measured with the 2-cell light meter, internally corrected to measure wavelengths from 400 to 700 nm (photosynthetically active radiation, PAR). We estimated the portion of an exposed algal mat that should have been capable of net carbon fixation for given ambient light intensities by using the photosynthetic compensation and saturation intensities reported for *Enteromorpha* spp. (King & Schramm 1976, Arnold & Murray 1980).

For estimates of algal-mat production, photosynthetic biomass was adjusted daily by interpolation between monthly field collections as suggested by Brinkhuis (1977). Since all tissue of *Enteromorpha* is photosynthetic, a geometric growth pattern was presumed, with the rate of growth or decline calculated from the ratio of standing crops in successive months. In an attempt to incorporate some of the great spatial variation in algal abundance into the production estimates, growth rates and production values were calculated for each of the 20 areas in which algal mat biomass was measured at the field site. The progressive degree of desiccation of emersed green algal mats on sunny and lightly overcast days during the growing season was predicted for each elevation sampled using the daily adjustment of algal density and values of daylight emersion. The degree of desiccation at each successive hour of emersion was then used to estimate the carbon fixation rate of *Enteromorpha* after Pregnall (1983).

Submerged production. Total submerged production should be a product of the duration of daylight submergence, the photosynthetic rate of algae, and the

photosynthetic biomass. The duration of submergence in daylight was calculated, using the tidal simulations described below, for each of the 5 elevations at which algal biomass measurements were made. The average depth of water during the period of daylight submergence was also computed for each elevation in order to determine the potential for attenuation of light by the water column. Light available to the submerged algal mat was estimated after Smith (1981) using an average extinction coefficient, *k*, of 0.69 m^{-1}, as computed by Walker (1980) from Secchi disk measurements (mean 2.08 ± 0.50 m, N = 20). Measurements of light penetration with the 2-cell light meter gave very similar extinction coefficients.

Photosynthetic rates of *Enteromorpha* spp. were determined by measuring incorporation of ^{14}C during 3 h incubations (Pregnall 1983). Water temperature was maintained at 16 °C, which was the mean temperature measured in the field from June to October. Artificial sea water for the photosynthetic incubations was prepared over a range of salinities from 2 to 35 ‰; salinity of South Slough water varied between 2 ‰ (Mar) and 30 ‰ (Jul through Sep) during the growing season of 1982. Light intensities during photosynthetic incubations varied from 3 to 75 mW cm^{-2}, which encompassed the range of ambient light intensities measured at the field site. Dark controls were wrapped in black plastic. Algal density in the 1.5 l chambers ranged from 0.025 to 0.40 g dry wt l^{-1}, which corresponded to algal standing crops of approximately 35 to 375 g dry wt m^{-2} by the conversion based on field measurements.

Daily production for each month interval was computed by extrapolation of the laboratory-measured rates of carbon fixation using the mean values of water temperature, salinity and light penetration that were measured during each month's collections at the field site. Photosynthetic biomass was adjusted daily, as described for exposed production, for each of the 20 areas in which algal biomass was monitored.

Tidal simulations. Computer programs in Fortran that calculate and display the predicted durations of emergence and submergence during daylight and darkness for various elevations along a gradient of tidal height are available upon request from the authors. All programs are initially based on a simple tide prediction that fits a sine function between each successive pair of tides (low-to-high or high-to-low). The water level at each hour is determined and stored in an array. The daily times of sunrise and sunset are stored in another array. Tidal elevations of interest are sequentially compared against the tidal array, and the conditions of emergence or submergence in light or dark are augmented appropriately.

The raw data for these programs was drawn from

several tables in the National Ocean Survey's 'Tide Tables 1982, High and Low Water Predictions'. The predicted times and heights of the tides at the reference station nearest the field site of interest, the correction times and heights for the field site, and the times of sunrise and sunset are all used as input. The use of local correction factors permits rapid recalculation of tidal exposures for any field site within the domain of reference stations, such as different locations within an estuary or along a complex coastline.

