



*Padilla Bay*

National Estuarine Research Reserve

Reprint Series No. 10  
Reprinted October 1990

**BENTHIC PRIMARY PRODUCTION IN THE EELGRASS  
MEADOW AT THE PADILLA BAY NATIONAL ESTUARINE  
RESEARCH RESERVE, WASHINGTON**

Ronald M. Thom

February 1988



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Padilla Bay National Estuarine Research Reserve is managed by the Shorelands and Environmental Assistance Program, Washington State Department of Ecology, in cooperation with the Estuarine Reserves Division, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce. The preparation of this document was financially aided through a grant to the Washington State Department of Ecology with funds obtained from NOAA/Office of Ocean and Coastal Resource Management, and appropriated for Section 306 or 315 of the Coastal Zone Management Act of 1972, as amended.



FRI-UW-8808  
February 1988

**FISHERIES RESEARCH INSTITUTE**  
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**NOAA TECHNICAL REPORT SERIES OCRM/MEMD**

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RESEARCH RESERVE, WASHINGTON**

by

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This work is the result of research sponsored by the U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, National Ocean Service, Office of Ocean and Coastal Resource Management, Marine and Estuarine Management Division, under contract NA86AA-D-CZ027.

Approved

Date 5-16-88

R. C. Francis  
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**Bibliographic citation:** Thom, Ronald M. 1988. Benthic primary production in the eelgrass meadow at the Padilla Bay National Estuarine Research Reserve, Washington. Report to NOAA/OCRM/MEMD by Univ. Wash., Fisheries Research Institute (FRI-UW-8808). 33 pp. Seattle, Washington. Padilla Bay National Estuarine Research Reserve Reprint Series No. 10, 1990.



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<b>REPORT DOCUMENTATION PAGE</b>	<b>1. REPORT NO.</b>	<b>2.</b>	<b>3. Recipient's Accession No.</b>
<b>4. Title and Subtitle</b> Benthic Primary Production in the Eelgrass Meadow at the Padilla Bay National Estuarine Research Reserve, Washington		<b>5. Report Date</b> 12-87	
<b>7. Author(s)</b> Ronald M. Thom		<b>6.</b>	
<b>9. Performing Organization Name and Address</b> Fisheries Research Institute School of Fisheries, WH-10 University of Washington Seattle, WA 98195		<b>8. Performing Organization Rept. No.</b>	
<b>12. Sponsoring Organization Name and Address</b> NOAA/OCRM/MEMD 1825 Connecticut Ave NW Universal Building Washington, D.C. 20235		<b>10. Project/Task/Work Unit No.</b>	
Padilla Bay N.E.R.R. WA State Dept. of Ecology 1043 Bayview-Edison Rd. Mt. Vernon, WA 98273		<b>11. Contract(C) or Grant(G) No.</b> (C) (G) NA86AA-D-CZ027	
<b>15. Supplementary Notes</b>		<b>13. Type of Report &amp; Period Covered</b> Final Report 6/86-12/87	
<b>16. Abstract (Limit: 200 words)</b> <p>The spatial patterns of standing stock and productivity of benthic autotrophic components (<i>Zostera marina</i> and <i>Zostera japonica</i>, epiphytic algae and benthic sediment associated algae) of the eelgrass meadow in Padilla Bay, Washington, were studied seasonally for one year. Eelgrass extended from approximately 1.0m above MLLW down to subtidal depths. However, standing stock decreased at depths below -0.5m MLLW. <i>Z. japonica</i> formed a band at upper elevations, and mixed with <i>Z. marina</i> at about 0.3m to 0.6m MLLW. Epiphytic algae were abundant in the meadow, and reached greatest standing stock between 0.3 and -0.4m MLLW. Sediment associated algae were abundant at all elevations as indicated by chlorophyll a concentrations. The standing stock of all components varied seasonally. Sediment algae reached peak abundance in early spring, followed by rapid growth of epiphytic macroalgae in early summer. Eelgrass biomass was greatest in early to late summer depending upon depth. Annual net primary productivity (NPP) for the system was 351 gC m<sup>-2</sup>. Epiphytic algae, <i>Z. japonica</i> and <i>Z. marina</i> were responsible for 50, 2 and 48% of this production, respectively. NPP by sediment algae was negligible due to high sediment associated respiration rates. Total annual production from the 3,000ha system was approximately 28,000mt dry plant matter.</p>		<b>14.</b>	
<b>17. Document Analysis a. Descriptors</b>  eelgrass, primary production, standing stock, seasonal dynamics, epiphyte production, estuarine primary production			
<b>b. Identifiers/Open-Ended Terms</b>			
<b>c. COSATI Field/Group</b>			
<b>18. Availability Statement</b>		<b>19. Security Class (This Report)</b>	<b>21. No. of Pages</b>
		<b>20. Security Class (This Page)</b>	<b>22. Price</b>



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## PREFACE

I gratefully acknowledge the assistance of J. Hampel, D. Groebecke, K. Li, D. Olden, L. Hallum and D. Shreffler in the field. J. Hampel, A. Shaffer, D. Shreffler and L. Hallum processed most of the samples. A. Shaffer entered a large proportion of the data onto computer files. J. Shapland drew the maps. T. Stevens provided the depth determinations for the study sites. The staff at the Padilla Bay Sanctuary was very helpful in providing equipment, logistical support and overnight accommodations during field trips. I especially thank T. Stevens, Director of the Padilla Bay Reserve, for help and support. R. Nakatani, T. Stevens and an anonymous reviewer provided helpful comments that considerably improved the manuscript. M. Duke did final editing of the manuscript.

The work reported herein documents the distribution and production of the dominant primary producers in the Reserve. This information is needed to understand the ecological importance and contribution of the major primary producers within the reserve. The data compliments work on the distribution of fish prey (C. Simenstad) and Dungeness crab (D. Armstrong) in the Bay, and research on the nutrient dynamics (S. Williams) and food web support (R. Wissmar) on the flats. Research which documents the total distribution of seagrasses in the Bay (T. Mumford, B. Webber) will utilize the present data to calculate the total primary production in the Bay. FY87 research focusing on primary production in the remaining benthic habitats, i.e. mudflats, gravel beds (R. Thom) and marshes (M. Burg), will be coupled with the seagrass data to document the relative and absolute contribution of benthic plants to the food web of the Bay.



## INTRODUCTION

Seagrasses are among the most common plants inhabiting shallow coastal ecosystems. Eelgrass (*Zostera* spp.) is the most common seagrass taxon in estuaries and embayments along temperate regions of North America (Phillips 1984). The relatively great importance of autotrophic components of seagrass systems to nearshore food webs is proven in several areas (e.g., Stoner 1980, Fry 1984). Further, the systems can act autonomously in terms of production and consumption processes (Asmus and Asmus 1985). Seagrass systems are utilized as habitat and nursery areas by many animals (e.g., Heck and Thoman 1984; Heijs 1985; Virnstein and Curren 1986).

Although dominant and ecologically important, fundamental information on eelgrass distribution and production is limited for the Pacific coast. Recently, Kentula and McIntire (1986) showed that *Zostera marina* L. in Netarts Bay, Oregon, exhibited a mean annual production rate of 383 gC m<sup>-2</sup>. The total production from the 176 ha bed amounted to 3,200 mt y<sup>-1</sup>. Of significance was the fact that the biomass was replaced 10 times during the growing season, which indicated substantial export of organic matter to surrounding habitats. Thom (1984) estimated that eelgrass accounted for over 50% of the annual primary production in Grays Harbor, a coastal estuary in Washington.

Seaweeds and diatoms epiphytic or closely associated with seagrasses can form a significant proportion of the total primary production in the system. Penhale (1977) calculated an 18% contribution by the epiphytic flora to the total productivity of the eelgrass system in New Jersey. Kentula (1982) found that maximum standing stock of epiphytes on eelgrass in Netarts Bay exceeded seagrass leaf biomass by 2.3 times during spring. The high importance of seagrass associated algae has been proven for one food web inhabiting estuaries of Hood Canal, Washington (Simenstad and Wissmar 1985).

The purpose of this work was to describe the spatial patterns and seasonal dynamics of standing stock and productivity of the major benthic intertidal plants in Padilla Bay (Fig. 1). An attempt was made to partition the production among the major components (i.e., two eelgrass species, seaweeds and sediment microflora), provide data from which predictions of production could be made in unsampled areas, and calculate a first order approximation of total annual primary production (i.e., the amount of carbon fixed by plants during photosynthesis) in the Bay.

