

Chapter 2

Eelgrass (*Zostera marina* L.) production in Buzzards Bay

Introduction

The contribution of *Zostera marina* L. (eelgrass) to primary production in Buzzards Bay has not been estimated. Elsewhere, *Zostera* beds contribute sizably to coastal primary production, especially in shallow embayments, where they may account for 50% of all primary production including benthic algae and phytoplankton (Sand-Jensen and Borum, 1983; Nienhuis and Van Ireland, 1978).

Because eelgrass grows subtidally, it is difficult to measure primary production in the field. Often production is estimated by multiplying peak summer biomass by a factor of 2 (McRoy and Phillips, 1977), or multiplying growth rate during a summer period by the length of a "growing season". Both of these approaches has limitations because growth rate changes during the year and many beds grow in winter.

Dennison (1985) measured carbon fixation and respiration by eelgrass in the laboratory under different light and temperatures, and estimated seasonal changes in production rates of eelgrass in Woods Hole, MA from local radiant energy and temperature data. This approach suggested that eelgrass production should be higher in late spring rather than late summer when water temperatures were warmer because a shorter photoperiod and higher respiration rates in late summer resulted lower net photosynthesis. These results are corroborated by eelgrass growth data in Woods Hole and elsewhere in similar climates (e.g Jacobs, 1979).

Dennison (1985) did not integrate this production data to estimate annual production, but I reanalyzed of his published data and estimated net production as $3225 \text{ mg C g}^{-1} \text{ leaf tissue y}^{-1}$. Dennison (1985)

provided a regression between carbon fixation and biomass production, and this carbon fixation value translates to 6000 mg dry g^{-1} leaf y^{-1} . Because mean leaf biomass in Woods Hole is $\approx 100\text{-}200$ g dry wt m^{-2} (see below), this suggests local production equals 600-1200 g dry wt m^{-2} .

There are several difficulties extrapolating Dennisons' data in this way. His conversion from net photosynthesis to biomass production was based on only 4 data points, and though the fit is good, the confidence interval of this relationship is necessarily large. Second, the temperature and light measurements were made on leaf tissue collected in July, acclimatized to experimental light and temperature for only hours before changes in oxygen output were measured. Summer collected *Zostera* may not respond to winter conditions in the same way as acclimatized plant tissue collected during the winter. Even with this limitations, this data is valuable because it is the best estimate of annual eelgrass growth and production in this region to date.

In this paper I relate field data on eelgrass growth to local light and insolation to generate a production curve for eelgrass in the region. I use this unit area production data, and eelgrass bed cover in Buzzards Bay that I have reported elsewhere (Costa, 1987), to estimate the total contribution of eelgrass in Buzzards Bay compared to estimates of other primary producers. The growth of eelgrass has been described elsewhere, and in some cases correlated to light or temperature. Because this paper relates to these other studies, a brief description of eelgrass growth and results of other studies are warranted.

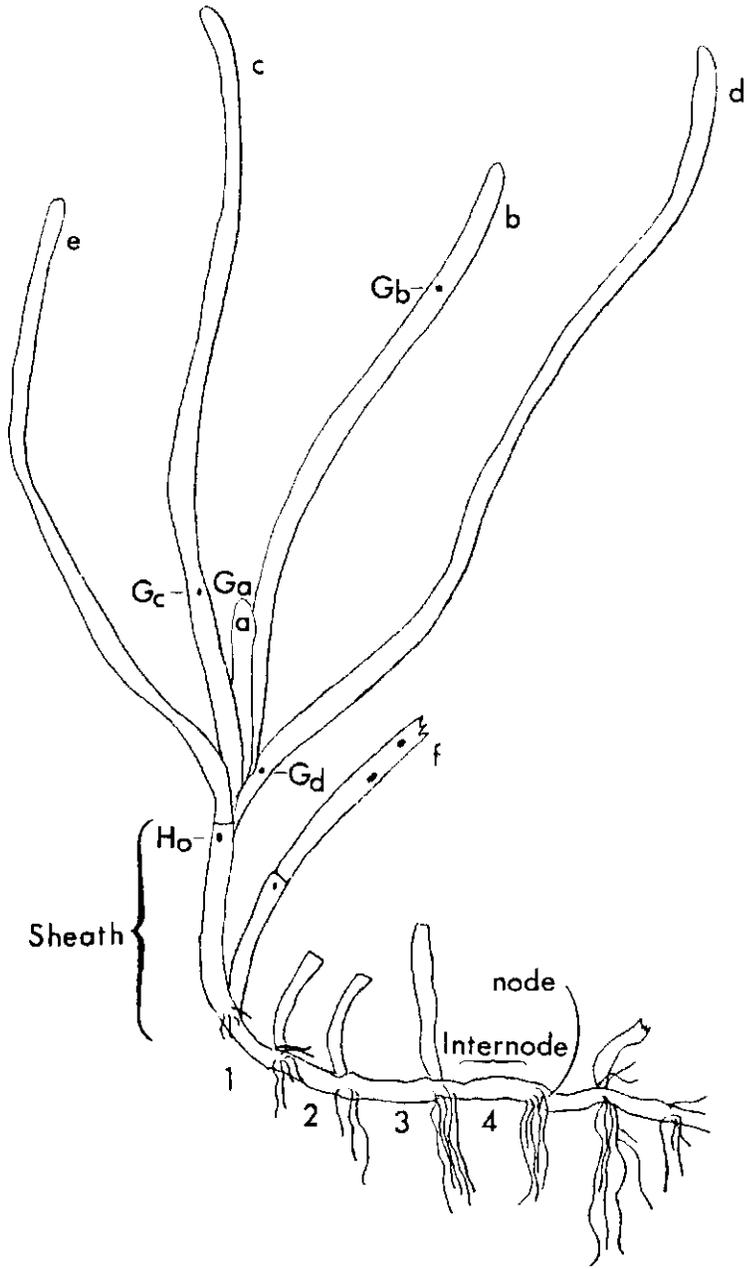
Measuring eelgrass production

The most widely accepted and reliable method for estimating seagrass production in the field are direct leaf marking techniques (Zieman and Wetzel, 1980). There are several variations of this method, but all are based on marking a leaf (punching a small hole, attaching a staple) in the field, and returning after 1 to 4 weeks to measure production of new leaf biomass (usually after harvesting).

