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PLANT STANDING STOCK AND PRODUCTIVITY ON TIDAL FLATS IN PADILLA BAY, WASHINGTON: A TEMPERATE NORTH PACIFIC ESTUARINE EMBAYMENT

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The standing stock productivity and respiration rates of sediment associated microalgae and macrophytes occurring in (a) sparse pickleweed (*Salicornia virginica*) marsh, (b) sand-mudflat, and (3) gravel patch habitats located in a Pacific Northwest estuarine bay were measured over an annual cycle in 1987-1988. Annual gross primary productivity (GPP) for the sand-mud flats, marsh habitat and gravel patch was 149, 277 and 355 g C m^{-2}. Biomass, net primary productivity and respiration (R) were greatest in spring, intermediate in summer and lowest in autumn-winter in all habitats. The seasonality was related to varying irradiance, temperature and inorganic nutrient concentrations (particularly nitrate nitrogen). Sites with the coarsest sediments had the greatest productivity rates, and sites with the finest sediments had the greatest R. The data from the present study were combined with data from the eelgrass system in the bay. The greatest proportion of total bay annual GPP was attributed to the *Zostera marina* system (59%), followed by the *Zostera japonica* system (23%), the sand-mud habitat (8%), the gravel patch (0.2%) and the marsh habitat (0.1%). NPP, respiration and GPP averaged 166, 211 and 377 g C m^{-2} yr^{-1}, respectively. GPP:R ratio (1.8) indicated that the bay system was autotrophic and exported 44% of the annual productivity. All component systems except the eelgrass meadow sediments were autotrophic on an annual basis. The bay system had an annual turnover rate of 7.0.

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ABSTRACT

The standing stock productivity and respiration rates of sediment associated microalgae and macrophytes occurring in (a) sparse pickleweed (*Salicornia virginica*) marsh, (b) sand-mudflat, and (3) gravel patch habitats located in a Pacific Northwest estuarine bay were measured over an annual cycle in 1987-1988. Annual gross primary productivity (GPP) for the sand-mud flats, marsh habitat and gravel patch was 149, 277 and 355 g C m^{-2}. Biomass, net primary productivity and respiration (R) were greatest in spring, intermediate in summer and lowest in autumn-winter in all habitats. The seasonality was related to varying irradiance, temperature and inorganic nutrient concentrations (particularly nitrate nitrogen). Sites with the coarsest sediments had the greatest productivity rates, and sites with the finest sediments had the greatest R. The data from the present study were combined with data from the eelgrass system in the bay. The greatest proportion of total bay annual GPP was attributed to the *Zostera marina* system (59%), followed by the *Zostera japonica* system (23%), the sand-mud habitat (8%), the gravel patch (0.2%) and the marsh habitat (0.1%). NPP, respiration and GPP averaged 166, 211 and 377 g C m^{-2} yr^{-1}, respectively. GPP:R ratio (1.8) indicated that the bay system was autotrophic and exported 44% of the annual productivity. All component systems except the eelgrass meadow sediments were autotrophic on an annual basis. The bay system had an annual turnover rate of 7.0.

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INTRODUCTION

Once thought of as stinking mires, estuarine tidal flats are now understood to harbor autotrophs of significant importance to estuarine systems. Annual gross primary productivity rates for tidal flats generally range from 50 to 200 g C m^{-2} (Colijn and de Jonge 1984), which compares to rates of 300 to 1000 g C m^{-2} for phytoplankton, macroalgal assemblages, seagrass meadows and marshes (summarized in Valiela 1984). Secondary productivity, consumption and nutrient cycling are significant processes on tidal flats (e.g., Pamatmat 1968).

Although they are sometimes spatially dominant, tidal flats are rarely the only habitat type within a defined ecosystem. An ecosystem landscape typical in Pacific Northwest estuaries, the region where my study was conducted, consists of broad mid-intertidal flats bounded by a fringing marsh at higher elevations and eelgrass (*Zostera marina* L., *Z. japonica* Aschers. & Graebn.) at low intertidal and shallow subtidal depths (Thom 1988). Autotrophic components of such a system vary in their productivity rates, seasonal dynamics, spatial distribution, decomposition rates, and energy content (Mann 1988). Hence, each species or assemblage has a unique role in space and time (e.g., carbon fixation, energy transfer) in the system.