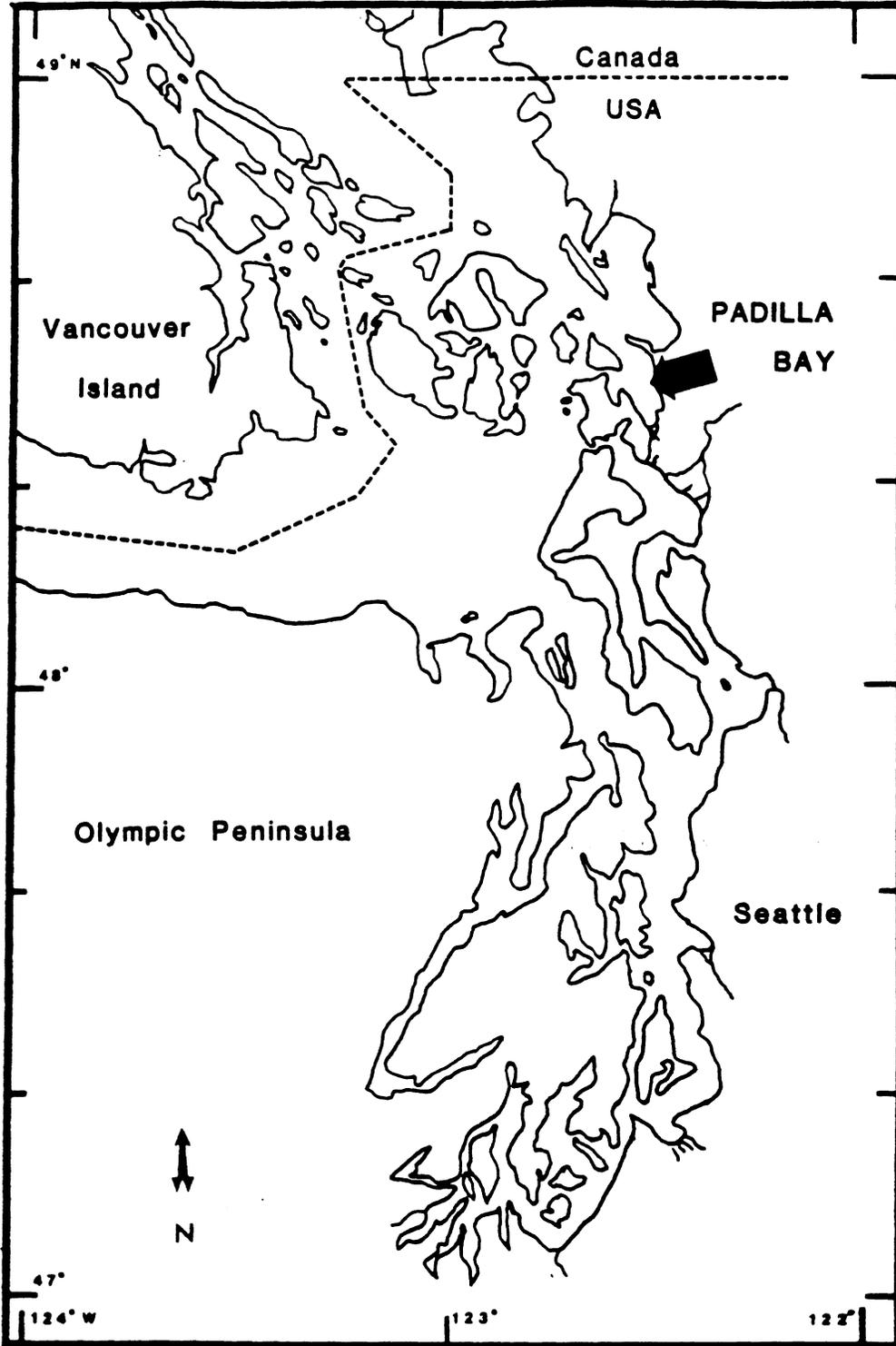


Figure 1. Location of Padilla Bay.

## STUDY AREA DESCRIPTION

Padilla Bay is a shallow embayment located on northern Puget Sound (Fig. 1). The Bay covers approximately 4,200 ha, and is surrounded by agricultural lands, forested uplands and narrow fringing marshes (Fig. 2). The broad intertidal flats in the Bay are dissected by shallow channels which drain the flats during falling tides. The mean tide range and mean spring tidal range for the area are 1.55 and 2.56 m, respectively. Riverine input is primarily from the Skagit River via Swinomish channel, and secondarily from small sloughs draining local uplands. Salinity in the Bay ranges from 15 ppt to 30 ppt depending upon river flow and tidal influences (Cassidy and McKeen 1986 and unpublished data). Water temperature varies from 7°C in December-February to as high as 25°C in large pools of standing water on the flats during warm mid-summer (July) days. Inorganic nitrogen values are typically low throughout the year. Nitrate concentration rarely exceeds 5  $\mu\text{M}$  and is usually less than 1  $\mu\text{M}$ . (unpublished data). Low nitrogen to phosphorous ratios (range 3-6) exist in spring and summer in the water over the seagrass meadow (Wissmar 1986).

The most conspicuous autotrophic component of the intertidal area is eelgrass, which occupies approximately 3,500 ha, and represents one of the largest contiguous eelgrass meadows on the Pacific coast of North America. The eelgrass species present in Padilla Bay are *Zostera marina* and *Zostera japonica* Aschers. & Graebn. *Z. japonica* is an annual species, and is believed to have been introduced to the region inadvertently with the importation of oyster seed from Japan in the 1930s (Harrison 1976). This latter seagrass species is generally smaller in size and occupies higher intertidal elevations as compared to *Z. marina* (Harrison 1982a).

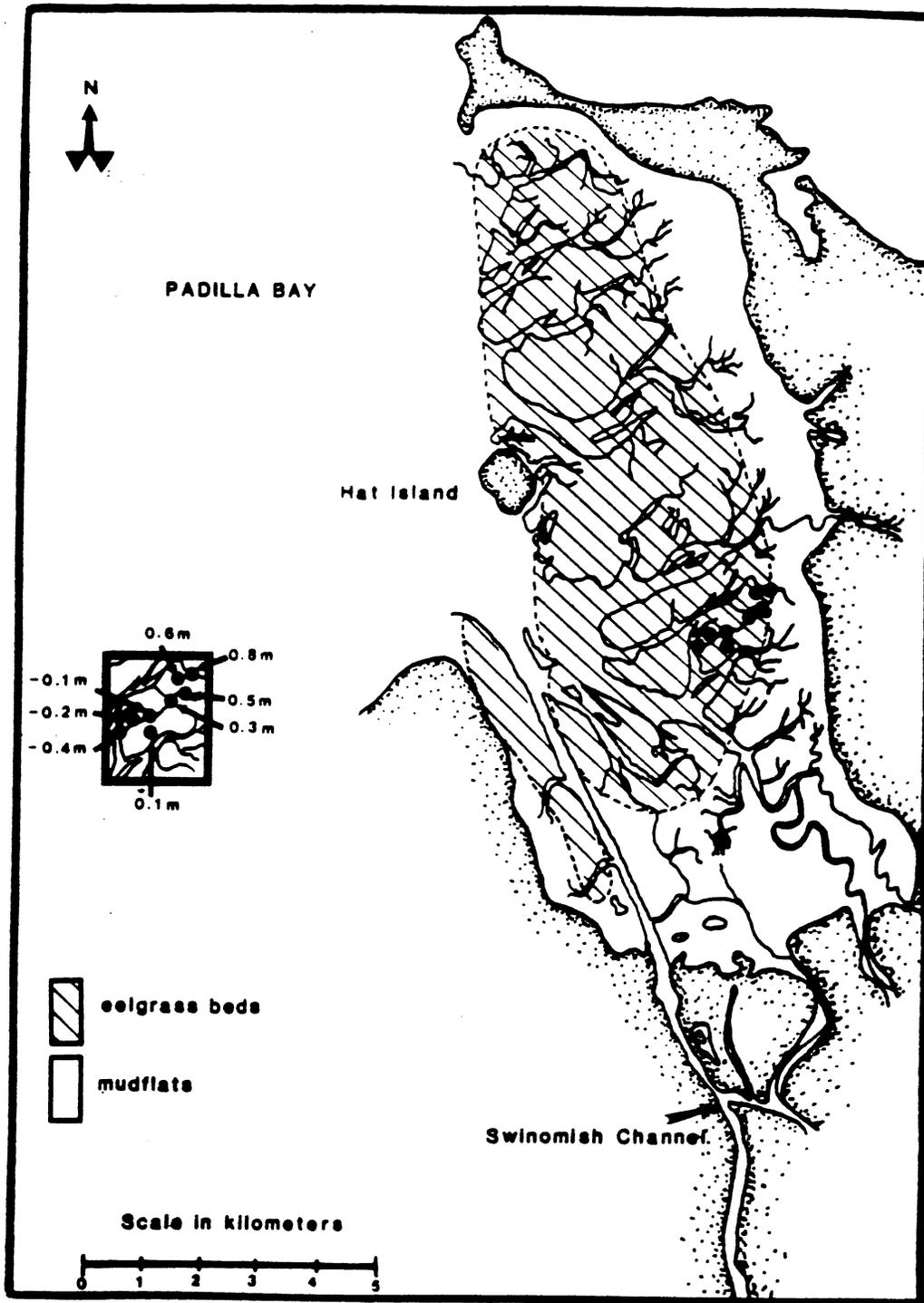


Figure 2. Padilla Bay and the study sites. The inset shows depths of sites relative to MLLW. The line delineating channels and flats within the Bay indicates the approximate seaward extent of the intertidal zone (-1.0m MLLW). The outline of eelgrass is also approximate. Little information exists on the distribution of eelgrass in the channels.

## MATERIALS AND METHODS

### Sampling Sites

Eight study sites were located in the mid portion of the Bay (Fig. 2). The sites covered a depth gradient that spanned from the landward edge of *Z. japonica* to the edge of a subtidal channel. The depths of the sites, relative to MLLW, were 0.8m, 0.6m, 0.5m, 0.3m, 0.1m, -0.1m, -0.2m and -0.4m. The site at -0.2m was located in the middle of a shallow, narrow (ca. 15m wide) channel, and the site at -0.4m was positioned at the edge of a wider channel that extended to subtidal depths. Water flowed relatively rapidly through these channels during falling tides. Preliminary observations showed that the sites were representative of the range of seagrass standing stock and morphology in the Bay. Each site consisted of a 10m transect line positioned parallel to the edge of the water. The sites were marked by wooden stakes placed at each end of the 10m line. Sampling was carried out using 0.1 m<sup>2</sup> quadrat placed at random points along either side of the line.

### Density and Standing Stock Sampling

Eelgrass shoots within the quadrat were harvested by cutting at their base. The plant material was placed in labelled plastic bags. A small plastic tube was used to extract a sediment core (1cm diameter x 1cm deep) from the quadrat for analysis of chlorophyll a and phaeopigment concentrations. All samples were frozen in the dark for later analysis. In general, three quadrats (one was also used for productivity measurements, see below) were sampled at each site. Sampling was conducted on 9 and 23 June, 22 July, 5 and 18 August and 7 October 1986, and 26 January, 25 February, 16 April and 1 May 1987. All sites were sampled during the June, July, August and May visits. Three sites (i.e., 0.6, 0.1, -0.4m) representative of the two main habitats (i.e., *Z. japonica* and *Z. marina*) were sampled during all visits.

Frozen samples of macrophytes were thawed in the laboratory, rinsed gently in tap water to remove sediments, and separated by species. The epiphytes, consisting of seaweeds and filamentous and tube dwelling diatoms were carefully removed from the seagrass leaves by scraping with a spatula. The freezing process facilitated easy removal of the epiphytes. The number of shoots of each eelgrass species was recorded for each sample. The weight of each species was recorded following drying at 90°C for at least 48 hours. To describe morphological differences in eelgrass populations among the sites, the

length, width, leaf area and dry weight were determined for five random shoots from each sample collected in June 1986. Chlorophyll a and phaeopigment concentrations were determined from 90% acetone extractions of sediments using a fluorometer (Strickland and Parsons 1972).