Eelgrass leaves have basal growth, and new leaves are produced in the center of the leaf cluster, and each time a leaf is produced by a shoot, a new rhizome node and root cluster is also produced on the rhizome (Fig. 1). This one-to-one correspondence of leaf parts simplifies production calculations, and the weight of a mature leaf, mature rhizome internode, and root cluster are usually termed plastochrone units (Tomlinson, 1974, Jacobs, 1979). Each time a new leaf appears, the equivalent of one new plastochrone unit (PU) is produced, and the duration between leaf production is termed the plastochrone interval (PI). Because leaf growth occurs simultaneously on several younger leaves, rhizomes, and root internodes, and because the oldest leaf does not always drop off when a new leaf appears, and leaf lifespan is roughly 5 times the PI, the term PI is preferable to "leaf turnover" time, and its use is retained in this paper.

PI during the year and typically ranges 7 - 20 days during spring and summer, but may exceed 40 days during winter (Jacobs, 1979; Robertson and Mann, 1984). Jacobs (1979) reported that PI in Denmark eelgrass beds correlated well with daily insolation, and production peaked in June, whereas Robertson and Mann (1984) reported that PI in Nova Scotia was a function of temperature and production peaked in May.

Figure 1. A typical vegetative eelgrass shoot (ramet) showing major anatomical features and marking technique. Leaf 'a' is the youngest, 'f' the oldest. Each node is associated with the production of one leaf, fragments of which often remain attached. The leaf hole in the meristem (Ho) is the original pinhole punched approximately one leaf width below the sheath ligule at the top of the meristem. Outgrowth scars on older leaves show typical 2 week summer growth. PI in this study equals third leaf area / new leaf tissue ($\Sigma[(ah-Ho) + (bh-Ho) + (ch-Ho) + \dots] \times \text{marking days}$).



Plant growth is a function of both light and temperature the discrepancy between these interpretations can be explained by climatic differences because in both areas, eelgrass grew faster in May and June than in late Summer. In the Northern Hemisphere at the latitude of these sites there is considerably more light in May and June the late summer, however in Denmark water temperatures are higher in July and August, whereas in Nova Scotia, water temperatures are higher in May and June. I reanalyzed Jacobs data and found that PI correlates better with both light and temperature [$r^2 = 0.89$; $PI = 14.5 - 0.734 \times (\text{light as } 10^{-3} \text{ J m}^{-2} \text{ d}^{-1}) - 1.14 \times (C^\circ)$], than with light alone ($r^2 = 0.67$). These coefficients, however, do not result in a reasonable PI curve when used with Woods Hole temperature and insolation data (data not shown), and may only apply to beds in Denmark.

The objective of this study was to estimate annual production of eelgrass in Woods Hole by correlating changes in plastochrone interval with local light and temperature data. Based on the relationship between these parameters, an annual PI curve can be modeled and integrated to obtain the total number of PUs produced each year.

Methods

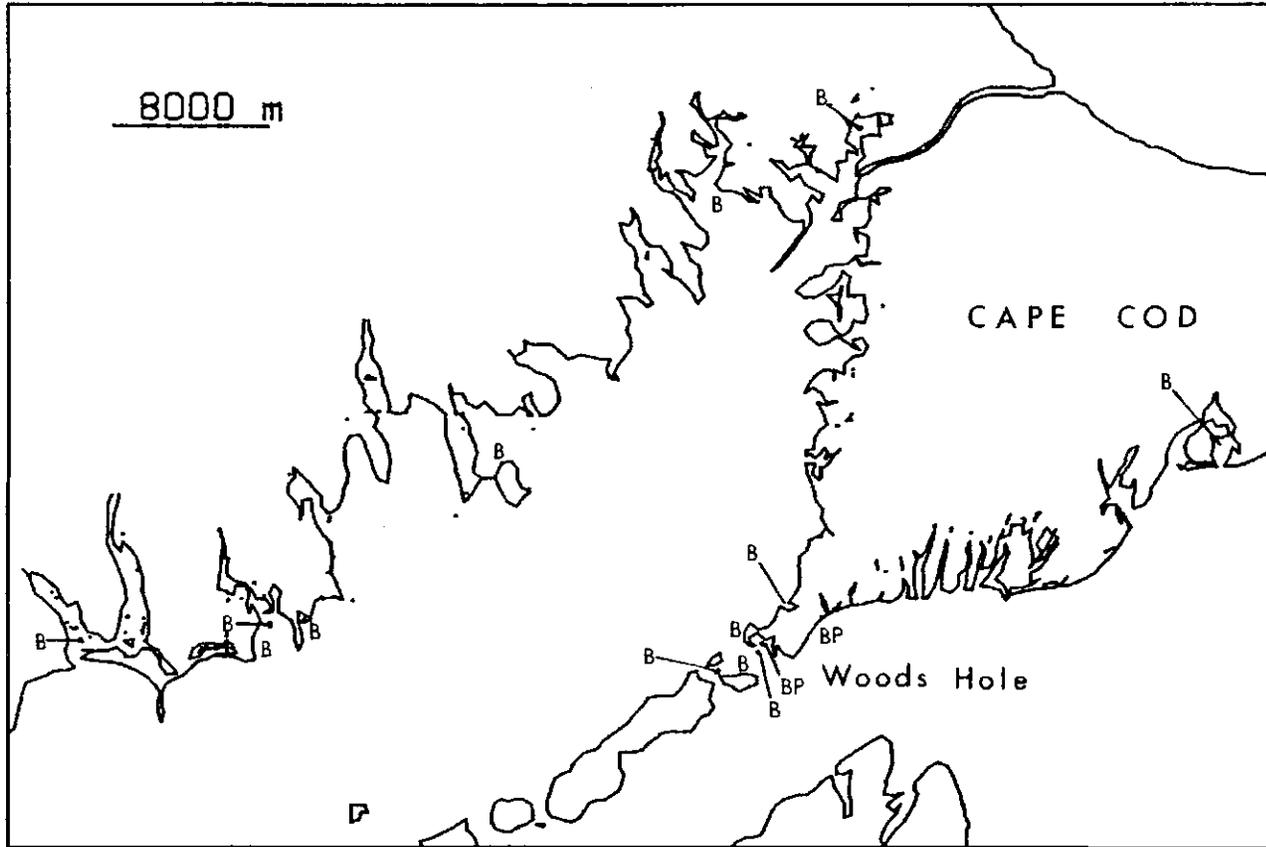
Total annual net production of eelgrass in Buzzards Bay was estimated by multiplying eelgrass bed production area by the mean number of plastochrone units produced each year times the mean plastochrone unit weight per area.