RESULTS

Algal mat dynamics

Green macroalgal populations in the Coos Bay estuary have a distinct seasonal pattern of abundance (Fig. 2). Initial growth in South Slough begins in April and May, maximum abundance occurs in late August, and

Fig. 3. Changes in species composition of green macroalgal mats at the South Slough field site from May to November of the 1982 growing season
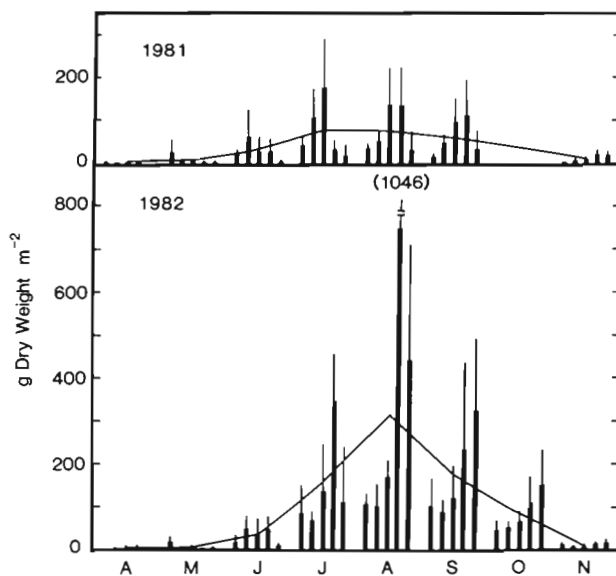

Fig. 2. Seasonal changes in standing crop of benthic green macroalgal mats at the South Slough field site. The 5 bars presented for each month indicate the mean biomass at the 5 elevations sampled (MLLW at the left to + 1.2 m at the right). Error bars: 1 SD computed from the 4 areas sampled at each elevation. The continuous line indicates mean biomass for all elevations

early winter storms remove nearly all algae by November. Growth rates from May through July averaged 6.5 % d^{-1}, declined to about 1.9 % d^{-1} into August, and were negative through the fall. Algal distributions were nearly identical from March through June of 1981 and 1982, but large blooms of the filamentous species *Enteromorpha prolifera* (Mull.) J. Ag. and *E. clathrata* (Roth) Grev. in July and August of
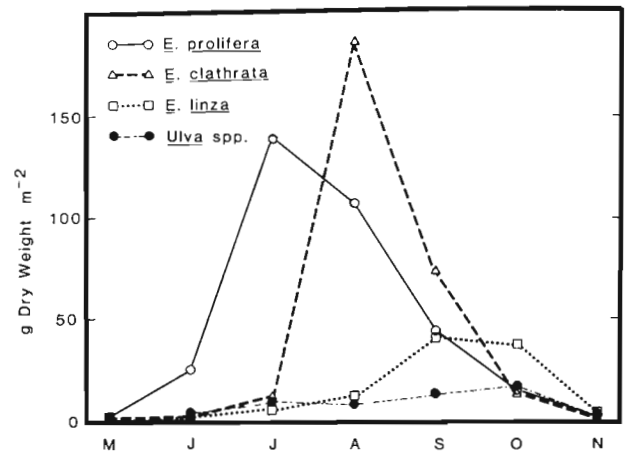
1982 (Fig. 3) created a much greater maximum standing crop than in the previous year. In both years, the algal mat was initially confined to the lowest elevations sampled (MLLW and +0.3 m), but it progressed upwards through the growing season until well over half of the algal biomass occurred at or above an elevation of +0.9 m (Fig. 2). While the mean standing crop for all elevations sampled in August 1982 was about 310 g dry wt m^{-2}, the overall mean biomass at +0.9 m was about 750 g dry wt m^{-2}, and in 1 of the 4 sampling areas at that elevation was nearly 960 g dry wt m^{-2}. The algal mat on the exposed mudflat was occasionally more than 10 cm thick. The filamentous species declined dramatically in September of both years, while the sheet-like forms, *E. linza* (L.) J. Ag. and *Ulva* spp., increased in abundance through October (Fig. 3).