Primary productivity on estuarine tidal flats in the Pacific Northwest is substantial (Pamatmat 1968, Pomeroy and Stockner 1976, Riznyk and Phinney 1972, Davis and McIntire 1983, McIntire and Amspoker 1986). However, few studies place tidal flat productivity in context with the productivity of other components of the system. Naiman and Sibert (1978) estimated that marsh (*Carex* spp.), eelgrass, benthic microalgae, phytoplankton and macroalgae contributed 495, 100, 22.5, 12.1 and 0.9 g C m^{-2} yr^{-1}, respectively, to the Nanaimo River estuary in British Columbia. Thom (1984) calculated that marshes, eelgrass, phytoplankton, benthic microalgae and macroalgae contributed 22.4, 59.2, 2.5, 10.8 and 5.1%, respectively, of total annual productivity (62,462 x 10^3 kg C) in Grays Harbor, Washington. Pacific Northwest estuarine systems are diverse in physical structure and hydrology, and include fjords (e.g., Puget Sound), broad embayments with little riverine influence (e.g., Padilla Bay), and river-dominated systems (e.g., Columbia River estuary). A comparison using limited information showed that the systems differ considerably in the relative mix and contribution of primary producers to total annual system productivity (Thom 1987). Data are lacking on several system types to further the understanding of the relative and absolute importance of autotrophs in Northwest estuaries. Furthermore, scientists and environmental planners in the Northwest are not unique in their need for system-specific data on fundamental ecosystem processes such as primary productivity, which will help them to better manage their estuaries.

The thrust of the work presented here was to measure the seasonal dynamics of the standing stock and productivity of major autotrophs on non-eelgrass dominated portions of tidal flats in

Padilla Bay. I combined data from the present study with similar data for the seagrass meadow (Thom 1988) in developing an estimate of total annual system benthic primary productivity. Sediment grain size has a documented but poorly understood influence on sediment associated microalgae (Amspoker and McIntire 1978, 1986, Davis and McIntire 1983, McIntire and Amspoker 1986). I therefore evaluated the effects of sediment particle size on sediment algae standing stock and productivity. I also measured respiration for the various components in the system, and calculated productivity to respiration ratios for the components and for the entire system. This ratio indicates whether a system is a net source or sink of fixed carbon. Padilla Bay is an excellent study area for several reasons: (1) It contains a mix of several vegetation types; (2) fisheries resources depend upon the estuary for food and habitat; (3) it is a National Estuarine Research Reserve with management as a high priority; and (4) nutrient and pesticide inputs from nearby agriculture pose a potential threat to the system. Information on benthic primary productivity can be used to assess impacts of these and other perturbations on the system.

STUDY AREA

Padilla Bay, located in northern Puget Sound, encompasses 4.5 km^2 (Figure 1). Roughly 90% of the bay is intertidal, with the remaining area comprised of a shallow channels. Eelgrass completely covers ca. 3,500 ha of the flats (Webber et al. 1987). Sand and mud, with small patches of gravel, cover the remaining area. Tides are mixed semi-diurnal with a mean range of 1.6 m. Mean tide level is 1.6 m MLLW (National Ocean Service 1989). The lowest tides occur during mid-day in spring and summer and at night during autumn and winter. Principal freshwater input comes from the Skagit River via Swinomish Slough, located south of the bay.

METHODS

STUDY SITES

Sites were positioned along two transects. The first transect ran from a shore base point located approximately in the mid-bay (see Appendix A) at an angle of 268° mag (from site 1) toward the southern tip of Hat Island (Figure 1). The shore base point was the same as used by Thom (1988) for similar studies on eelgrass productivity. However, the eelgrass transect was oriented at an angle of 212° mag from the shore base point. Twelve sites were established along the Hat Island transect and permanently marked with wooden stakes. The sites extended from a sparse (mean cover = 18.8%, n = 12, for June-August, unpublished data) pickleweed (*Salicornia virginica*) marsh out to the landward edge of the distribution of *Z. japonica* (Table 1). Sites 1-4