## Productivity Measurements

### Eelgrass

Net shoot primary productivity (NPP) of *Z. marina* was measured using a modification of the method of Kentula and McIntire (1986). A 0.1 m<sup>2</sup> area was marked at each site containing this species by anchoring a quadrat using stiff wire (i.e., clothes hanger) pushed into the sediment. A shoot was marked by poking a hypodermic needle through the leaves at a point immediately above the youngest sheath. Different diameter needles were used depending on the width of the leaves not only to minimize damage to the plant but to also assure relocation of the marks at a later date. The majority of shoots within the quadrat were marked. All vegetation in the quadrat was harvested during the next visit to the site, and frozen for later analysis. In the laboratory, the samples were treated exactly like the samples for standing stock. However, the marked shoots were separated from the remainder of the sample. The shoot was cut at the level of the mark in the oldest leaf. Next, the portion of leaf distal to the mark on that leaf was removed. The material between the level of the mark on the oldest leaf and the distal mark consisted of the biomass produced during the time between the original marking and the harvesting. It was assumed that no leaf loss occurred during the 13-15 day intervals. Loss of the oldest leaf was apparent in a few cases in that a mark was found in the basal portion of the outer senescent leaf, but the upper portion of the leaf was lost. In addition, using the mark in the oldest leaf as a baseline assumed that no growth took place in the oldest leaf. Very little (<10%) of the annual *Z. marina* NPP was due to growth in the oldest leaf in Netarts Bay (Mary Kentula, personal communication, 1986). The dry weight of the new material produced during the growth interval was recorded. Finally, the data on shoot density and biomass of component plants from the quadrat were included as a third replicate sample of standing stock from each site. Production experiments were carried out during June, July and August 1986, and April-May 1987; a period covering the growing season for the plants (Kentula and McIntire 1986, Harrison 1982a).

The shoot marking technique was attempted on *Z. japonica* employing very fine needles and pins, but proved unsuccessful due to difficulties in confidently relocating marks in the very narrow (<2mm) leaves. In addition, damage to the leaves appeared significant, even with the smallest diameter pin. Thus, change in mean biomass was used as an indicator of NPP. *Z. japonica* is an annual, and is virtually absent from the Bay in winter. This fact, coupled with the relatively short intervals between samplings during the growing season, minimized the error in estimating NPP using biomass changes. Limited experiments were conducted with both eelgrass species using oxygen flux (see below) to provide a comparison of methods measuring NPP using oxygen flux versus shoot marking and biomass changes. Because of evidence from physiological and environmental work, the use of oxygen flux to measure net production was strongly discouraged by Zieman and Wetzel (1980). Therefore, I used leaf marking and biomass changes to estimate eelgrass NPP in Padilla Bay.

#### Benthic Algae

The NPP of algae epiphytic on the eelgrass was measured using standard light and dark bottle incubations following the methodology in Littler and Arnold (1985). Healthy specimens of epiphytic algae were collected from the sites and transported to laboratory facilities at the Padilla Bay Interpretive Center. Portions of specimens were placed in 300 ml BOD bottles containing water collected from the Bay. The initial dissolved oxygen (DO) was measured using an oxygen meter (YSI dissolved oxygen meter model 58). The bottles were placed in a water bath held at ambient sea temperature, and incubated under ambient mid-day light for 1-3 hours. Bottles containing water only were run to account for plankton metabolism. Following the incubation, the final DO was recorded. The specimens were removed from the bottles, dried and weighed. NPP was calculated for each species using the formulas in Littler and Arnold (1985). Two-four replicates were run for each species. The experiments took place on 9 June, 23 June, 22 July and 18 August 1986, and 30 April 1987. Shoots of both seagrass species were incubated in a similar manner during some experiments.

Sediment NPP was measured in clear plexiglass cylinders. The cylinders were 20cm long and had an inside diameter of 10 cm. An undisturbed sediment core (5cm deep) was carefully removed from within one random  $0.1 \text{ m}^2$  standing stock quadrat at each site using the cylinder. The bottom was sealed with a rubber bung. The top of the cylinder was closed with a plexiglass plate except for a hole (1.3 cm diameter) through which the oxygen

probe could be inserted. This hole was sealed with a rubber stopper during incubations. The sediments were incubated under the same conditions as the epiphytes in the BOD bottles.

#### System Productivity Calculations

The *Z. marina* growth data was extrapolated to NPP per unit area by multiplying mean NPP per shoot by the mean shoot density. *Z. japonica* production was calculated as the difference in mean biomass between successive collection dates. Epiphyte production per unit area was determined by multiplying mean production per g of tissue by mean g dry weight of tissue per unit area. Sediment production was directly measured per unit area of sediment. Epiphyte and sediment hourly production was expanded to daily rates by multiplying hourly rates by 8 to simulate the duration of non-light limited photosynthesis (unpublished data). Total daily NPP for a site was the sum of per unit area rates for the species occurring at the site during the sampling period. A factor of 0.38 gC = 1 g dry wt was used to inter-convert plant dry weight with carbon content (Westlake 1963).

## RESULTS

### Eelgrass Morphometrics

Coefficient of determination values based on linear regressions showed that pairs of morphometric parameters were more strongly related for *Z. marina* as compared to *Z. japonica* (Table 1). Shoot length and leaf area of both species increased with increasing depth, although a relatively wide range in shoot lengths for *Z. marina* especially at the deepest sites resulted in a relatively weak relationship (Table 1). Non-linear models applied to the data did not yield appreciably greater  $R^2$  values over that of the linear model.

### Density and Standing Stock

#### Eelgrass

Shoot density for both species showed a strong relationship to depth during the growing season (Fig. 3a, b), with *Z. japonica* reaching peak density between 0.5 and 0.8m depth and *Z. marina* having peak density at -0.2m depth. Based on the density vs depth curves, the depth of maximum overlap of the two species was at about 0.3m.

The dramatic seasonality of *Z. japonica* is typified by the change in mean density from a maximum in June of approximately 3200 shoots  $m^{-2}$  to a minimum of less than 100 shoots  $m^{-2}$  in winter at the site at 0.6m depth (Fig. 4). Seasonal changes in the density of *Z. marina* was much less pronounced (Fig. 4).

Mean biomass was strongly related to depth also (Fig. 5a, b). For *Z. japonica*, biomass was greatest at depths between 0.3 and 0.8m. An interesting shift in biomass is evident during the growing season, however. At 0.6m, biomass was lowest in May, greatest in June and intermediate in August. The difference between May and August values at 0.5m is also relatively great. Seasonal differences at the other elevations are less pronounced. Peak biomass of *Z. marina* occurred at the lowest depth (-0.4m) in May and June, and at a much shallower site (0.1m) in August. The relatively great leaf area of plants at the lowest elevation explains the high biomass at relatively low density (Fig. 3b) condition at the lowest elevation. As with density, the greatest overlap of the two species with regard to biomass was at the 0.3m depth (Fig. 5a, b). Although peak densities were quite dissimilar between the two species (Fig. 3a, b), the maximum mean biomass measured was similar (Fig. 5a, b).

Table 1. Linear regressions for seagrass morphometric parameters. The model is of the form  $Y = a + bX$ .  $R^2$  = coefficient of determination

Species	Y	X	b	a	$R^2$
<i>Z. japonica</i>	shoot wt.(mg)	length (cm)	3.32	0.60	0.49
	leaf area (cm <sup>2</sup> )	length (cm)	1.89	2.50	0.46
	shoot wt. (mg)	leaf area (cm <sup>2</sup> )	1.75	-3.00	0.32
	length (cm)	depth (m) <sup>a</sup>	-6.43	7.26	0.55
<i>Z. marina</i>	shoot wt.(mg)	length (cm)	43.86	-362.61	0.74
	leaf area (cm <sup>2</sup> )	length (cm)	19.31	-120.41	0.78
	shoot wt. (mg)	leaf area (cm <sup>2</sup> )	2.00	-59.10	0.85
	length (cm)	depth (m) <sup>a</sup>	-13.84	15.81	0.26

<sup>a</sup>Relative to MLLW.

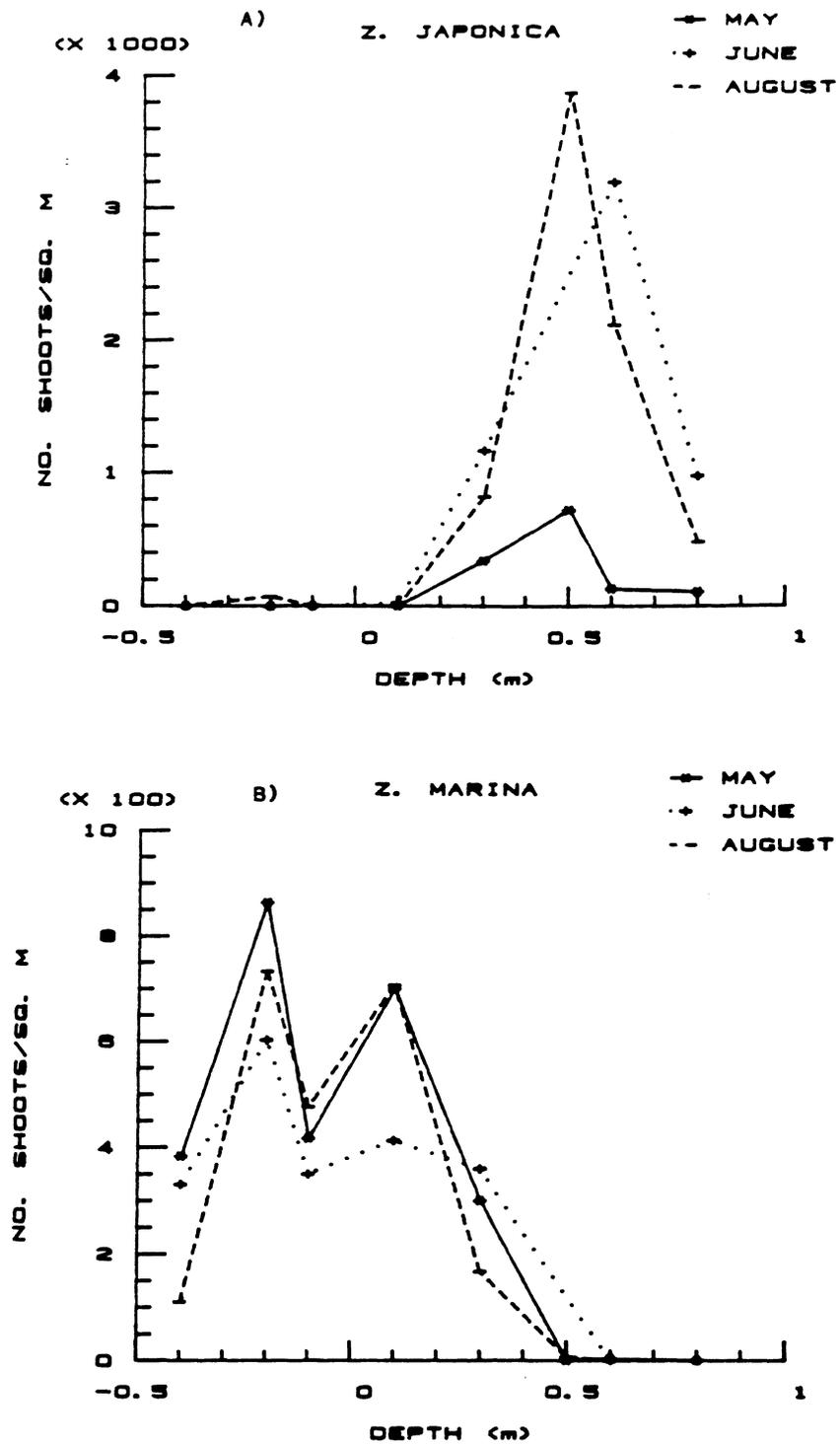


Figure 3. Eelgrass mean density vs depth. A) *Z. japonica*; B) *Z. marina*.