Elsewhere I have calculated the total eelgrass bed area in Buzzards Bay (2920 ha; Costa, 1988). This estimate was calculated from

photographs of $\approx 1:25,000$ scale photographs, and adjusted for percent cover as perceived on that scale imagery. This process ignores bare patches within eelgrass beds that are too small to be seen on those photographs, and which are only visible underwater or with small scale imagery. It is impossible to quantify small scale patchiness in every bed in this region, so a correction factor was estimated based on field experience and microscopic study of photographs was factored into the estimate of bed area.

Vegetative and flowering shoot densities, were measured at $92 \frac{1}{16}$ m² quadrats taken randomly or along transects at 16 sites in Buzzards Bay and Cape Cod (Fig. 2) spanning a wide range of habitat diversity. Most observations and biomass collections were made in the center of the depth distribution of each eelgrass bed, rather than at bed margins. To determine mean plastochrone biomass, above and below ground biomass was collected in 64 of these quadrats. Vegetative biomass was separated into third leaves, other leaves, meristems, and mature rhizome internodes (generally the 4th internode). Reproductive shoots were treated separately, and seed and flower counts were noted. The dimensions of the biomass clippings were recorded, then leaves were cleaned, first by removing large epiphytes by hand or razor, then by soaking in 10% phosphoric acid for several minutes to remove encrusting and smaller epiphytes (Jacobs, 1979). Leaves were rinsed in tap water, blotted dry, damp weight taken, then dried at 50 °C for at least 36 hr. Total aboveground plastochrone unit weight for each quadrat was calculated as total 3rd leaf weight + (total sheath weight/mean leaf no.).

Figure 2. Map of southeastern Massachusetts showing where biomass samples were harvested (B) and sites for measurement of production rates (P).



In some samples, adequate rhizome material was not collected for every shoot. In these cases, total rhizome plastochrone unit weight was calculated as shoot no. per quadrat x mean collected mature rhizome weight. Roots were not harvested, but assumed to be equal to 50% of rhizome biomass (Jacobs, 1979).

PI on various dates between May 1984 and March 1985 was measured off Quisset Beach, and Garbage Beach in Woods Hole (Fig. 2). To measure plastochrone interval, quadrats ($1/16 \text{ m}^2$) were set at different stations in the bed. A hole was punched one leaf width below the top of the leaf sheath of most shoots in the quadrat using a fine pin (Fig. 1). After two to three weeks, all the plants in the quadrat were harvested, and plant tissue was processed as described above.

PI was calculated for each punched shoot in the quadrat by measuring the distance each leaf hole grew from the residual scar on the sheath. If a young leaf had no scar, it was completely new growth. PI was calculated as follows:

$$\text{PI days} = (\text{marking period days}) \times (\text{area of a mature leaf})$$

(total new leaf area produced)

Leaf area was used to calculate PI because older leaves have a higher weight per unit area than younger leaves (Jacobs, 1979; Pregnall, unpub.) because of encrusting algae and dissolved salts, which leads to underestimates of PI. Leaf area of oldest mature older shoots was not always suitable, especially in spring, because winter leaf lengths are

somewhat shorter than summer leaf lengths, and this would lead to overestimates of production. The area of the third leaf, or sometimes the average of third and fourth leaves if there was considerable variability among mature leaves, was used as mature leaf area.

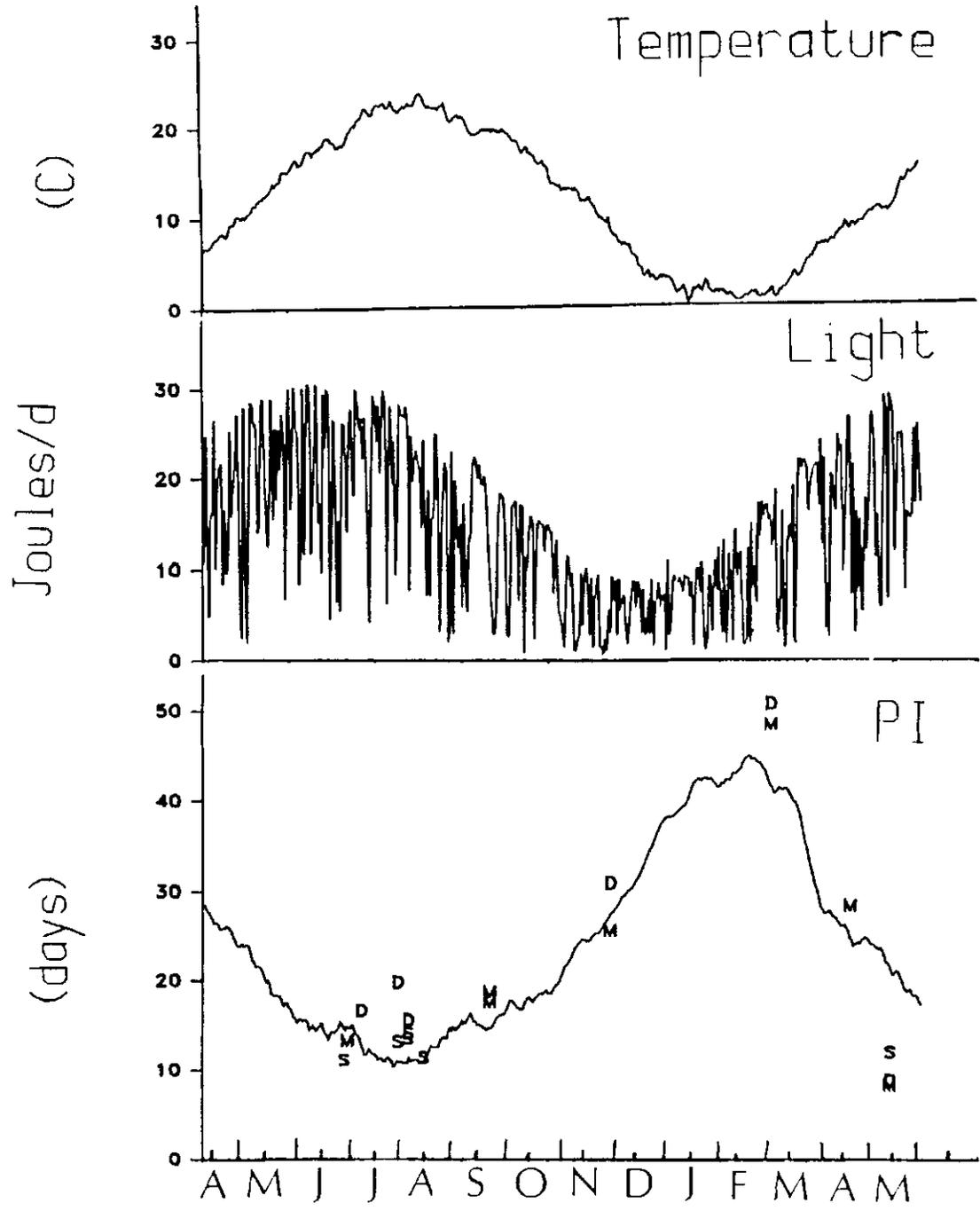
To obtain temperature and light coefficients of growth, PI was correlated with local insolation and water temperature (Woods Hole Oceanographic Institution) during the leaf marking interval. The coefficients were applied to the year long record of light and temperature to model eelgrass growth for 1985. To obtain the total number of PU's produced that year, the inverse of the PI curve was integrated. This number was multiplied times the mean vegetative PU weight at the 16 sites to determine annual vegetative production per unit area. Reproductive shoot production was calculated as 2 x summer biomass and added to vegetative production to obtain total annual aboveground production (Robertson and Mann, 1984).