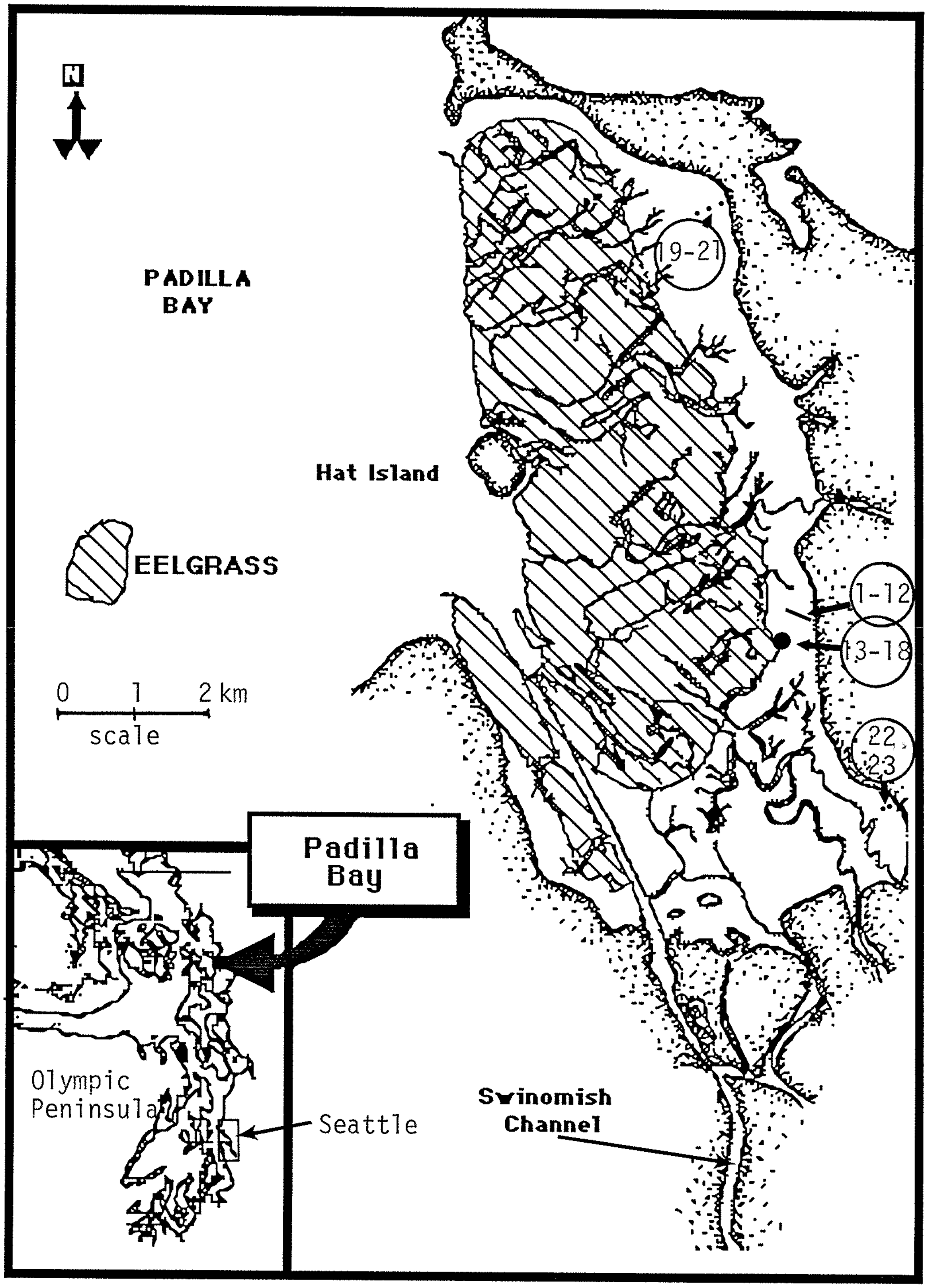

Figure 1. Padilla Bay and the study sites.

Table 1. Descriptions of sampling sites. Elevation is in m relative to MLLW. ND = not determined.