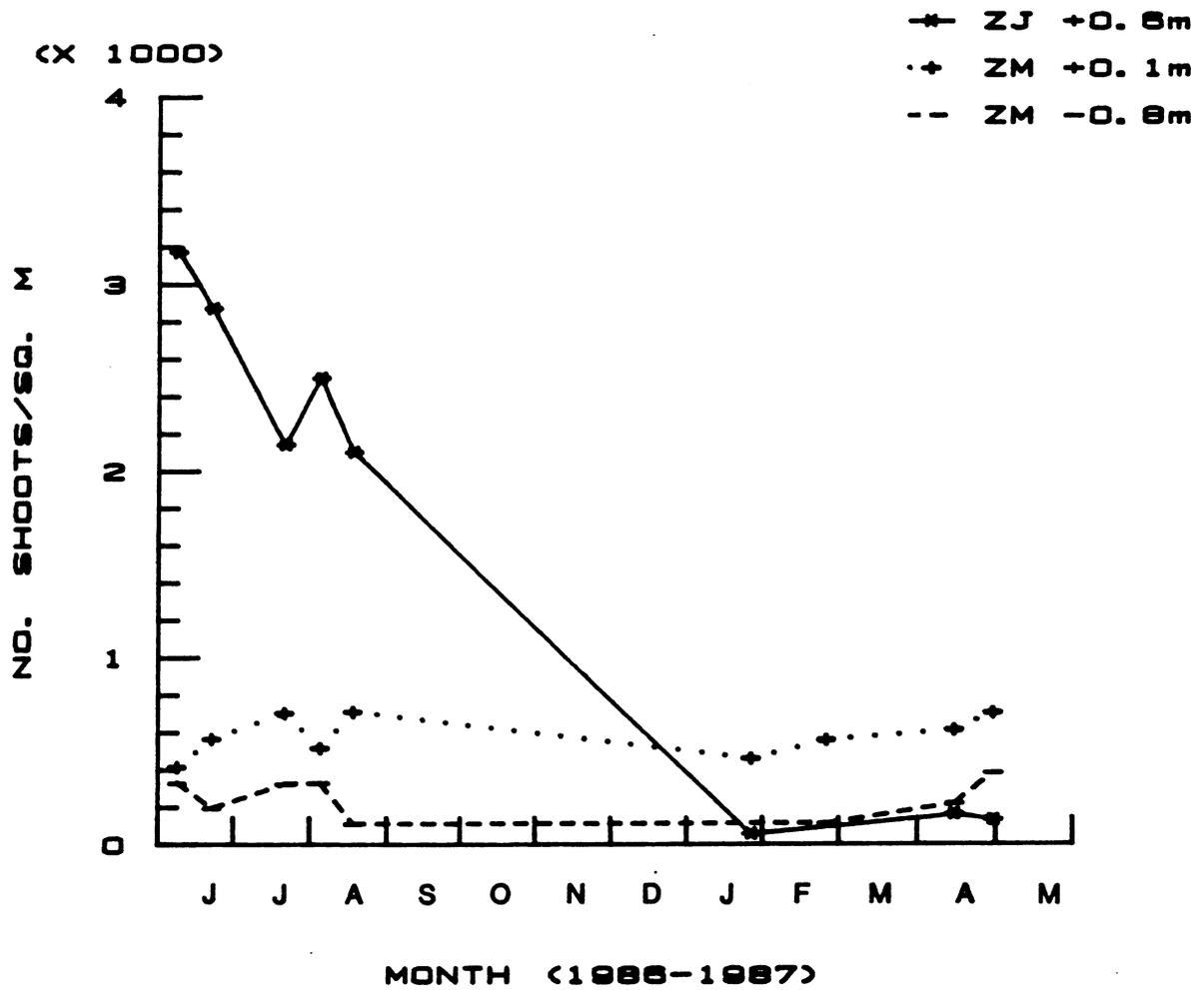


Figure 4. Eelgrass mean density at three depths vs time. ZJ = *Z. japonica*; ZM = *Z. marina*.

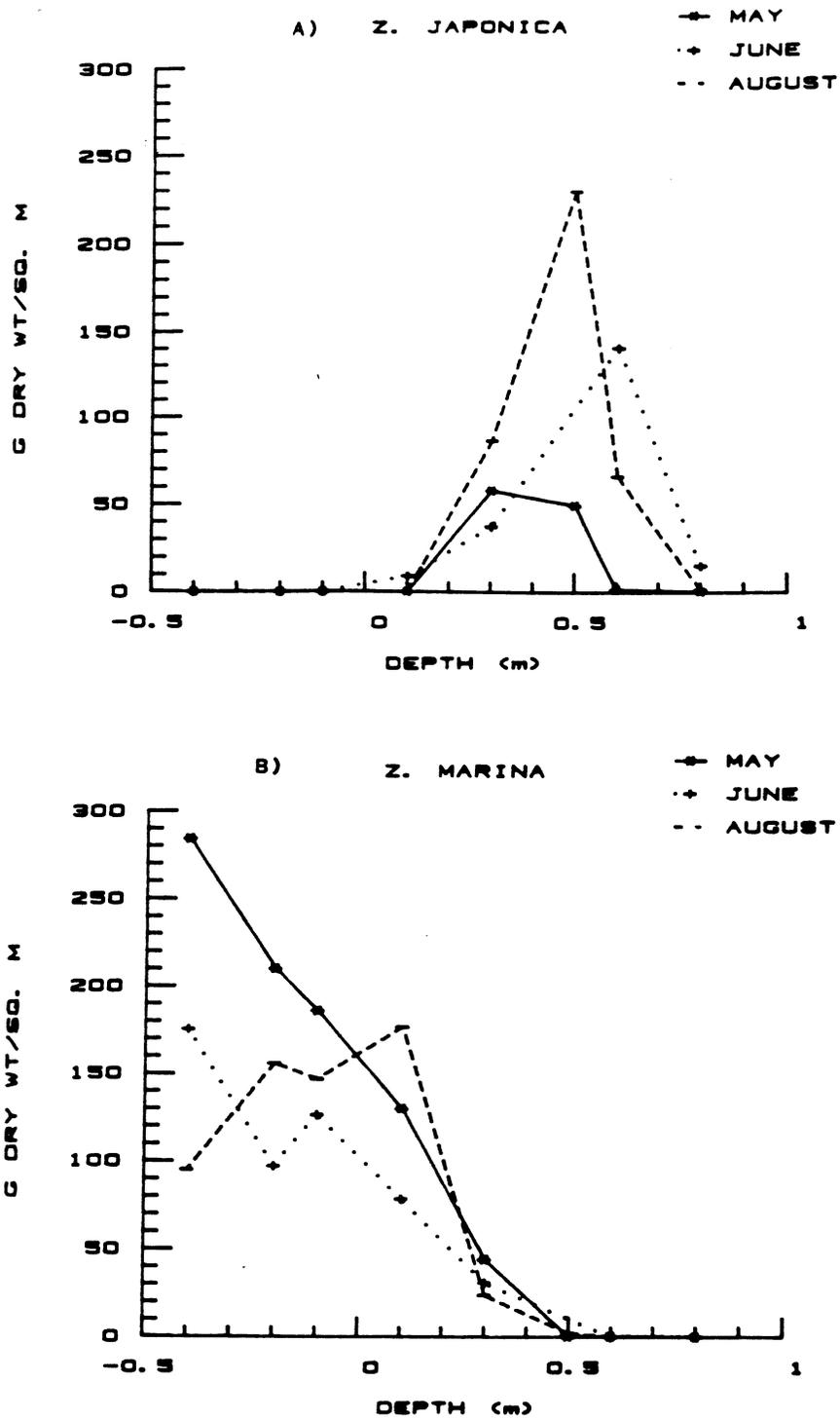


Figure 5. Eelgrass mean biomass vs depth. A) *Z. japonica*; B) *Z. marina*.

The seasonal shift in biomass for both species was evident, with maximum biomass occurring in early summer for *Z. japonica* (Fig. 6). *Z. marina* biomass peaked in spring at the lowest elevation and in late summer in the high elevation site (0.1m). The site at -0.4m maintained the greatest biomass throughout the winter.

### Epiphytes

Maximum mean epiphyte biomass, which included both seaweeds and filamentous and tube dwelling diatoms epiphytic on eelgrass and associated with the base of the eelgrass shoots, occurred at the site at 0.1m depth in June (Fig 7). There was a pronounced peak of relatively short duration of epiphyte biomass during early summer (June) at the three intensively studies sites (Fig. 8). The June peak was dominated by diatoms, the red alga *Ceramium pacificum* and the green alga *Ulva fenestrata*. Diatom biomass was greatest at 0.1m (248.9 g dry wt m<sup>-2</sup>). The biomass of *C. pacificum* was greatest at -0.2m (45.6 g dry wt m<sup>-2</sup>). *U. fenestrata* biomass was greatest at -0.1m (34.2 g dry wt m<sup>-2</sup>). The green alga *Enteromorpha intestinalis* was abundant in late June, and reached at peak mean biomass of 113.6 g dry wt m<sup>-2</sup> at -0.4m during this period. Other species recorded in the epiphyte samples included the green alga *Cladophora* sp., the brown alga *Laminaria saccharina* and the red alga *Gracilaria pacifica*. *C. pacificum*, *U. fenestrata* and *G. pacifica* were common members of the understory assemblage in the *Z. marina* portion of the bed.

### Sediment Microalgae

There was no apparent trend in sediment chlorophyll a concentration relative to depth during any of the samplings in spring-summer (Fig. 9a). Concentrations did change among the months, and this change appeared most pronounced at the highest site. Phaeopigment concentration was greatest at 7 of the 8 sites in May as compared to June and August (Fig. 9b). Phaeopigment concentration showed little relationship to depth during the latter two months.

Chlorophyll a concentration was highest at the three intensive study sites in late winter through early spring (i.e., February-April) (Fig. 10). This peak precedes the early summer increase in seagrass (Fig. 6) and seaweed (Fig. 8) biomass.