Emersed photosynthesis

The degree of desiccation of *Enteromorpha* and *Ulva* spp. at low tide is dependent upon the amount of algae present and the duration of exposure. A least-squares multiple regression of the percent fresh weight loss of algae (% FWL) on both algal density (Algden) and exposure time (T) yields a very highly significant function ($r^2 = 0.72$, N = 135) for which both the slope and the intercept are functions of T:

$$\text{\% FWL} = \text{Slope} \cdot \text{Log}_e \text{(Algden)} + \text{Intercept} \quad (1)$$
$$\text{where Slope} = -25.063 \cdot e^{-0.4037/T} \quad (2)$$
$$\text{and Intercept} = 220.626 \cdot e^{-0.4037/T} - 4.805 \quad (3)$$

Some of the data used to derive these functions have been presented elsewhere (Pregnall 1983).

Light is attenuated within a compressed algal mat (Fig. 4). The curve probably overestimates the photo-
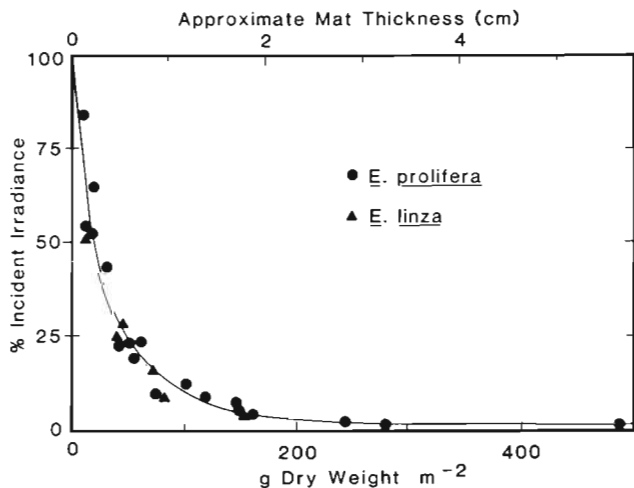
Fig. 4. Attenuation of light (percent of surface light that penetrates through the algae) by an *Enteromorpha* mat

synthetically useful light available to the lowermost algal filaments, since all wavelengths from 400 to 700 nm were weighted equally by the light meter cells. Even at midday in summer, photosynthetic saturation and compensation light intensities reported for *Enteromorpha* spp. (King & Schramm 1976, Arnold & Murray 1980) occurred within the upper few centimeters of an exposed algal mat.

Water collected from depressions on the mudflat containing thickly matted algae possessed total dissolved inorganic carbon concentrations of ∼ 350 μM. Photosynthetic incubations using sea water with lowered inorganic carbon content showed an inverse relation between algal density and weight-specific carbon fixation rate (Fig. 5). The *Enteromorpha* fixed well over 90 % of added ^{14}C-bicarbonate during the 3 h incubations.

Submerged photosynthesis

Carbon fixation by *Enteromorpha* spp. from the Coos Bay estuary was highly dependent upon algal density and salinity in incubations with light intensities between 12 and 45 mW cm^{-2} (Fig. 6). Algal density was the more significant variable, with salinity explaining less of the total variation. Low salinity caused a slight but significant reduction in net carbon fixation, probably by increasing the release of dissolved organic carbon (Pregnall 1983). Additional photosynthetic incubations indicated that *Enteromorpha* spp. were light limited below about 8 mW cm^{-2} and photo-inhibited above 60 mW cm^{-2}. There was such great overlap of photosynthetic performance by the 3 species of *Enteromorpha* studied (*E. linza, E. prolifera,* and *E. clathrata*) that, instead of making separate estimates
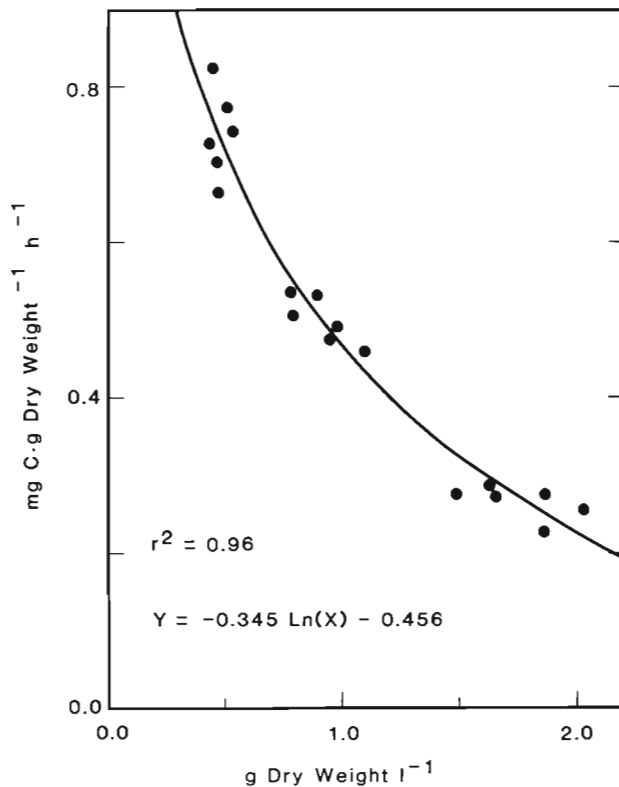