Results

PI was shortest in May 1986 (8.9 days) and longest in February 1986 (51 days for mid and deep beds, and ≈ 80 in shallow beds; Fig 3). PI correlates well with water temperature, insolation, and [$r^2 = 0.75$; $PI = 77.9 - 0.160 \times (\text{light as } 10^{-3} \text{ J m}^{-2} \text{ d}^{-1}) - 20.3 \times \text{Ln}(C^{\circ}+2)$, Fig. 3]. The adjustment of temperature in this equation was necessary because water temperature in Woods Hole may reach -2°C in winter. Using $^{\circ}\text{K}$ (e.g. Robertson and Mann, 1984) does not result in a good correlation ($r^2 = 0.55$), because as temperature approaches freezing, eelgrass growth slows dramatically.

Figure 3. Water temperature, surface insolation, plastochrone interval (PI) data and PI curve for Woods Hole, 1985-1986.

The PI curve was based on a multiple correlation between, PI, light, and water temperature from eight dates.



Integration of the inverse PI curve yielded 19 PUs, that is, each plant produces 19 leaves, rhizome segments and root clusters during the year. Alternate methods of generating a PI curve based on this data, such as by a fourth order polynomial, or integration of a hand drawn curve, changed this estimate by less than 15%.

The mean aboveground vegetative plastochrone unit weight for the harvested quadrats $38 \text{ g dry wt m}^{-2}$ ($SE=3.1$). If regional annual production is 19 PUs, then mean annual production is $722 \text{ g m}^2 \text{ yr}^{-1}$. When corrected for reproductive shoot production, total above-ground production is $892 \text{ g m}^{-2} \text{ yr}^{-1}$. If the mean below ground production is included, and root biomass estimated as 50% of rhizome production (Jacobs, 1979), then mean total above and belowground production equals $1008 \text{ g dry m}^2 \text{ yr}^{-1}$. Carbon composition measured from eelgrass tissue collected in Woods Hole during Spring 1981 was 39%, thus above ground production is $347 \text{ g C m}^{-2} \text{ yr}^{-1}$ and above + below ground production is $393 \text{ g C m}^{-2} \text{ yr}^{-1}$.

There are several differences between beds at the upper limits of growth and the deep edges of beds. Except in winter, shallow stations have shorter PIs than deeper stations (Fig. 3), but insufficient data was collected from shallow stations to generate a separate curve. The quicker summer growth rates of shallow beds do not result in higher production than mid-depth beds, because above-ground plastochrone unit weight is somewhat less at shallow sites (Table 1). The differences between production in shallow and mid-depth bed may be less than indicated because shallow beds devote more production to roots than do mid-depth beds (Thayer et. al., 1984). Both mid-depth and shallow beds,

Table 1. Measures of biomass (means \pm SE) in shallow, mid-depth and deep beds off Quisset beach.

To calculation total PU weight, root weight was assumed to equal 50% of rhizome weight.

Parameter	Shallow (1-2 m MLW)	Mid (\approx 3 m MLW)	Deep (\approx 5 m MLW)
density:	704 \pm 97	445 \pm 52	141 \pm 17
aboveground biomass: (g dry m ⁻²):	128 \pm 30	162 \pm 27	85 \pm 12
mean shoot dry wt: (mg)	187 \pm 44	427 \pm 122	611 \pm 68
aboveground PU wt: (g m ⁻²):	34.3 \pm 11.7	37.6 \pm 8.0	14.9 \pm 3.9
rhizome PU weight: (g m ⁻²):	9.9 \pm 2.2	8.8 \pm 1.3	3.6 \pm 1.2
Total PU wt (g m ⁻²)	48.7	49.8	20.8

Figure 4. Regional frequencies of various measures of eelgrass biomass.

Top: Aboveground biomass (mean = 149 g dry wt m⁻², SE= 8.7, n=67),
Middle: Shoot density, and Bottom: Aboveground annual production.