### Productivity

Calculation of NPP was divided into spring (i.e., April-June) and summer (i.e., July-August) to cover the growing season and to emphasize apparent seasonal differences in

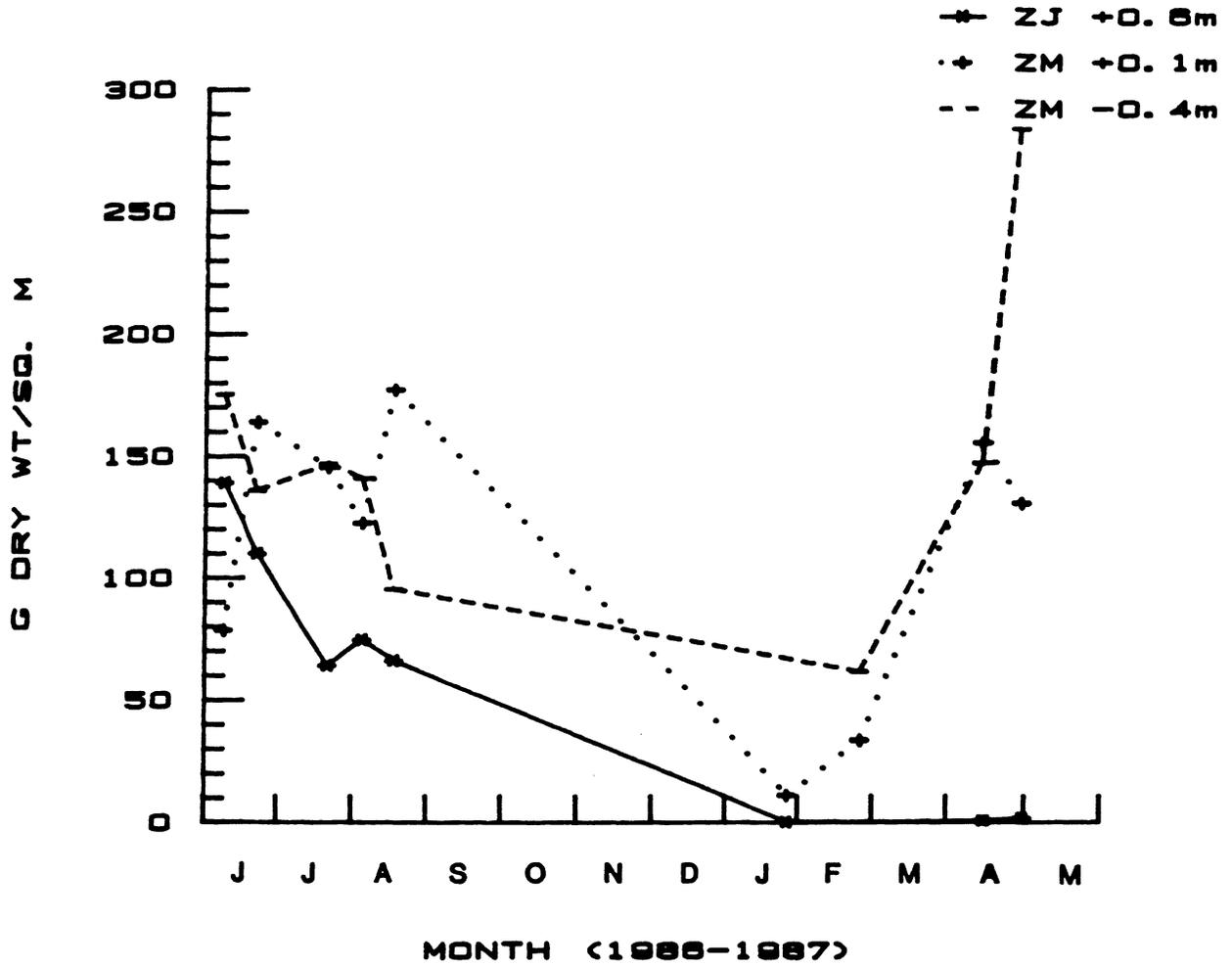


Figure 6. Eelgrass mean biomass at three depths vs time. ZJ = *Z. japonica*; ZM = *Z. marina*.

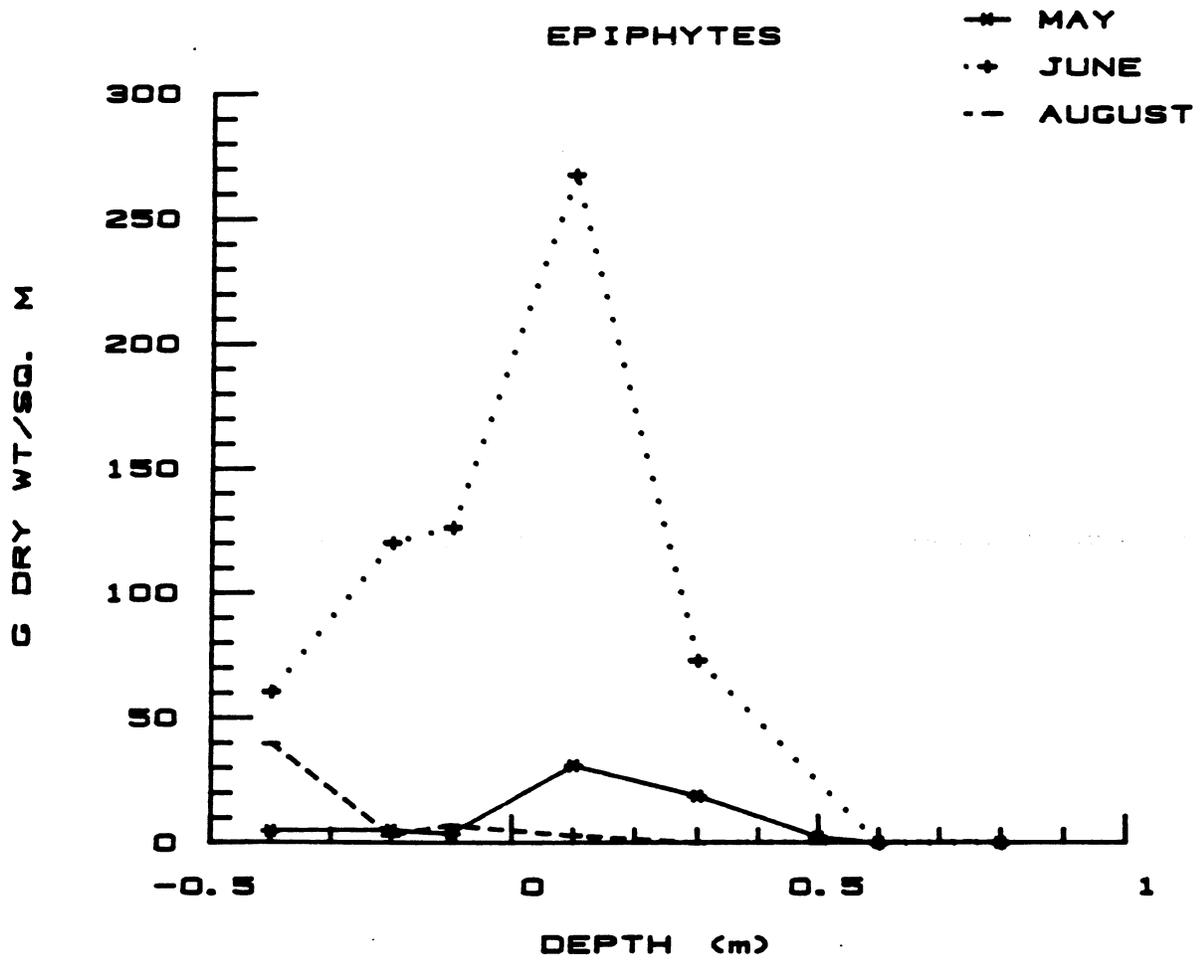


Figure 7. Epiphyte mean biomass vs depth.

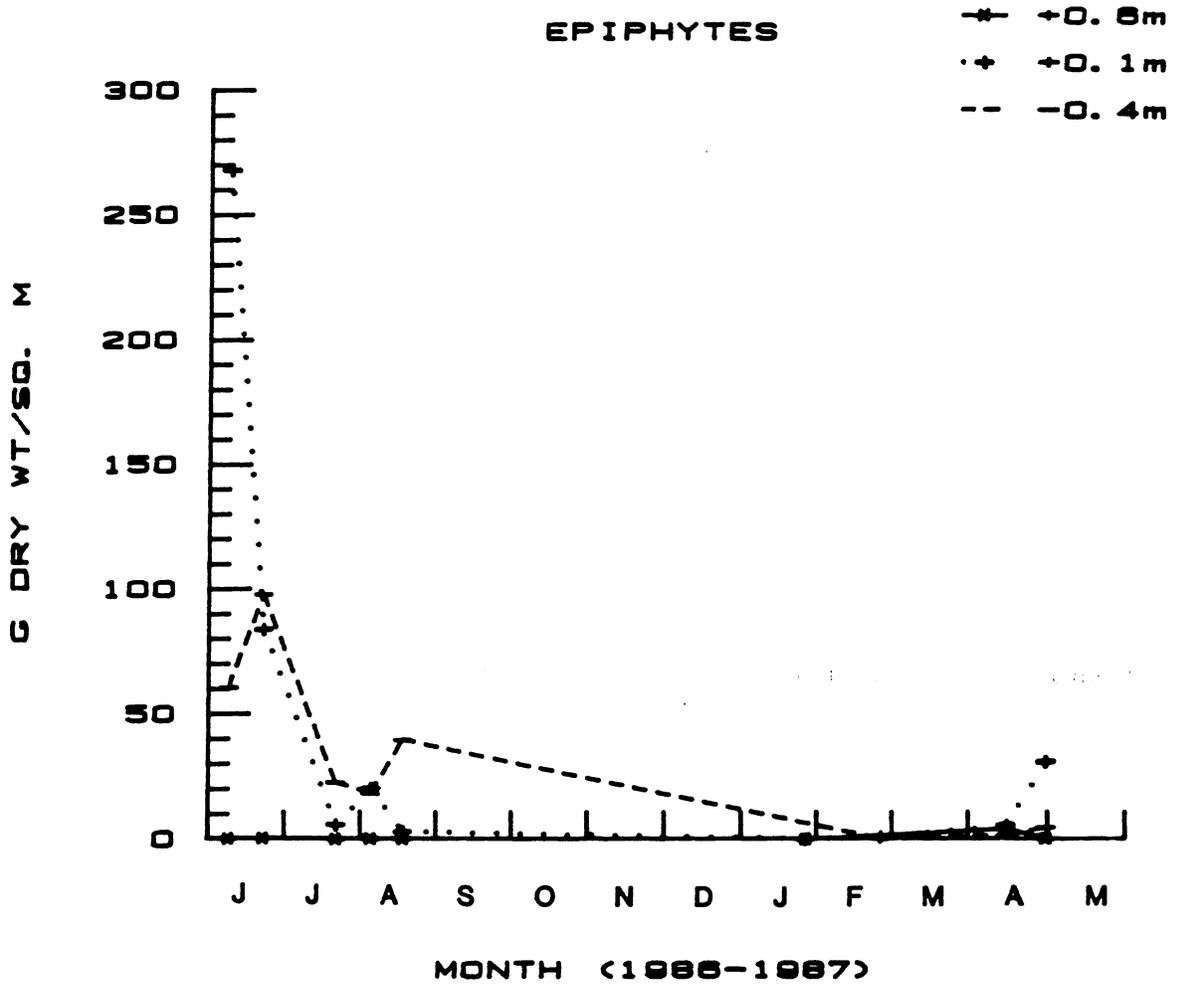


Figure 8. Epiphyte mean biomass at three depths vs time.