Fig. 5. *Enteromorpha prolifera.* Carbon fixation rates as a function of algal density during incubations. The synthetic sea water had previously been flushed with CO_2-free air to provide a dissolved inorganic carbon concentration of ∼ 400μM
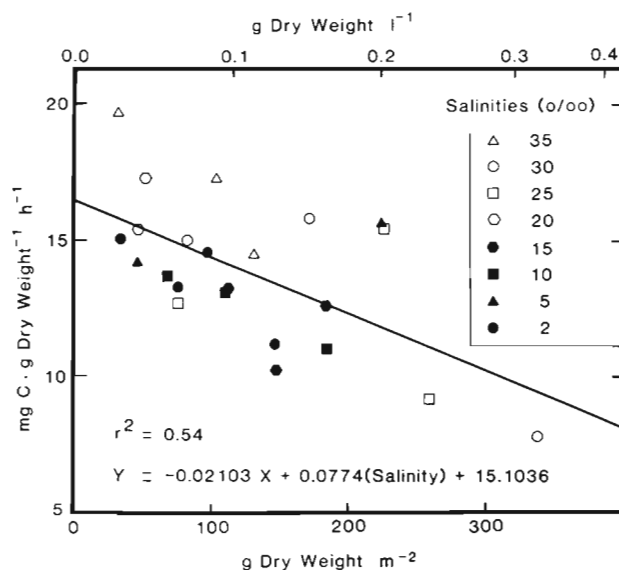

Fig. 6. *Enteromorpha* spp. Carbon fixation rates under submerged conditions as a function of algal density and salinity. Algal density is presented here as both g dry wt l^{-1} (from photosynthetic incubations) and as g dry wt m^{-2} (estimated from calculations of the volume of water occupied by known densities of algae at high tide)

for each species, production was estimated from total algal biomass.

As incoming tides lifted the algal mat off the mudflat surface, light penetrated to the lower parts of the mat that had been shaded at low tide. However, light attenuation by the water column was sufficient to limit photosynthesis by algae at the 2 lower elevations sampled (MLLW and +0.3 m) for short periods after dawn and before dusk. Turbidity was slightly greater at the water line owing to resuspension of fine sediments and detritus by small waves, but declined as water depth increased away from shore. Despite the increased water turbidity experienced by algae at the higher elevations (owing to more frequent encounters with the water's edge from tidal submergence and exposure), light penetration through the thinner water column was sufficient to sustain high rates of photosynthesis during nearly all periods of daylight submergence.
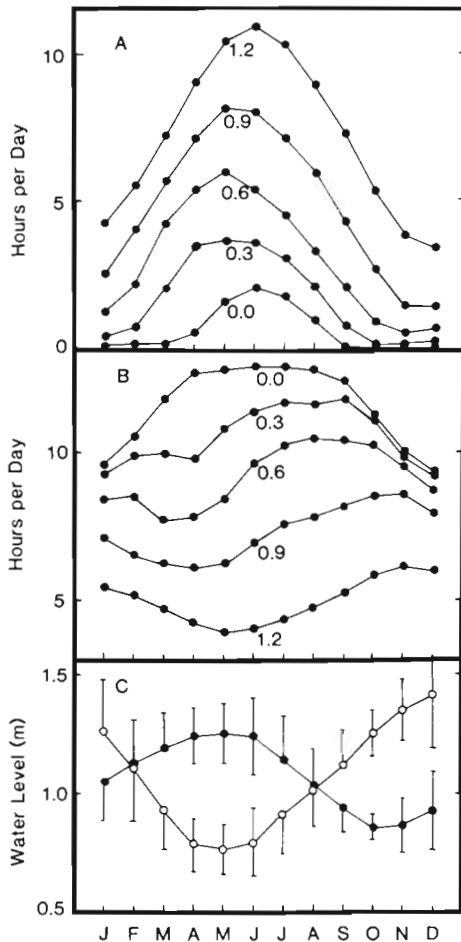