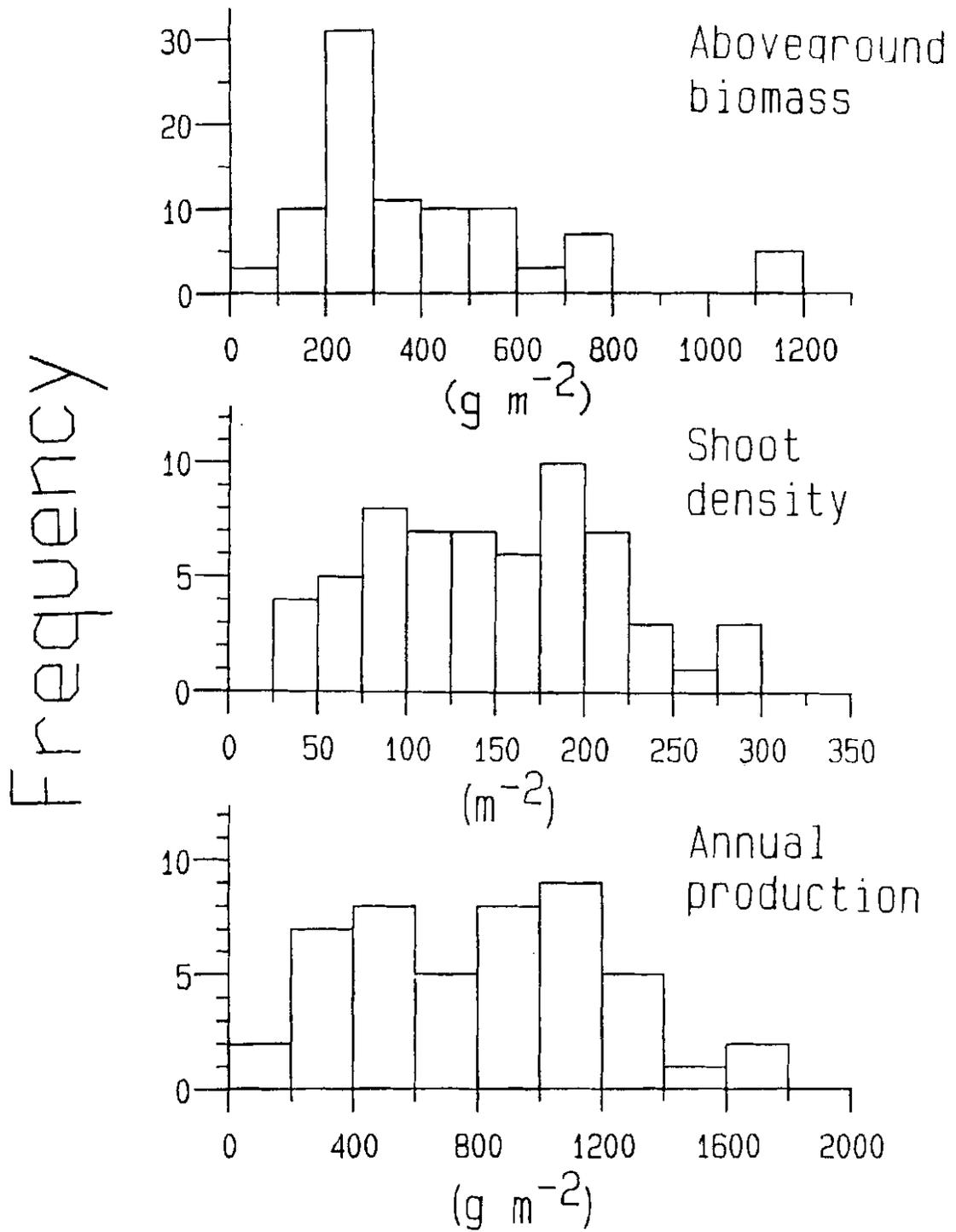
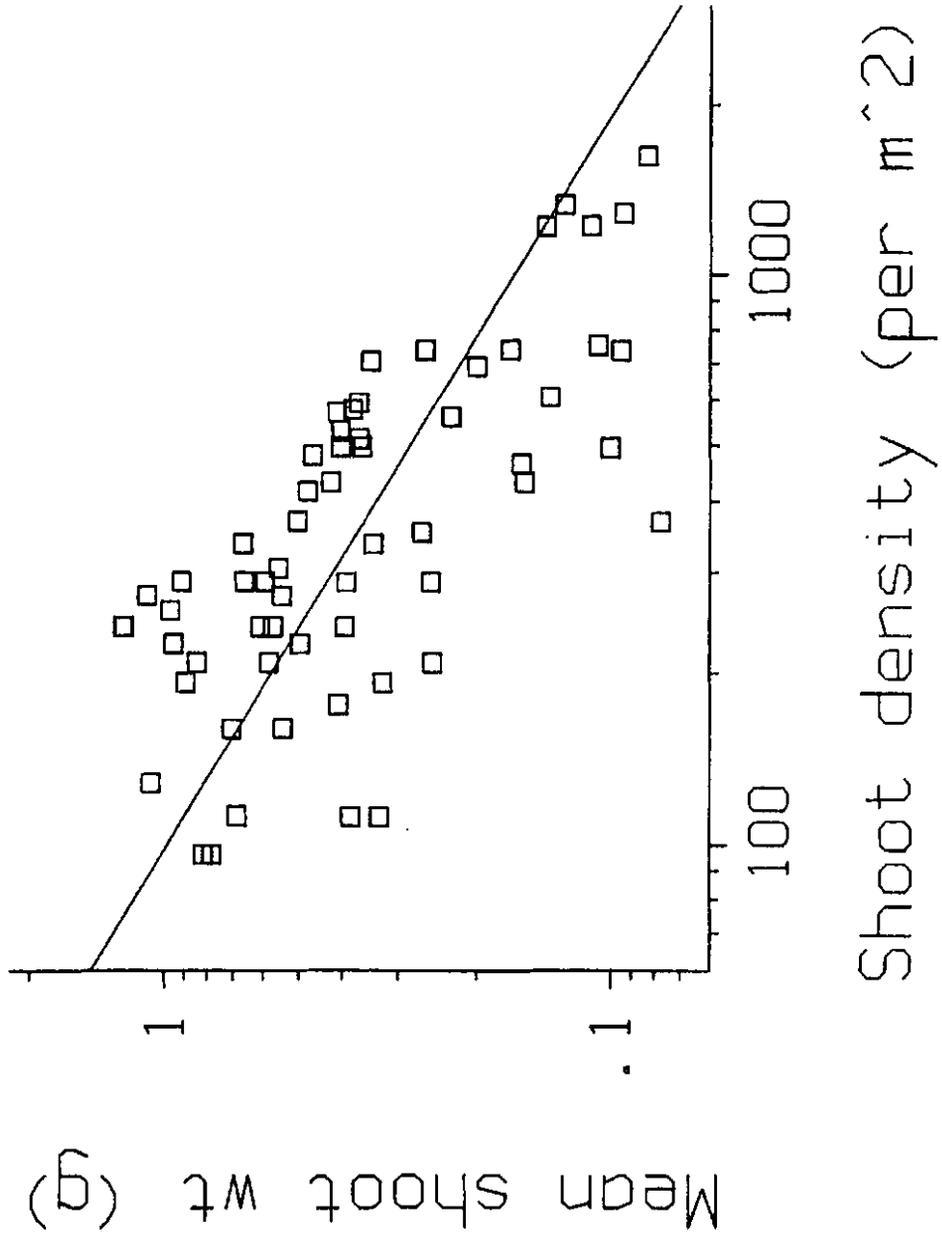