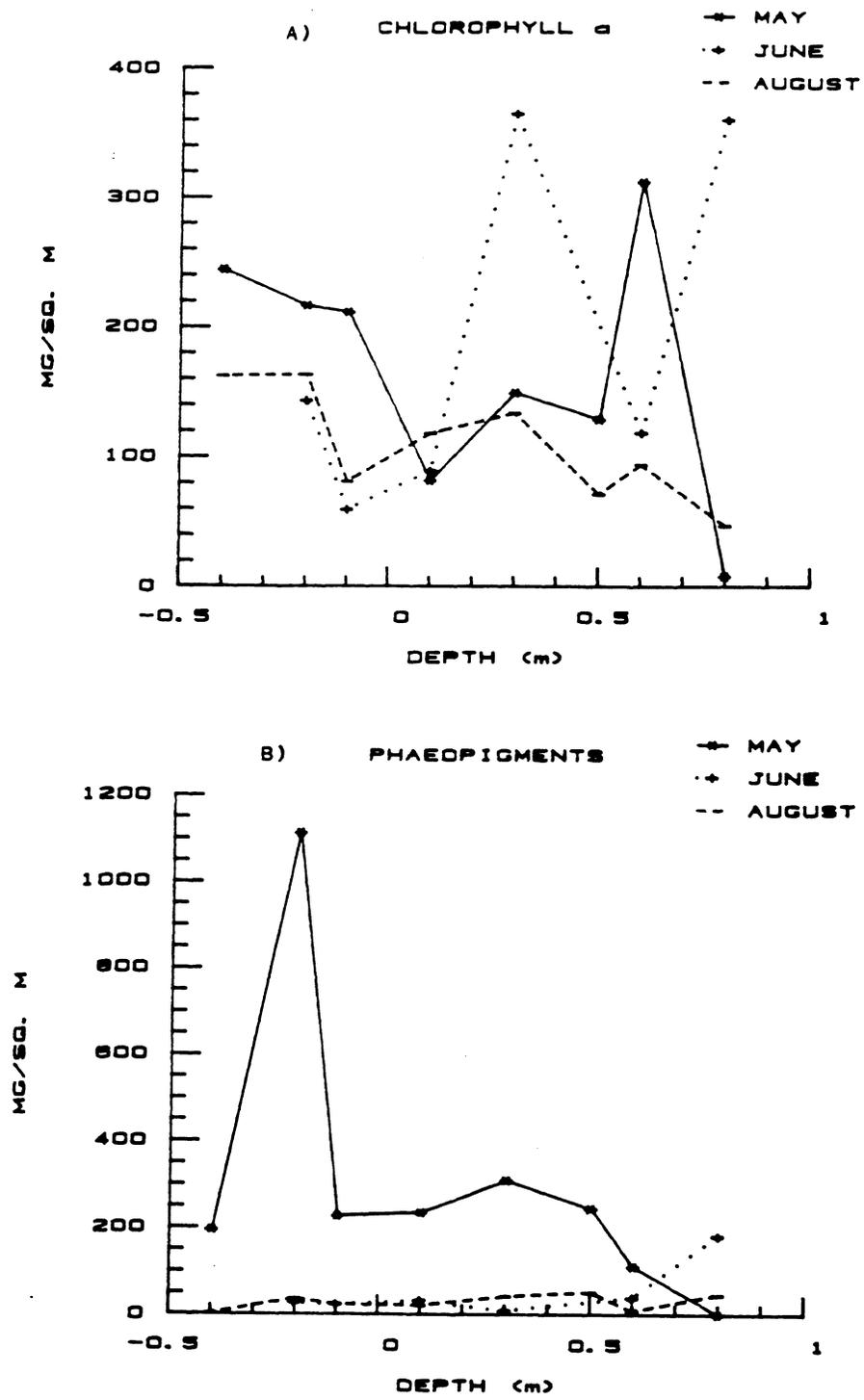


Figure 9. Mean sediment plant pigment concentrations vs depth. A) Chlorophyll a; B) Phaeopigments.

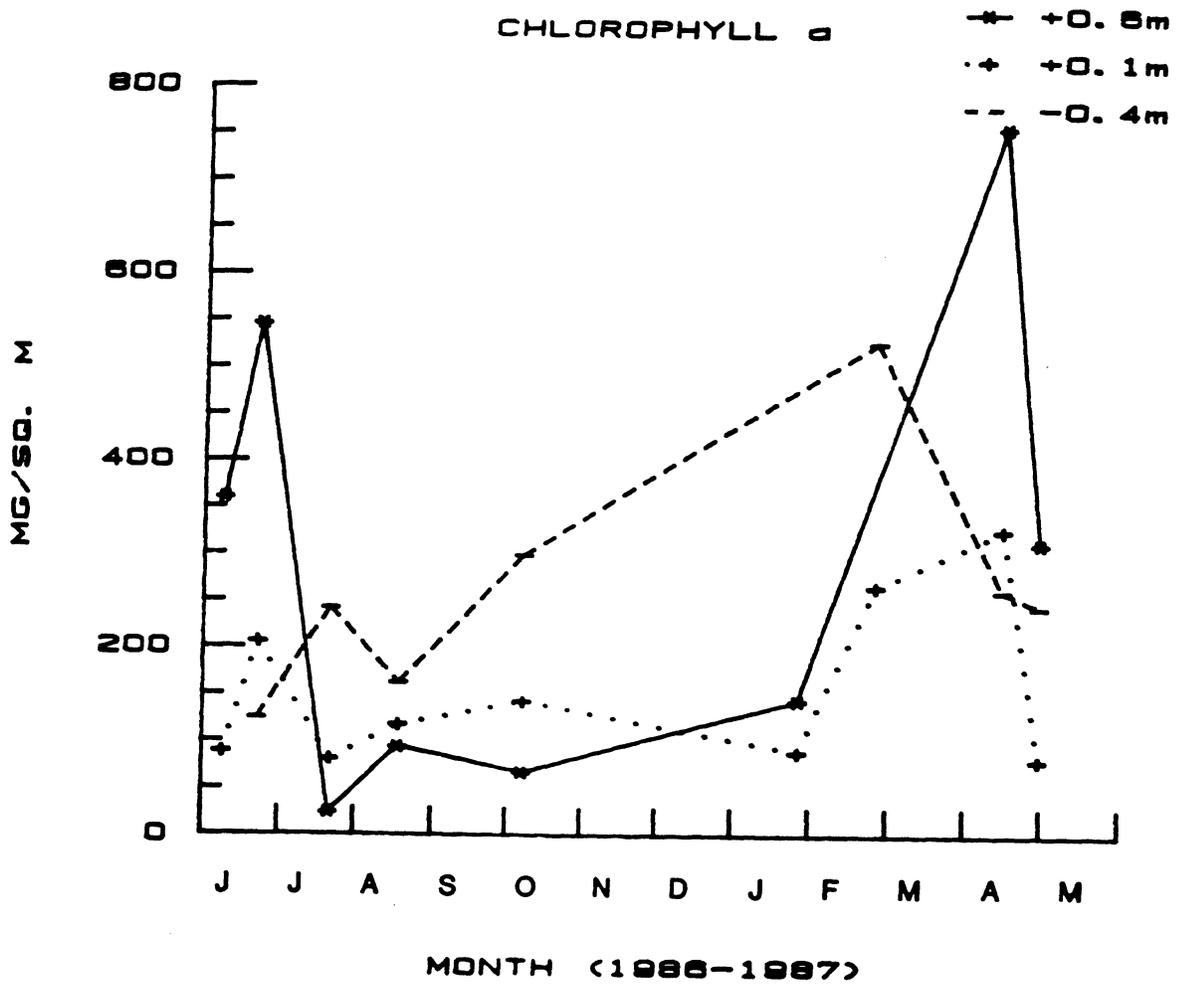


Figure 10. Mean sediment chlorophyll a concentration at three depths vs time.

NPP among major component autotrophs. In spring, NPP was dominated by epiphytes at sites between 0.3 and -0.2m elevation (Fig. 11a). Assemblage NPP was greatest between elevations 0.1 and -0.1m. *Z. marina* NPP was greatest at the two lowest elevations, and *Z. japonica* NPP peaked at 0.6m. In summer, epiphyte NPP exceeded seagrass productivity only at the lowest elevation (Fig. 11b). Greatest NPP for *Z. marina* shifted to higher elevations as compared to spring. In contrast, maximum NPP for *Z. japonica* shifted to a lower elevation as compared to spring. NPP declined at all sites between spring and summer except at 0.5 and -0.2m. NPP declined to zero at the two highest elevations (*Z. japonica* dominated sites) in summer.

Annual NPP varied with depth, with a maximum NPP at -0.1m (Fig. 11c). Seaweed NPP predominated, on an annual basis, at intermediate elevations. Maximum NPP by *Z. marina* and *Z. japonica* occurred at -0.2 and 0.5m elevations, respectively.

Mean NPP by sediment associated microflora was negative during all samplings and is not presented. Very high oxygen demand (unpublished data) associated with the sediments accounted for the negative values.

Total annual NPP estimated from the Padilla Bay eelgrass system was  $10,557 \times 10^3$  kg C (Table 2). Ninety-seven percent of this production occurs in the *Z. marina* bed at elevations below 0.3m. A total of 50% of the production in the system was attributed to epiphytes. The average annual NPP for the macrophyte component of the system was  $351 \text{ gC m}^{-2}$  ( $= 924 \text{ gdry wt m}^{-2}$ ).

### Production to Biomass

Epiphyte annual NPP to average annual biomass ratio was greatest among all components at all sites except the highest two (Table 3). These high values are explained by the relatively low annual biomass of epiphytes due to their markedly seasonal appearance (Fig. 8). There was little variation in NPP:B for the seagrass species over the depth gradient. The turnover rate for the entire system, calculated by dividing total average annual NPP by total average annual biomass, was 9.2. This means that the entire biomass of the system was replaced approximately 9 times during the year of study.