Fig. 7. Annual tidal exposure patterns for the entrance to the Coos Bay estuary. (A) daylight emergence (monthly means) at the 5 elevations sampled for algal abundance; (B) mean monthly daylight submergence; (C) mean water levels in daylight (open circles) and darkness (filled circles) ± 1 SD calculated from daily values

Tidal exposures

In May and June emersion during daylight is at its maximum for the year at the Coos Bay estuary entrance (Fig. 7 A). In contrast, daylight submergence gradually increases from April or May through September or October (Fig. 7 B). From July on, only the uppermost tidal elevation sampled (+1.2 m) experiences more emergence than submergence in daylight. The mean water level in daylight, and consequently the depth of water over the submerged algal mat, also increases through the growing season (Fig. 7 C).

At Coos Bay, the daily time-lag of the tides is almost precisely matched by the successive alternation of the higher and lower low tides through a spring-neap-spring series (Fig. 8), maintaining the time of day at
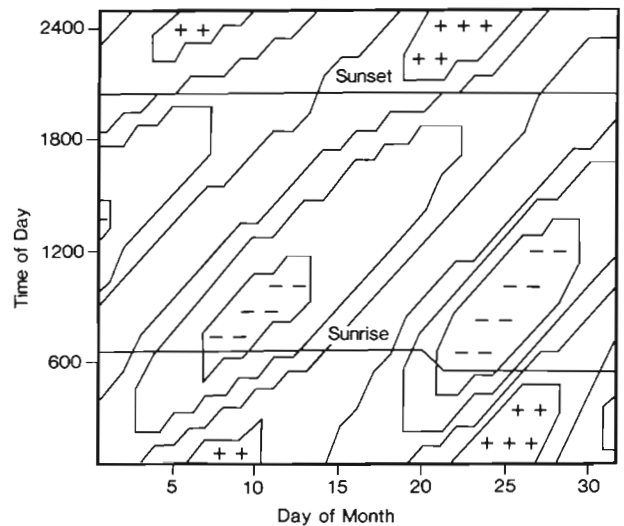

Fig. 8. Tidal elevations computed for Coos Bay entrance in May 1982. The 'topographic map' has a contour interval of 0.6 m. Periods with water levels below MLLW are indicated with minus signs; plus signs indicate water levels above +1.8 m. Approximate times of sunrise and sunset are indicated. Note the occurrence of 2 high-tide 'ridges' and 2 low-tide 'valleys' each day (read vertically)

which extremely high or low tides occur during a given month. From March through August, the extreme low tides occur during daylight hours; the extreme high tides which precede them occur mostly at night. From September through February, the opposite is true, and both the higher high tides and the higher low tides occur during daylight.

Estimated algal mat production

Estimated algal-mat production for each elevation and month interval from May to December of 1982 is presented in Table 1. Annual production was high,