Figure 5. Log-Log plot of mean shoot weight vs shoot density. Slope = -0.78.



however, have higher production than deep beds which have both less above and below-ground plastochrone unit weight and grow more slowly.

Eelgrass beds in Buzzards Bay are remarkably varied in terms of aboveground biomass, shoot density, and total annual production (Fig. 4); but certain biomass relationships are consistent throughout the region. Shoot densities are higher in shallow and high energy environments, but shoots size is smaller (Table 1.). Consequently, aboveground biomass does not change appreciably with changing shoot densities. A log-log plot of these two variables results in a linear relationship with a slope of -0.78 (Fig. 5).

Eelgrass bed area in Buzzards Bay (corrected for large scale percent cover) is 2920 ha (Costa, 1988). Based on transects in the field and detailed analysis of low scale photographs (unpublished observations), 0.85 was used as a correction factor to account for small bare areas ($<2 \text{ m}^2$) that exist in eelgrass beds, but are not resolved in large scale aerial photographs. Thus "production area" of eelgrass beds in Buzzards Bay is 2482 ha. If mean annual production is $393 \text{ g C m}^{-2} \text{ yr}^{-1}$, total annual production in this region is $2.4 \times 10^{10} \text{ g dry}$, or $9.2 \times 10^9 \text{ g C}$. Aboveground annual production alone is $2.1 \times 10^{10} \text{ g dry}$ or $8.1 \times 10^9 \text{ g C}$.

Discussion

Production of organic matter is just one contribution of *Zostera* beds to coastal ecosystems. Eelgrass beds also act as a refuge, habitat, and nursery for a diverse assemblage of algae, plants, and animals and important in binding and stabilizing sediments. Knowledge

of rates of production by *Zostera* and other primary producers, however, is fundamental for understanding carbon flow in coastal ecosystems.

The estimate of production of eelgrass in Buzzards Bays bay depends upon three assumptions: the area of eelgrass is accurate, the concept of a regional PI curve is valid, and the mean weight of plastochrone units used in the calculations are representative of the diverse habitats of the region. Clearly there are difficulties with each of these premises, but a realistic range can be ascribed to the estimate of regional production.

Biomass of plastochrone unit area weight is variable both within and between beds, and only further sampling of beds in this area can shed light on whether these biomass samples represent a regional average for eelgrass biomass. The range of biomass (Fig 4, 42-298 g m⁻²) and production (210 -1540 g m⁻² yr⁻¹) reported here is well within the range of values reported elsewhere (Kentula, 1985; Robertson and Mann, 1982).

The largest uncertainty in estimating production is the calculation of total plastochrone events per year, and the assumption that one curve is characteristic for the whole region. The plastochrone curve was based on data collected from well flushed somewhat exposed beds, typical of most eelgrass bed cover in Buzzards Bay. But PI even within these beds changes with depth, and shallow beds appear to grow quicker in summer and slower in winter.

The cause of these differences in growth rate may be due to both light and temperature effects. In summer, water overlying the shallow beds is often 1 or 3 °C warmer in the summer than deeper beds even in well flushed areas as along surf drive and although not measured,

shallow areas may exhibit more cooling in winter. Moreover, shallow beds receive a longer duration of light above saturation (longer "Hsat"), and this affects growth rate as well (Dennison and Alberte, 1985). Of course, other factors such as physical damage and nutrient availability may play a role in explaining these growth rate differences.

Differences in summer production between shallow and mid-depth beds are small because total plastochrone unit size in shallow areas is slightly less than mid-depth beds (Table 1). Root production was not measured, and if root production in shallow beds is double mid-depth root production, then total plastochrone unit weight may be equal in the two areas, however. This may be the case because beds in shallow wave swept areas have considerably more biomass in below ground production than deeper beds in undisturbed areas (Thayer, et al. 1984; pers. obser.). Shallow and mid-depth beds have higher growth rates and plastochrone units than deep beds where annual production is considerably less.

The relationship between shoot weight and density has been extensively studied in terrestrial systems, and virtually all agricultural and forestry studies show that the slope of a log-log plot is near -1.5, and this has become known as the "-3/2 power law" (White and Harper, 1970). That is, shoot weight = $cp^{-3/2}$, where p=density, and c is a species specific constant. It is remarkable that eelgrass does not conform to this relationship, and instead shows a -0.78 power relationship. This is not because eelgrass is a clonal species, because this relationship applies to terrestrial clonal grasses as well (Kays

and Harper, 1973). Kays and Harper, however, found that terrestrial grass exposed to 30% ambient sunlight showed a depression of the curve to ≈ -1 slope. This also results in biomass to be constant, independent of density. These authors concluded that low light intensity induces density dependant growth and mortality because of mutual self-shading, and this may also explain the unusual shoot density relationship in eelgrass as well.