The relationship between mean shoot weight (regardless of species) for the sampling having the greatest mean eelgrass standing stock (August) and annual NPP is linear for shoot weights up to approximately 300 mg (Fig. 12). Higher shoot weights appeared to

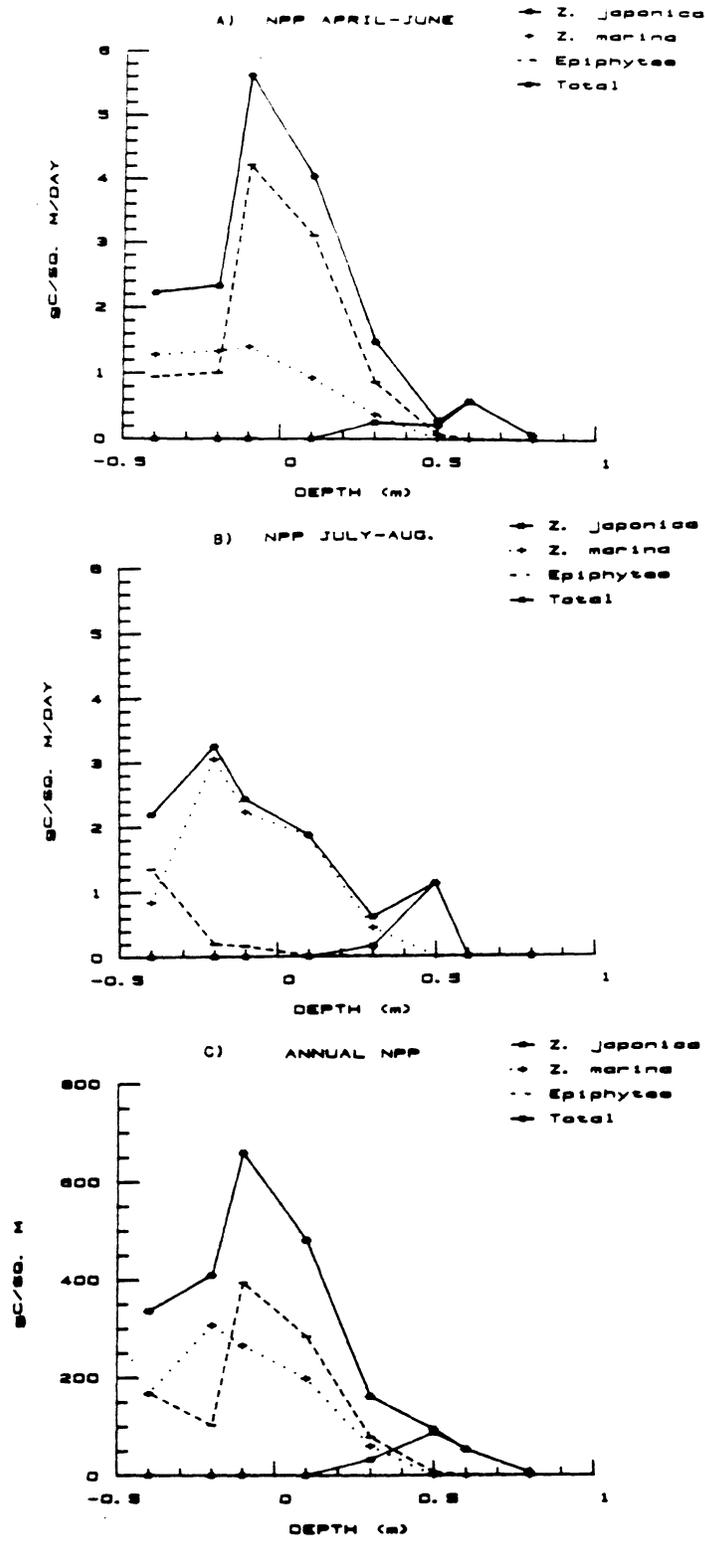


Figure 11. NPP vs depth. A) April - June; B) July - August; C) Annual NPP.

Table 2. Estimate of total NPP in the eelgrass system. Averages are for 12 months. Total intertidal area = 4176 ha. Total *Zostera* area = 72% of intertidal area = 3007 ha. Total *Z. japonica* area = 16% of *Zostera* area = 481 ha. Total *Z. marina* area = 84% of *Zostera* area = 2526 ha.

Component and Depth	Average NPP (gC/m <sup>2</sup> /yr)	Area (ha)	Total NPP (x10 <sup>3</sup> kgC/yr)	Percent of Total
<i>Z. japonica</i> (0.8 to 0.3m)	44.7	481	215	2
Epiphytes (0.8 to 0.3m)	21.3	481	102	1
<i>Z. marina</i> (0.3 to -0.4m)	199.7	2526	5044	48
Epiphytes (0.3 to -0.4m)	205.7	2526	<u>5196</u>	49
			Total = 10557	

Table 3. Average annual biomass (B), NPP and production to biomass ratio (NPP:B) for the primary producers at the study sites. Percentage of total NPP for each site is given in parentheses. Average biomass was calculated on a 12 month basis using interpolation for months with no data. ZJ = *Z. japonica*; ZM = *Z. marina*; E = epiphytes.

Depth (m)	Average Biomass (g m <sup>-2</sup> )				Annual NPP (gdry wt m <sup>-2</sup> )				Annual NPP:B		
	ZJ	ZM	E	Tot.	ZJ	ZM	E	Tot.	ZJ	ZM	E
0.8	2	0	0.2	2.2	15.8 (95)	0 (0)	0.8 (5)	16.6	7.9	-	4.0
0.6	22	0	0.7	22.7	138.9 (100)	0 (0)	0.5 (<1)	139.4	6.3	-	0.7
0.5	49	0	0.7	50.6	230.0 (93)	0 (0)	17.1 (7)	247.1	4.7	-	353.0
0.3	24	33	8	65.0	85.5 (19)	159.0 (35)	206.1 (46)	450.6	3.6	4.8	25.8
0.1	0	93	21	114	0 (0)	520.2 (41)	746.8 (59)	1267.0	-	5.6	35.6
-0.1	0	102	13	115	0 (0)	698.4 (40)	1037.1 (60)	1735.5	-	6.8	79.8
-0.2	0	115	13	128	0 (0)	807.7 (75)	271.1 (25)	1078.8	-	7.0	20.9
-0.4	0	118	15	133	0 (0)	440.6 (50)	443.4 (50)	884.0	-	3.7	29.6

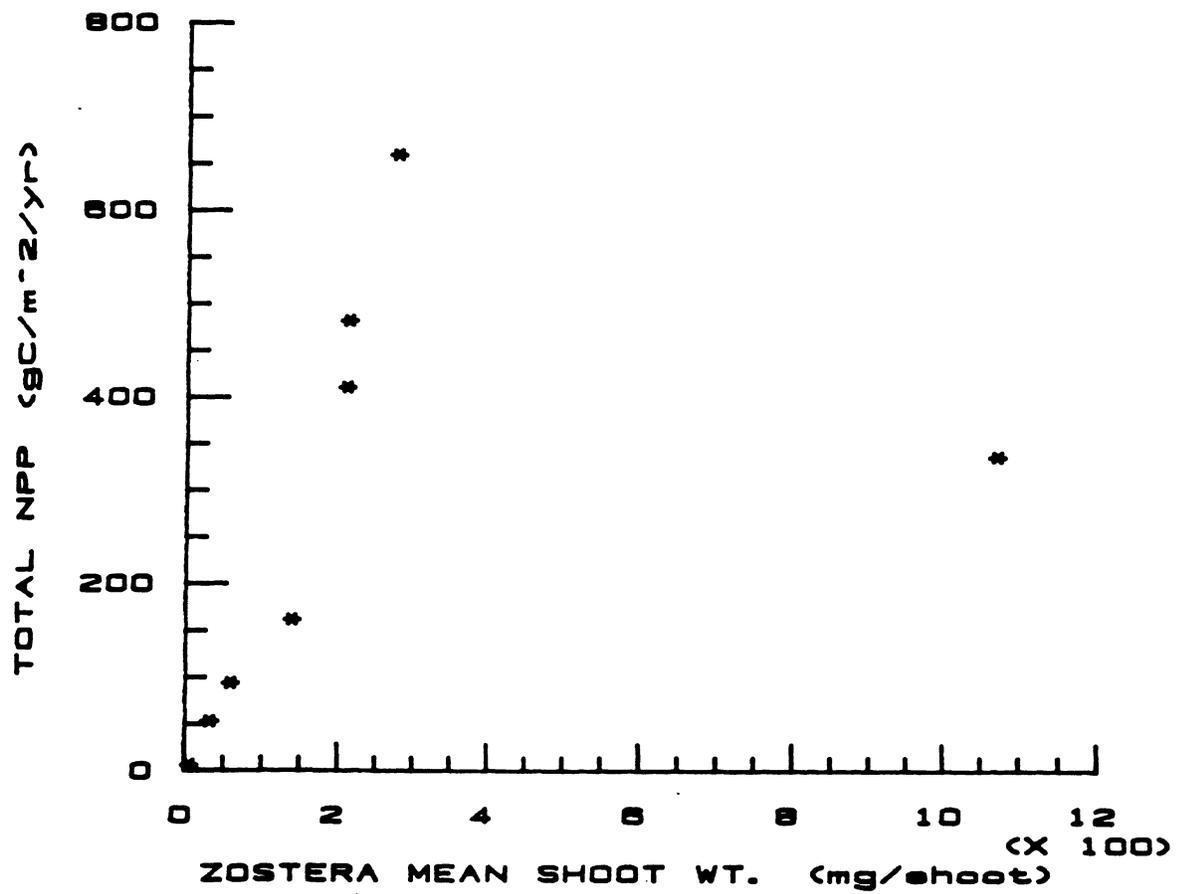


Figure 12. Eelgrass shoot weight vs annual system NPP. Shoot weights are means from samples collected in August 1986.

have a negative affect on annual NPP. Shoot weight is positively related to leaf area (Table 1), and the site with the greatest mean shoot weight was located at the lowest elevation sampled.

### Comparison of Methods

Limited comparisons of oxygen flux data with shoot marking and biomass change estimates of NPP showed that oxygen flux resulted in greater NPP values for both eelgrass species and epiphytic algae. Daily NPP for *Z. marina* (at 0.1m MLLW) estimated by oxygen flux was 4.37 and 1.30 times higher than the estimate from shoot marking in June and August, respectively. For *Z. japonica* (at 0.5m MLLW) in August, oxygen flux produced a daily NPP value that was 3.66 times that calculated on the basis of change in biomass. In comparison, total daily epiphyte NPP estimated by oxygen flux at 0.6m MLLW was 2.50 times that estimated by biomass change during the period of April-June. The ratio of estimates based on the two methods at 0.1m MLLW was 2.78 during the same period.