Table 1. Estimated algal-mat production for the South Slough field site during the 1982 growing season, given for each elevation sampled and for each month interval between field censuses. Production is presented as the mean ± 1 standard deviation (calculated from the 4 areas sampled per elevation) in g C m^{-2}. Percent value indicates the proportion of total estimated production occurring during periods of emersion

| Month | Elevation (m) | | | | | |
interval	0.0	0.3	0.6	0.9	1.2	Mean
May						
	59.5 ± 7.3	38.3 ± 23.5	42.3 ± 41.0	27.5 ± 23.4	1.4 ± 0.3	33.8 ± 21.5
	0.6 %	1.2 %	2.0 %	3.1 %	0.6 %	1.5 %
Jun						
	170.5 ± 107.5	209.2 ± 44.7	208.8 ± 140.0	298.2 ± 106.7	40.7 ± 39.0	185.5 ± 93.5
	1.0 %	2.0 %	3.0 %	6.9 %	10.2 %	4.6 %
Jul						
	270.2 ± 103.4	234.9 ± 17.0	386.3 ± 154.0	415.0 ± 57.2	214.8 ± 75.0	304.2 ± 90.8
	1.2 %	2.0 %	2.5 %	7.1 %	19.7 %	5.7 %
Aug						
	238.4 ± 64.3	230.4 ± 59.5	327.3 ± 89.4	369.9 ± 81.8	240.4 ± 75.0	280.5 ± 62.0
	1.3 %	1.3 %	2.0 %	6.9 %	14.7 %	5.2 %
Sep						
	137.2 ± 82.4	155.6 ± 38.7	197.6 ± 77.6	260.4 ± 120.8	211.1 ± 69.2	192.4 ± 48.5
	1.0 %	1.4 %	1.3 %	3.6 %	8.7 %	3.3 %
Oct						
	38.0 ± 18.3	31.3 ± 9.6	47.1 ± 14.5	68.5 ± 28.5	68.8 ± 30.2	50.7 ± 17.3
	0.4 %	1.0 %	1.3 %	2.5 %	5.6 %	2.0 %
Nov						
	10.7 ± 3.7	3.2 ± 1.7	4.8 ± 2.0	5.3 ± 1.6	3.5 ± 1.4	5.5 ± 3.0
	0.0 %	0.4 %	0.9 %	1.3 %	1.7 %	0.7 %
Dec						
Total	924.5	902.9	1214.2	1440.9	816.0	1059.7 ± 260.5
	1.1 %	1.6 %	2.2 %	6.0 %	11.7 %	4.4 %

with a mean for the entire field site of about 1100 g C m^{-2}. The mid-intertidal elevations (0.6 to 0.9 m) were more productive than higher or lower elevations, and July-August was the period of greatest algal production. The estimated contribution of production during tidal emersion was minor, even at the highest elevation considered.

Production was much higher than the maximum standing crop observed at the field site. The ratio of production to observed monthly increase in standing crop for the early months of the growing season indicated turnover rates of 0.9 to 8.7 mo^{-1}. The difference between estimated production and observed change in standing crop should indicate excess algal production that was contributed to the estuarine system during the growing season (Table 2). Again, the mid-intertidal elevations appeared to be more important, but greatest total contribution to the estuary did not occur until after the August biomass maximum. Much of the algal contribution after August was due to the decline in biomass on the mudflats.

DISCUSSION

Benthic green macroalgae typically exhibit rapid population growth and decline and substantial between-year variation in peak biomass (Price & Hylleberg 1982, Shellum & Josselyn 1982, Owens & Stewart 1983). The great spatial variability in algal biomass observed in the present study, both among and within elevations, also appears to be highly characteristic of these populations. Year-to-year fluctuation in abundance and activity of small grazers, particularly benthic amphipods, may be partially responsible for the observed variation in maximum algal population development (Pomeroy & Levings 1980, Price & Hylleberg 1982, Warwick et al. 1982).

The factors that influence production by *Enteromorpha* mats emersed at low tide include desiccation, light attenuation within the algal mat, and inorganic carbon availability for large amounts of algae trapped in shallow depressions. Desiccation of filamentous and sheet-like macroalgae generally causes a significant reduction in photosynthetic rate (Wiltens et al. 1978, Quadir et al. 1979, Beer & Eshel 1983a, Pregnall 1983). The degree of desiccation of *Enteromorpha* and *Ulva* spp., and consequently the photosynthetic rate,

Table 2. Estimated algal-mat contribution to the Coos Bay estuary during the 1982 growing season, given for each elevation sampled and for each month interval between field censuses, in units of g C m^{-2}. Contribution is calculated by subtracting the observed change in standing crop from the estimated production, assuming an algal carbon content of 30 % of dry weight