Locally, eelgrass production is approximately 6.5 x aboveground biomass (Fig. 6). Thus the extrapolation of Dennisons data (1985) showing yearly production to be 6x active leaf weight seems reasonable.

Comparison of eelgrass and other primary producers in Buzzards Bay

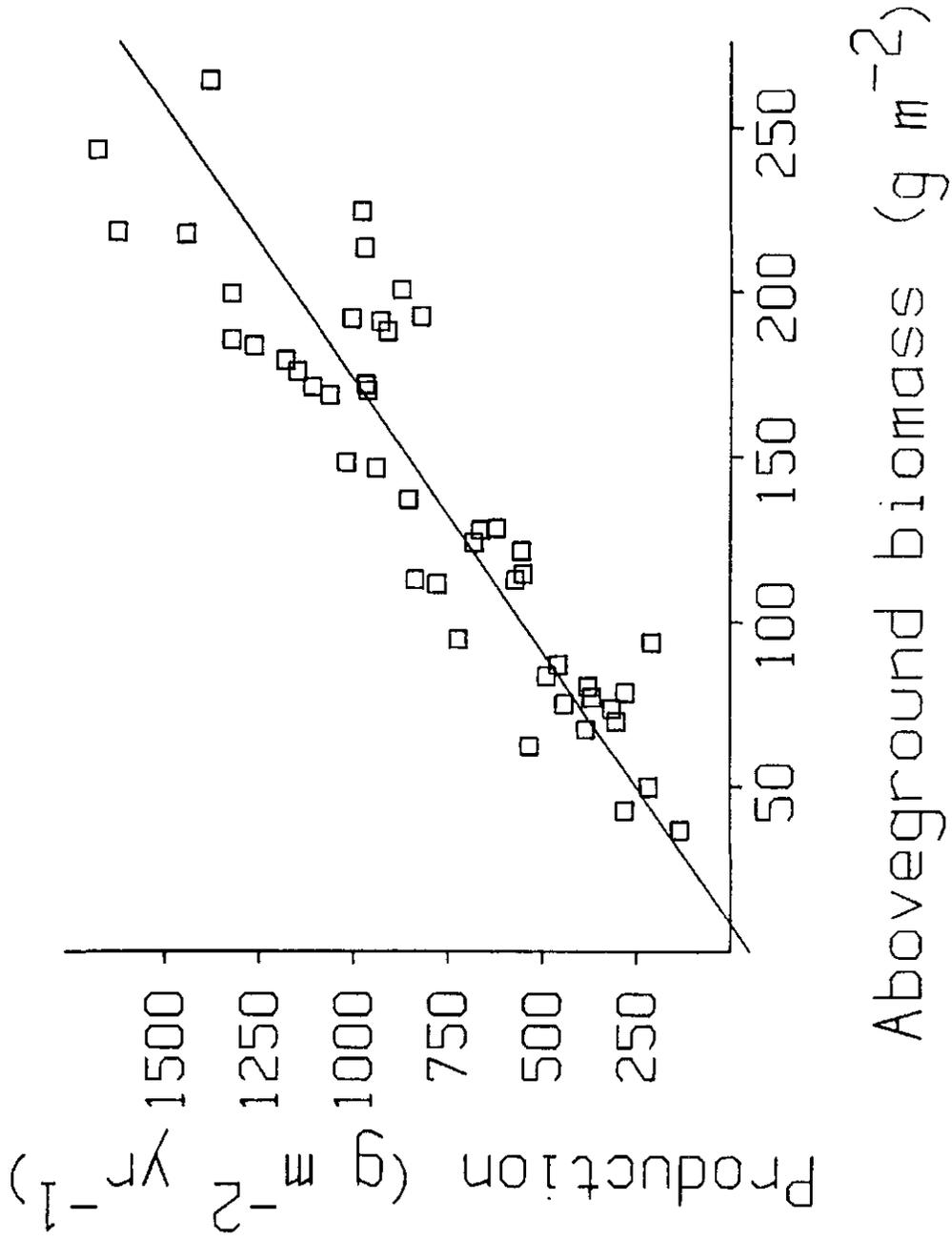
Phytoplankton

Carbon fixation in Buzzards Bay is approximately 10^7 g C m^{-2} y^{-1} (Roman and Tenore, 1978). Because the area of Buzzards Bay and its adjoining bays and estuaries is 5.5×10^8 m^2 (Signell, 1987), phytoplankton annual production in Buzzards Bay is $\approx 5.9 \times 10^{10}$ g C.

Macroalgae

Many macroalgae grow deeper than eelgrass, and drift algae often accumulate on the bottoms of quiescent bays. Nonetheless, macroalgal cover, like eelgrass, is not appreciable in Buzzards Bay because most of the Bay is greater than 10 m deep, and light penetration is insufficient at that depth to support a large biomass of benthic algae. Furthermore, in the open bay, most algae are restricted to solid substrate, and rocky areas are only extensive around the Elizabeth Islands, offshore of

Figure 6. Regression between total aboveground biomass and above and belowground annual production ($r^2 = 0.82$, $m = 6.5$).



Westport and Dartmouth, and in shallow areas, especially within 100 m of shore. The vast majority of the shallow margins of the Bay bottom is mud and sand, and is suitable only for eelgrass colonization. Based on aerial photographs, it appears that algae cover less than 10% of the habitat area of eelgrass, or about 400 ha.

Production estimates for attached algae in temperate waters are quite variable and generally range from 100 - 1000 g C m⁻² y⁻¹ (Ferguson et al., 1980; Josselyn and Mathieson, 1978; Mann, 1972; Wassman and Rasmuss, 1973). Estimates of drift algae production are infrequent. Thorne-Miller et al (1983) found summer biomass of unattached benthic algae in Rhode Island Coastal lagoons to be 14 - 125 g dry m² but did not estimate annual production. Sand-Jensen and Borum (1983) estimated macroalgal production in coastal waters with eelgrass beds 200-500 g C m⁻² y⁻¹. In this paper, 500 g C m⁻² y⁻¹ was conservatively estimated for both drift and attached macroalgae, where they are dense. Thus macroalgal production in Buzzards Bay is $\approx 20 \times 10^8$.