Site No.	Predominant habitat name	Vegetation type	Elevation (m)	Sediment mean phi	Volatile solids (%)	Sediment description[1]
1	SAL/ENT	*Salicornia & Enteromorpha*	2.0	0.43	4.5	very coarse sand
2	SAL/ENT		1.9	-0.16	13.5	very coarse sand
3	SAL/ENT		1.6	0.27	4.3	very coarse sand
4	SAL/ENT		1.3	-0.48	1.2	very coarse sand
5	SAND/MUD	Sediment & diatoms	0.8	1.04	10.0	coarse sand
6	SAND/MUD		0.8	2.33	2.0	med.-fine sand
7	SAND/MUD		0.8	2.66	1.9	med.-fine sand
8	SAND/MUD		0.8	2.49	3.2	med.-fine sand
9	SAND/MUD		0.8	2.50	0.2	med.-fine sand
10	SAND/MUD		0.8	2.52	2.3	med.-fine sand
11	SAND/MUD		0.8	2.14	2.9	med.-fine sand
12	SAND/MUD		0.8	2.89	0.2	med.-fine sand
13	GRAV	*Ulva*	0.8	0.43	3.5	very coarse sand
14	GRAV		0.7	-0.29	1.3	very coarse sand
15	GRAV		0.7	1.03	0.4	coarse sand
16	GRAV		0.7	0.47	2.6	very coarse sand
17	GRAV		0.6	-0.29	0.8	very coarse sand
18	GRAV		0.5	-0.75	0.1	granule
19	SAND/MUD	Sediment & diatoms	ND	3.10	3.1	fine sand
20	SAND/MUD		ND	3.10	0.2	fine sand
21	SAND/MUD		ND	3.03	1.8	fine sand
22	SAND/MUD		ND	3.61	3.6	fine sand
23	SAND/MUD		ND	4.48	44.6	very fine sand

[1] From Gray (1981)

1-4 (designated SAL/ENT habitat) were located in the *S. virginica* marsh, which contained some (11.3% cover, n = 12, for June-August, unpublished data) tubular green alga, *Enteromorpha intestinalis*, during summer. Sites 5-12 (designated SAND/MUD habitat) were located on the portion of the flat representing the sand and mud flats of the bay. The distance between site 1 and 12 was 192.5 m.

A second series of 6 sites (sites 13-18) was permanently marked along a 40-m long transect positioned within a gravel patch (GRAV habitat; ca. area = 6,000 m^2) such that the sites spanned the elevation range of the patch (Figure 1, Table 1).

A final group of five sites (sites 19-23), located in SAND/MUD habitats in northern and southern portions of the bay (see Appendix A), was sampled only in July 1987 to determine how representative sites 5-12 were of other areas in the bay.

Sediment core samples, collected at all sites on 7 July 1987, were analyzed for sediment particle size (using sieve and pipette analysis) and percent volatile solids (as weight lost by ashing at 500°C for 4 hr). Particle size and volatile solids content was determined for the top 10 and 2 cm of the sediments, respectively.

Elevation of sites 1-18 (Table 1) was determined using a hand level with reference to sites for which elevations were previously determined (Thom 1988).

SAMPLING METHODS

Sampling of vegetation standing stock (i.e., dry weight biomass for macrophytes and chlorophyll *a* for sediment associated microalgae) and productivity was conducted at sites 1-18 in June, July, August, September and November 1987, and February, March, April and May 1988.

At each site, a tape measure was extended perpendicular to the main transect line between two wooden stakes that were spaced 5 m apart. A random sampling point (determined using a random numbers table) was located either 0.5 m landward or seaward from the 5-m tape measure. The area within the 0.5 m on either side of the tape was not sampled but was used to access the random sampling points. Care was taken to avoid walking on, or otherwise disturbing, potential sampling points.

A 0.1-m^2 square quadrat was placed at each point, and a small core (1.25-cm diameter x 1-cm deep) of sediment for chlorophyll *a* analysis was extracted from the approximate center of the quadrat. The sample was placed in a numbered plastic vial. All seaweeds and eelgrass attached within the quadrat were then removed and placed in a labelled plastic bag. Specimens of healthy seaweed species and of *Z. japonica* that were abundant (i.e., covered at least 5% of the area of any one quadrat) were collected for productivity incubations. Finally, a core (8.8-cm diameter x 5-cm deep) for productivity incubations was extracted immediately next to the location of the chlorophyll *a* sample using a plexiglass cylinder. This cylinder, which was used as the incubation chamber for productivity incubations of sediment, was 20 cm tall. The top was sealed with a plexiglass plate, except for a 1.5-cm diameter hole used for filling the chamber with water. Once the sediment sample was removed from the sediment, the bottom of the chamber was sealed with a rubber bung. Care was taken to minimize disturbance of the surface of the sediment samples during collection, transport and productivity incubations. The chlorophyll samples and macrophyte biomass samples were frozen and kept in the dark until analysis in the laboratory.