Month interval	Elevation (m)					
	0.0	0.3	0.6	0.9	1.2	Mean
May						
	54.9 ± 9.5	20.6 ± 18.7	32.2 ± 27.2	14.3 ± 12.0	0.6 ± 0.8	24.9 ± 20.6
Jun						
	146.5 ± 85.8	203.4 ± 62.4	164.6 ± 129.3	168.0 ± 101.7	−5.1 ± 13.9	135.5 ± 81.3
Jul						
	291.0 ± 77.0	230.9 ± 17.3	404.6 ± 120.0	406.2 ± 55.4	93.1 ± 65.2	285.2 ± 131.1
Aug						
	239.2 ± 36.8	230.6 ± 76.7	338.3 ± 76.4	703.8 ± 168.0	334.3 ± 143.6	369.2 ± 193.8
Sep						
	140.6 ± 22.4	171.5 ± 29.6	222.7 ± 71.5	309.5 ± 152.0	279.5 ± 101.3	224.8 ± 70.9
Oct						
	50.0 ± 22.3	50.0 ± 15.6	70.4 ± 8.3	108.7 ± 39.6	122.8 ± 78.2	80.4 ± 33.7
Nov						
	13.4 ± 8.4	4.0 ± 1.6	6.9 ± 1.9	8.9 ± 3.6	9.5 ± 4.7	8.5 ± 3.5
Dec						
Total	935.5	910.9	1241.7	1719.4	834.7	1128.4 ± 365.0

depends greatly upon the amount of algae present, the duration of exposure, and the ambient temperature and humidity (Beer & Eshel 1983a, Pregnall 1983).

Dense mats of green macroalgae do not dry out rapidly when emersed, but light attenuation within the mats may limit production. Only the surface layers of algae, which are most susceptible to rainfall or desiccation stress, may be photosynthesizing at low tide. The light that passes through *Enteromorpha* and *Ulva* spp. is greatly skewed towards the green wavelengths, which are less efficiently used in photosynthesis. Photosynthesis by the estuarine green alga *Cladophora* also declines in the lower portions of thick mats (Bach & Josselyn 1978, Gordon et al. 1980).

Measurements of inorganic carbon in water from algae-filled depressions suggested that photosynthesis could also be limited by carbon availability (Beer & Eshel 1983b). The reduced rates of carbon fixation by algae at high density probably result from a combination of self-shading, increased stability of boundary layers, and severe inorganic carbon depletion. It is unlikely that respiration by lower layers of algae and sediment microbes and fauna is sufficient to match carbon demand by the upper algal filaments. The rates of carbon fixation by carbon-limited *Enteromorpha* at increased density were even lower than those of desiccating thalli.

As the growing season progresses, the algae experience fewer hours of daylight emersion, further limiting exposed production. Factors that restrict emersed algal production (desiccation stress, light limitation in a compressed mat, and insufficient carbon availability) occur less frequently after May or June in Coos Bay. In contrast, the duration of daylight submergence increases through the growing season even as the total daylight period decreases. Thus, factors that enhance total algal mat production (daylight submergence with the concomitant continuous water flow, light penetration to all parts of the algal filaments, and high carbon availability) increase in duration and frequency from May through September.

The low contribution of emersed algae to total *Enteromorpha*-mat productivity, even at elevations that experience nearly equal amounts of daylight emersion and submergence, emphasizes the importance of partitioning intertidal algal production estimates between emersed and submerged conditions as opposed to extrapolating submerged production rates to the entire daylight period. Since diurnal exposure patterns can exhibit distinct and predictable seasonal fluctuations, total annual emersion curves may lead to inaccurate partitioning of production conditions. The tide-simulating program used in the present study does not yet incorporate effects of wave action, which can substantially alter true exposure regimes. However, the tidal predictions should be quite valid for our sheltered, gently sloping estuarine site, for effects of wave activity on tidal exposures are greatly diminished as the slope of the intertidal zone decreases (Druehl & Green 1982).