Epiphytic algae

Numerous species of algae are epiphytic on eelgrass (Harlin, 1980), and production estimates range from 1 to 100% of eelgrass production, although 20 - 40% are most frequently reported (Borum and Wium-Anderson, 1980; Mazella and Alberte, 1986, Penhale, 1977; Sand-Jensen and Borum, 1983). In Buzzards Bay, dense accumulations of epiphytic algae are usually found in poorly flushed areas, especially near sources of nutrient inputs. Offshore eelgrass beds typically have much lower accumulations of algal epiphytes, and because these beds make

up approximately 70% of eelgrass cover in Buzzards Bay, total overall epiphytic algal production was conservatively estimated to be 20% of eelgrass production.

Periphyton

Periphyton production on the surface of sediments and solid surfaces range from 4 to 200 g C m⁻² y⁻¹ and are most abundant on muddy sediments in shallow waters without macrophytes, and are less productive in sand (Hickman and Round, 1970; Marshall et al., 1971; Ferguson, et al., 1980, Revsbeck et al., 1981; Sand-Jensen and Borum, 1983). Sand-Jensen and Borum (1983) found in Danish waters that microbenthic algal production peaked at 120 g C m⁻² y⁻¹ at 0.5 m MLW, dropped to 35 g C m⁻² y⁻¹ at 2 m MLW, and decline to negligible values below 5 m..

The production rate of periphyton declines more rapidly than macrophytes. Thus, the total shallow (photic) substrate area in Buzzards Bay (10,380 ha, Chapter 1) overestimates the areal extent of periphyton production area, because more than 80% of this substrate is covered with eelgrass beds, rock fields, or sand flats without appreciable periphyton densities. If the remaining area has a mean production rate of 45 g C m⁻² y⁻¹, then periphyton contribute 9 x 10⁸ g C y⁻¹ in Buzzards Bay.

Salt marshes

Salt marshes cover 1900 ha in Buzzards Bay (Hankin et al, 1985). These communities are productive, but they do not export appreciable amounts of organic matter (Nixon, 1980). One well studied salt marsh in

Buzzards Bay has a mean annual production of $160 \text{ g C m}^{-2} \text{ y}^{-1}$ (Valiela et al., 1975), however, only 20% of its production is released into Buzzards Bay (Valiela and Teal, 1979). If this marsh is typical for the region, then the contribution of salt marshes to Buzzards Bay is $6.0 \times 10^8 \text{ g C m}^{-2} \text{ y}^{-1}$.

Relative contribution of eelgrass production in Buzzards Bay and adjoining shallow embayments

Most of Buzzards Bay is too deep to support eelgrass growth, hence eelgrass and epiphytic algae contribute only 15% of the total production in Buzzards Bay (Table 2). In contrast, eelgrass communities may account for a larger portion of total production in shallow embayments.

For example, Buttermilk Bay is a 210 ha lagoon at the north end of Buzzards Bay with a mean depth of 1.0 m (Costa, 1988; Valiela and Costa, in press), and 47 ha of eelgrass production area (Appendix III). Assuming eelgrass production rates described above, then *Zostera* production in Buttermilk Bay equals $1.8 \times 10^8 \text{ g C y}^{-1}$.

Other producers can also be estimated as before. Algal epiphytes are very abundant in parts of Buttermilk Bay, and if they equal 40% of *Zostera* production (Penhale, 1977), they account for an additional $0.7 \times 10^8 \text{ g C y}^{-1}$. In a shallow, enriched Rhode Island lagoon, Nowicki and Nixon (1985) estimated phytoplankton production to $120 \text{ g C m}^{-2} \text{ y}^{-1}$. If Buttermilk Bay has similar rates of production, then phytoplankton produce $2.5 \times 10^8 \text{ g C y}^{-1}$.

Drift algae are abundant in some areas of Buttermilk Bay, (Costa, 1988). Algal biomass in 1985 was $77 \text{ g dry wt m}^{-2}$ ($n=8$, $SE=22$) in a

Table 2. Eelgrass production in Buzzards Bay compared to estimates of other producers.

Salt marsh production for Falmouth and the Elizabeth Islands was based on the area salt marsh adjoining Buzzards Bay (from Hankin et al., 1985).

Component	Production (g C y ⁻¹ x 10 ⁸)	Percent of Total
Phytoplankton	588	80
Eelgrass	92	13
Eelgrass epiphytes	18	2.5
Other periphyton	9.0	1.2
Macroalgae	20	2.7
Salt marshes	6.1	0.8
TOTAL	733	

transect from mid-bay to Red Brook. If annual production is 6x summer biomass then annual production is $\approx 500 \text{ g C m}^{-2} \text{ y}^{-1}$. This transect was centered near a major source of nutrients, and probably overestimates algal abundance in the Bay. In Buttermilk Bay, drift algae occur mostly in quiescent areas, depressions, or tangled within eelgrass shoots, especially near nutrient sources. Total drift algae area was conservatively estimated to be 20% of eelgrass cover, and therefore contributes $0.5 \times 10^8 \text{ g m}^{-2} \text{ y}^{-1}$ to Buttermilk Bay.

Attached algal production in Buttermilk Bay is negligible, because rock and cobble are common in only a few areas. Altogether there is less than 6.5 ha of attached algae habitat in this Bay, or $0.3 \text{ g C} \times 10^8 \text{ y}^{-1}$. Epipellic periphyton are more important in Buttermilk Bay because there are ≈ 50 ha of unvegetated mud bottom where periphytic algae may be abundant. Assuming production rates of $100 \text{ g C m}^{-2} \text{ y}^{-1}$, then this component may equal $0.5 \times 10^8 \text{ g C y}^{-1}$.

Based on these estimates, eelgrass beds and their epiphytes account for 40% of all production in Buttermilk Bay (Table 3).

Table 3. Eelgrass production in Buttermilk Bay compared to estimates of other producers.

No estimates of salt marsh production were made.

Production Component	Percent of (g C y ⁻¹ x 10 ⁸)	Total
Phytoplankton	2.4	39
Eelgrass	1.8	29
Eelgrass epiphytes	0.7	11
Drift algae	0.5	8.1
Macroalgae	0.3	4.8
Other periphyton	0.5	8.1
TOTAL	6.2	