Seaweed biomass samples were thawed, sorted to species, dried at 80°C to a constant weight and weighed to the nearest mg. Chlorophyll samples were thawed, ground in ca. 5 ml of 90% acetone with a mortar and pestle, and poured into screw cap test tubes containing a total of 10 ml of 90% acetone to extract sediment pigments. The tubes were kept at 3°C in the dark for 24 hrs. Chlorophyll *a* and phaeopigments were determined using a fluorometer (Turner Model 112) and the formulas in Lorenzen (1966).

PRODUCTIVITY INCUBATIONS

All incubations were carried out in ambient sunlight at the Breazeale Interpretive Center laboratory located ca. 1 km from the sites. The sediment chambers were carefully filled with water gathered in 19-liter buckets from Padilla Bay (1.5 km from the sites) and the fill hole closed with a rubber stopper. The chambers were then placed in ice chests filled with water at ambient Padilla Bay temperature. Whole thalli, or pieces of thalli, of macrophyte specimens collected at the sites were placed in glass 300-ml BOD bottles, which were then filled with bay water. Three replicate bottles for each species were run each sampling trip except April, when two replicates were run for each species. The bottles were capped and placed into ice chests large enough to accommodate several chambers or BOD bottles or both per chest. The chambers and the BOD bottles were suspended within the ice chests such that the surface of sediments and macrophyte specimens were exposed to direct sunlight. The initial dissolved oxygen (DO) was determined on water samples in chambers containing no sediment and BOD bottles without algae using a polarographic oxygen probe and meter (YSI Model 58). All bottles and chambers were gently shaken every 15-20 min to minimize the development of steep gas and nutrient gradients near the specimens (Littler and Arnold 1985). Blank (water only) controls were run to correct for plankton metabolism. The final DO in each BOD bottle and chamber was determined after 1-3 hrs of incubation in the light. The chambers had small (0.5-cm diameter) holes located in the wall mid-way between the top of the sediment and the top of the chamber to which was affixed a flexible plastic tubing and a pinch clamp. At the end of an incubation period, water in the chambers was slowly (to minimize splashing) drained into a BOD bottle through the tubing, and the end DO was determined from this sample. The light bottle incubations were conducted in the morning (08:00-12:00 hrs) and again in the afternoon (from 13:00-16:00 hrs). Dark bottle incubations, to measure respiration rates, were conducted by placing the chambers and bottles in closed ice chests and were run at night (23:00-06:00 hrs). In general, respiration rates were low, thus requiring longer incubation periods to produce measurable results. I carried out the experiments during a full diel cycle to minimize the effects of time of day on the productivity estimates (Shaffer and Onuf 1985, Rizzo and Wetzel 1986). Following the incubations, macrophyte specimens were removed from the bottles and placed in plastic bags and frozen. The dry weight was later determined as above. New water was collected for each incubation run. Salinity was measured for each water sample using a salinity probe (YSI Model 33 S-C-T meter). Samples were collected from each water sample for nutrient analysis and frozen until analyzed. Phosphate, silicate, nitrate, nitrite and ammonia concentrations were determined using an autoanalyzer (Technicon Autoanalyzer II) following the methods of Whitledge et al. (1981). Water temperature was recorded at 15-20 min intervals during the light incubations, and at the beginning and end of the dark incubations using a mercury thermometer. Irradiance was also recorded during the light incubations every 15-20 min, and periodically at other times during the day, using a light meter (Licor Model LI-185).

DATA ANALYSIS

Calculations of primary productivity, respiration and gross primary productivity followed the formulas in Littler and Arnold (1985). Because sediment net productivity and respiration (R) include animal metabolism, the following relationships must be defined further to more accurately reflect what I measured:

GPP = gross primary productivity
NPP = net primary productivity
CR = community respiration
AR = autotrophic respiration
HR = heterotrophic respiration
NEP = net ecosystem productivity,

which are related as follows:

$$\begin{aligned} NPP &= GPP - AR \\ CR &= AR + HR \\ NEP &= GPP - CR \\ NEP &= NPP - HR. \end{aligned}$$

The seaweed light bottle and dark bottle incubations measured NPP and AR, respectively, whereas the sediment chamber light and dark incubations measured NEP and CR, respectively. Below I use NP (= net productivity) to mean the total of NEP plus NPP. Similarly, R = CR + AR. Where total NPP, NEP or NP are greater than zero, the system is defined as being autotrophic. Where total NPP, NEP or NP are less than zero, the system is heterotrophic. (Autotrophic systems produce more fixed carbon than is utilized, and heterotrophic systems utilize more fixed carbon than is produced.)