While estimated annual production at +1.2 m (the highest elevation sampled) was less than at any other elevation, peak standing crop at this elevation was much greater than at the lowest 3 elevations. This apparent paradox may derive from any of the following: the method of estimation is in error; the biomass

turnover rates are much slower at +1.2 m than at the lower elevations; or there is much greater loss of algae throughout the growing season in the lower intertidal zone. Consideration of the various mechanisms through which algal production leaves the mudflat population and enters the estuary provides some insight into this problem.

The fragile attaching filaments of *Enteromorpha* are readily broken by strong waves (Fitzgerald 1978), creating large amounts of drift algae. Senescence of light-limited lower sections of algal thalli also permits the buoyant upper sections to float free (Kier & Todd 1967). The likelihood that *Enteromorpha* will break free and enter the drift-algal population is certainly much greater in the low intertidal zone, where tidal currents sweep past the algae almost continuously, than at higher elevations, where algae are submerged for much shorter periods. Waves may remove large amounts of algae during storms, but the estuary is fairly sheltered at other times. Masses of green algae are observed floating about the Coos Bay estuary from August through December. The productivity of such macrophytoplankton is unknown but must be substantial.

Small herbivores, particularly benthic amphipods, may graze enough to remove large amounts of green macroalgae from estuarine populations (Pomeroy & Levings 1980, Price & Hylleberg 1982, Warwick et al. 1982). Algal fragments created by 'sloppy' grazing join the particulate detrital pool of the estuary. Amphipods living in the *Enteromorpha* mat in Coos Bay seemed most active during submerged conditions and at night, while they were usually clustered against the mudflat surface underneath all algae during daylight low tides. Certainly the effect of these grazers will be greater at the lower elevations studied.

Enteromorpha living at mid to upper intertidal elevations will be subjected to rainfall, desiccation, and tidal reimmersion much more frequently than algae in the low intertidal zone. Each of these stresses greatly increases the loss of photosynthate from *Enteromorpha* in the form of dissolved organic carbon (Pregnall 1983). Thus, for equal amounts of carbon fixed, the net carbon retention or gain of mid-intertidal algae will be reduced relative to low-intertidal algae, slowing growth and turnover rates. Microbes use this dissolved portion of the total algal production very rapidly.

The tangled filaments of the algal mat increase sedimentation by reducing the current velocity over the mudflat surface. Other workers have found substantial amounts of green algae buried in newly deposited estuarine sediments (Frostick & McCave 1979, Price & Hylleberg 1982, Owens & Stewart 1983). The mid-intertidal elevations sampled in Coos Bay had the greatest amounts of buried algae during the latter half of the growing season. The maximum standing crop here baffles water flow most effectively, and the high frequency of slack tides with water levels in the mid intertidal provides a ready source of recently suspended particulates. The buried portion of total algal production becomes available to the estuary through microbial regeneration of nutrients and storm-induced sediment turnover, even long after the seasonal decline of the *Enteromorpha* populations.

The production estimate for this *Enteromorpha* mat of approximately 1100 g C m^{-2} yr^{-1} is comparable to that of other highly productive benthic macroalgal populations (Mann et al. 1980 and references therein). Production during midsummer is about 10 g C m^{-2} d^{-1}. Thus, even though these green algal populations may flourish for only a few months, their total annual production matches that of large, perennial brown algae. Extrapolation of carbon-fixation rates measured during short incubations yields much greater production estimates than maximum observed biomass, as is also true for extrapolation of nitrogen uptake rates for *Enteromorpha* (Owen & Stewart 1983).

Gross production of the *Enteromorpha* populations examined in the present study is transformed through a variety of mechanisms whose importance changes in time and space. Some loss of photosynthate occurs almost immediately through respiration and release of dissolved organic carbon. Algal tissues may be consumed by herbivores or dispersed as propagules and particulate fragments throughout the growing season. Large amounts of algae, sometimes entire thalli, are exported from the mudflat through physical processes; the productivity of these floating masses has not yet been examined. The recycling of buried algae through microbial decomposition or storm-induced sediment turnover increases the period during which *Enteromorpha*-mat production is exported to the estuary. Such processes effectively moderate the magnitude of the pulse of production and extend algal contribution beyond the time when actively growing *Enteromorpha* populations are present on the tideflats.

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