## DISCUSSION

Padilla Bay is an example of an expansive shallow estuarine embayment in which the benthic environment is dominated by a dense seagrass system. My observations in the Bay and data from other research (T. Mumford, unpublished) indicate that the results from the present study are roughly applicable to the system in general.

The study sites spanned a gradient in seagrass leaf dimension, density and plant biomass and NPP that correlated with depth. Peak standing stocks of *Z. japonica* and *Z. marina* were centered at about 0.5 m and MLLW, respectively. The densities and depth distribution at Padilla Bay was similar to that reported for an expansive eelgrass system in Roberts Bank in southern British Columbia (Harrison 1982). In contrast, the upper limit of depth distribution of *Z. marina* in Netarts Bay, Oregon, was much shallower. Kentula and McIntire (1986) sampled that system at 1.1 to 1.4 m MLLW; an elevation range that spanned the intertidal portion of the bed. The upper limit of *Z. marina* at Padilla Bay was about 0.3 m MLLW (i.e., 0.8 m deeper than at Kentula and McIntire's deepest study site). A possible explanation is higher temperatures on the flats in Padilla Bay during low tides in summer (Bulthuis 1987). Harrison (1982b) showed experimentally that the upward limit of distribution of *Z. marina* is regulated by low resistance to desiccation in comparison to *Z. japonica*, and that *Z. japonica* can outcompete *Z. marina* for this reason at upper elevations. Kentula (1982) did not report *Z. japonica* from Netarts Bay, although it is known to occur in estuaries north and south of Netarts Bay (Harrison 1982b; Thom 1984 and personal observation).

Ponds form on Padilla Bay flats during low tides. Ponding was most evident in summer when standing stocks of eelgrass was greatest, which suggests that the mass of plant material functions as a sponge in inhibiting the rate at which the flats drain during ebbing tides. The deepest site (at -0.4m) was under 0.3 m of water even during extreme low tides of -1.3m MLLW. Sites located in areas of ponding at upper elevations (i.e 0.3 to 0.6m) contained the densest stands of *Z. japonica*. The site (0.8m) that was dry at low tide had a very low standing stock of plants in late summer; a time when NPP was negligible. In winter, when standing stock in the entire system was the least, very little ponding was evident. This further supports the sponge effect hypothesis. Ponding was noted by Harrison (1982a) on Roberts Bank, Kentula and McIntire (1986) in Netarts Bay and in England by

Wyer et al. (1977). The ecological significance of biologically mediated ponding that varies seasonally may be great, and requires study.

*Z. marina* density changed relatively little seasonally, whereas the density of *Z. japonica* exhibited wide fluctuations between an early summer maximum to a mid winter minimum near zero. Some individuals of *Z. japonica* were present during winter, and these were most evident at the sites at the lower end of its distribution. The biomass of both species changed with season. The most rapid increase occurred between April and June, when NPP was greatest. During this time light energy reaches maximum and water temperature is increasing rapidly in the region. Light energy at noon in mid-June (i.e., the time of the summer solstice) can be as high as  $4000 \mu\text{E m}^{-2} \text{s}^{-1}$ . Mid-winter noon values are commonly below  $100 \mu\text{E m}^{-2} \text{s}^{-1}$ . Several previous studies (Sand-Jensen 1975, Jacobs 1979, Kentula and McIntire 1986, Dennison 1987) have concluded that light energy was an important factor controlling shoot net production. The experimental work of Dennison and Alberte (1982) showed that variations in light intensity exhibited significant control of eelgrass photosynthesis. Peak shoot biomass occurred in June-August, which is the same period as reported for other north temperate systems (Phillips 1972, Sand-Jensen 1975, Wyer et al. 1977, Jacobs 1979). In addition, peak shoot density coincided with peak biomass. In Padilla Bay, seasonal biomass peaks varied by depth. Seasonal shifts in the location of these peaks may be related initially to how light energy requirements are met at the various depths.

The increase in biomass, especially evident in *Z. marina*, was due largely to an increase in leaf area. Plants had relatively narrow leaves in mid-winter and noticeably wider leaves in summer. Kentula and McIntire (1986) and others have shown that *Z. marina* plants have more and larger leaves in spring and summer as compared to winter. This latter condition is in response to increased light energy and photosynthetic rate, and perhaps decreased leaf export rate, in summer.

Annual NPP in Padilla Bay was  $351 \text{ gC m}^{-2}$  was similar to data from other temperate systems (see Zieman and Wetzel 1980). However, the epiphytes were responsible for 50% of the NPP, indicating that NPP by eelgrass was, on average, relatively low (ca.  $175 \text{ gC m}^{-2}$ ). Epiphyte NPP has been noted to be significant in many seagrass systems. Typical values for epiphyte production are between 7 and 58% (Morgan and Kitting 1984). The high relative importance of the seasonal appearance of the highly productive epiphyte taxa with substantial turnover rates to animals associated with seagrass was proven by stable

carbon isotope data in estuarine systems in Hood Canal, located near Padilla Bay (Simenstad and Wissmar 1985). Fry (1984), also using stable carbon isotopes, showed that algal epiphytes in a *Syringodium filiforme* meadow in Florida were the dominant source of carbon in that seagrass ecosystem.

Limited experiments showed that comparing NPP on the basis of the two methods employed must be done with caution. Substantially higher values were obtained using oxygen flux methods for eelgrass and epiphytes as compared to values obtained using biomass changes. The average difference factor for eelgrass during the growing season was 3.11. Using this factor, the estimate for eelgrass annual NPP would be increased from 175 to 546 gC m<sup>-2</sup>. Total annual NPP for the system would be 722 gC m<sup>-2</sup>, of which epiphytic algae would comprise 24% instead of 50% of the total. Recently, the arguments of Zieman and Wetzel (1980) against the use of metabolic techniques for measuring NPP in rooted aquatic macrophytes was examined by Kemp et al. (1986) using *Potamogeton perfoliatus* L. They found that the primary reasons given for not using metabolic techniques (i.e., problems associated with the storage, recycling and translocation of metabolic O<sub>2</sub> and CO<sub>2</sub>) were not significant sources of error. Obviously, these types of studies need to be carried out for eelgrass in order to better estimate eelgrass system productivity.

Epiphyte biomass, although substantially exceeding seagrass biomass at some sites during early summer, comprised only 11% of the total average annual biomass in the system. Values reported for seagrass systems in New Jersey (Penhale 1977), Netarts Bay (Kentula 1982) and south Texas (Morgan and Kitting 1984) were 23, 25 and 47%, respectively.

Greatest total system and epiphyte annual NPP was recorded at -0.1m depth. This site was located in the center of a small channel through which water from surrounding flats drained at during ebbing tides. This site also had the greatest epiphyte production to biomass ratio within the *Z. marina* portion of the meadow. I noted on several visits that water currents were swifter through this channel as compared to the surrounding flats, and that floating matter was rapidly removed. Based on limited data from near these sites (unpublished) inorganic nitrogen concentrations are quite low during the growing season. It may be that the rapid transport of water past the study site in the channel is supplying the plants in the channel with a constant, although low, amount of inorganic nutrients. This relatively high flux of nutrients past the epiphytic algae and seagrass may be responsible for

the relatively high production rates there (Fonseca and Kenworthy 1987). Nitrogen was shown to be limiting to *Z. marina* growth in Chesapeake Bay (Orth 1977). In addition, Short and McRoy (1984) have shown that *Z. marina* can uptake and utilize nutrients through its leaves. Further, the relatively high current rates in the channel may explain the lower average annual epiphyte and seagrass biomass at this site (Fonseca and Kenworthy 1987). Nutrient flux rates are known to be important with regard to total nutrient supply available to support algal growth (see review by Hanisak 1983).

Sediment associated microalgae, as measured by chlorophyll a concentration, were present. A rapid increase in chlorophyll a during late winter and early spring, prior to the period of rapid macrophyte growth, suggests that the sediment microflora is better adapted for rapid growth during the low temperatures and lower light conditions during the late winter. Competition for nutrients, and light, and photoinhibition, along with species succession may be factors slowing the growth of this assemblage in summer (Mills and Wilkerson 1986). High sediment associated oxygen demand resulted in low or negative calculations of NPP. These data suggest that gross primary productivity (GPP) for sediment associated assemblages may be substantial, and a significant source of carbon to the local sediment food web, and that the sediments are highly heterotrophic. GPP in a *Z. marina* bed in Chesapeake Bay by the sediment was  $225 \text{ gC m}^{-2}$  on an annual basis, which accounted for 14% of the annual GPP of the bed (Murray and Wetzel 1987). In comparison, respiration measurements made on eelgrass indicate that respiration is low relative to NPP during the growing season (unpublished data). Respiration rates of epiphytes on the seagrass were usually <10% of the NPP for these plants. Recent research in Padilla Bay (Thom, in preparation) focused on the production dynamics of sediment microflora on mudflats in Padilla Bay, and will couple the work from seagrass sediment production studies in evaluating the importance of this component to total production in the Bay.

The values for sediment chlorophyll a concentration measured in Padilla Bay were on the order of those reported for Netarts Bay (Davis and McIntire 1983) and higher than those reported for the Columbia River estuary (McIntire and Amspoker (1986). Sediment physical characteristics, and biological and physical processes have a strong but poorly understood influence on the benthic microflora (Davis and McIntire 1983).

Mean shoot weight, regardless of eelgrass species, in June (as an indicator of leaf area) and depth appeared to be good predictors of annual NPP for the system. Of significance was the threshold of annual NPP reached at approximately  $300 \text{ mg dry wt shoot}^{-1}$  and a

depth of -0.2 m. Higher shoot weights and increased depth resulted in lower NPP. Light penetration may best explain this threshold response (Dennison 1987).

The present data show that *Z. japonica* has a lower annual NPP as compared to *Z. marina*, and exhibits different patterns by season in terms of density distribution and growth. These latter differences probably only point out a few of the ecological consequences of the invasion of the introduced species. Of note is the fact that *Z. japonica* is very new to the area in geological and evolutionary time scales.

Finally, a total of approximately 28,000 mt of dry plant matter was produced in Padilla Bay seagrass system during the one year study. Values from Netarts Bay and Grays Harbor were 3,200 mt (Kentula and McIntire 1986) and 98,000 mt (Thom 1984), respectively. Although the estuaries differ in size and distribution of eelgrass, these values indicate that the amount of organic plant matter produced on an annual basis and potentially available for utilization in estuarine and nearshore marine systems is substantial.

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