Daily NPP and NEP were calculated by multiplying the average hourly rate (i.e., based on the morning and afternoon incubations) by the day length in hours. Annual NPP and NEP were calculated as follows: I assumed that limitation of photosynthesis occurred below 200 $\mu E\ m^{-2}\ sec^{-1}$ (Davis and McIntire 1983) and based the day length on the light data taken during sampling trips. This meant that day length varied from 10 hr in June and July to 3 hr in February (Figure 2). I used interpolated net productivity and day length values for days not sampled and assumed a linear change in these values between samplings. Annual net productivity was the sum of calculated daily rates between 10 June 1987 and 9 June 1988. Daily respiration was the hourly respiration multiplied by 24 hr/day. Annual respiration was computed similarly to annual net productivity, except that day length was a constant 24 hr. Daily GPP was the sum of daily net productivity and respiration. Annual GPP was the sum of daily rates for the year.

RESULTS

IRRADIANCE AND WATER PROPERTIES

Irradiance varied in the daily maximum and duration of time that irradiance was above 200 μE m^{-2} s^{-1} (Figure 2). Of note are the low levels in late autumn (November) and large relative increase in early spring (between March and April). Afternoon values were lower relative to morning

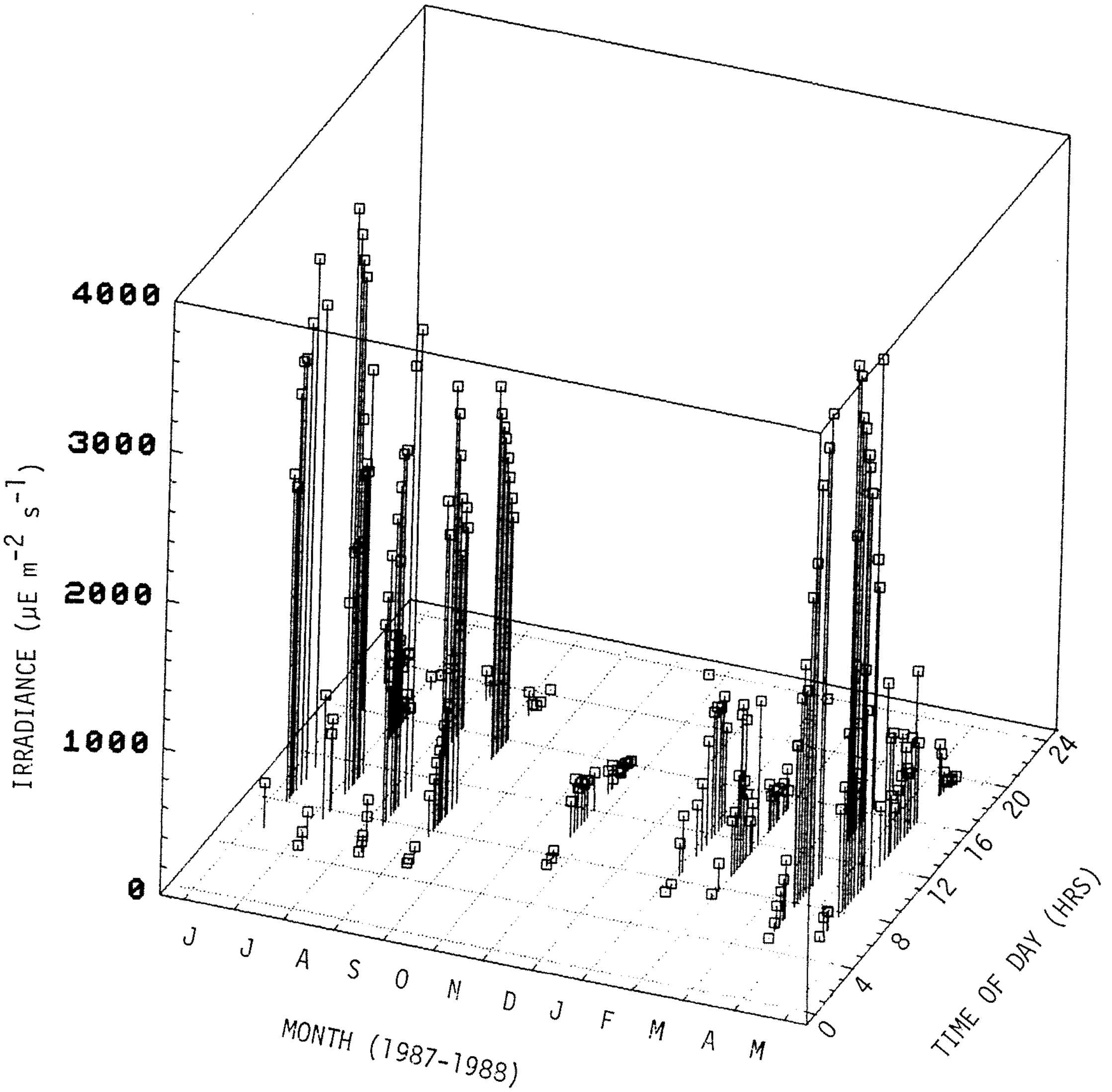

Figure 2. Solar insolation on the days when productivity experiments were conducted.

morning values during the April and May field trips, which reflected an increase in cloud cover during the afternoon.

All water properties showed seasonal changes (Figure 3), with the possible exception of phosphate (Figure 3c). Summer (June-September) was a period of highest water temperatures (Figure 3a), high salinity (Figure 3b), and lowest nitrate (Figure 3e), nitrite (Figure 3f), ammonia (Figure 3g) and total inorganic nitrogen to phosphate ratio (N:P) (Figure 3h). In general, water temperature and salinity were lowest, and inorganic nitrogen compounds were greatest, during autumn and winter (November-March). Silicate (Figure 3d) showed an increase from a late summer minimum to a late winter (February) maximum. Spring (March-May) was characterized by increasing water temperature and salinity, and rapidly decreasing nitrate, ammonia and N:P.

Notable correlations existed among several water properties (Table 2). A significant positive correlation between water temperature and salinity reflects a decline in freshwater input between the rainy winter season to the dry summer season. Salinity had a strong negative correlation with nitrate and N:P, suggesting that freshwater is the primary nitrate source. In contrast, ammonia and nitrite were not significantly correlated. Fluctuations in N:P were strongly linked to fluctuations in nitrate (R = 0.98), and to a much lesser extent to nitrite (R = 0.50) and ammonia (R = 0.37).

BIOMASS

Chlorophyll *a* concentration was greatest in sediments in the SAL/ENT and SAND/MUD habitats during spring and exhibited the largest relative increase between February and March samplings (Figure 4a). A slight increase in chlorophyll *a* concentration occurred in September in the SAND/MUD habitat. Summer chlorophyll *a* values were the lowest among all seasons. Mean chlorophyll *a* concentration in July for sites 5-12 did not differ significantly ($p = 0.05$, t-test) from that for the extra sites (19-23) sampled in July in the north and south portions of the bay. Phaeopigment concentration was also greatest in spring (Figure 4b). However, in the SAND/MUD habitat, phaeopigment concentration peaked in April as compared to the March peak in chlorophyll. Limited sampling in soft sediment comprising part of the gravel habitat showed that chlorophyll *a* and phaeopigment concentrations were comparable to those in the other habitats in April.

Total macrophyte vegetation biomass, like sediment pigments, showed a spring maximum (Figure 5). Summer values were substantially lower than spring values, and winter values were minimum. The biomass in the GRAV habitat was dominated by filamentous and tube-dwelling diatoms and the green-bladed alga *Enteromorpha linza* in April, and by the green-bladed alga *Ulva fenestrata* in May-July (Table 3). The red alga *Gracilaria pacifica* and *Z. japonica* were persistent members of the floral assemblage throughout the year in the GRAV patch. These species were generally found at the lowest site elevation located at the gravel-mud interface located at the edge of

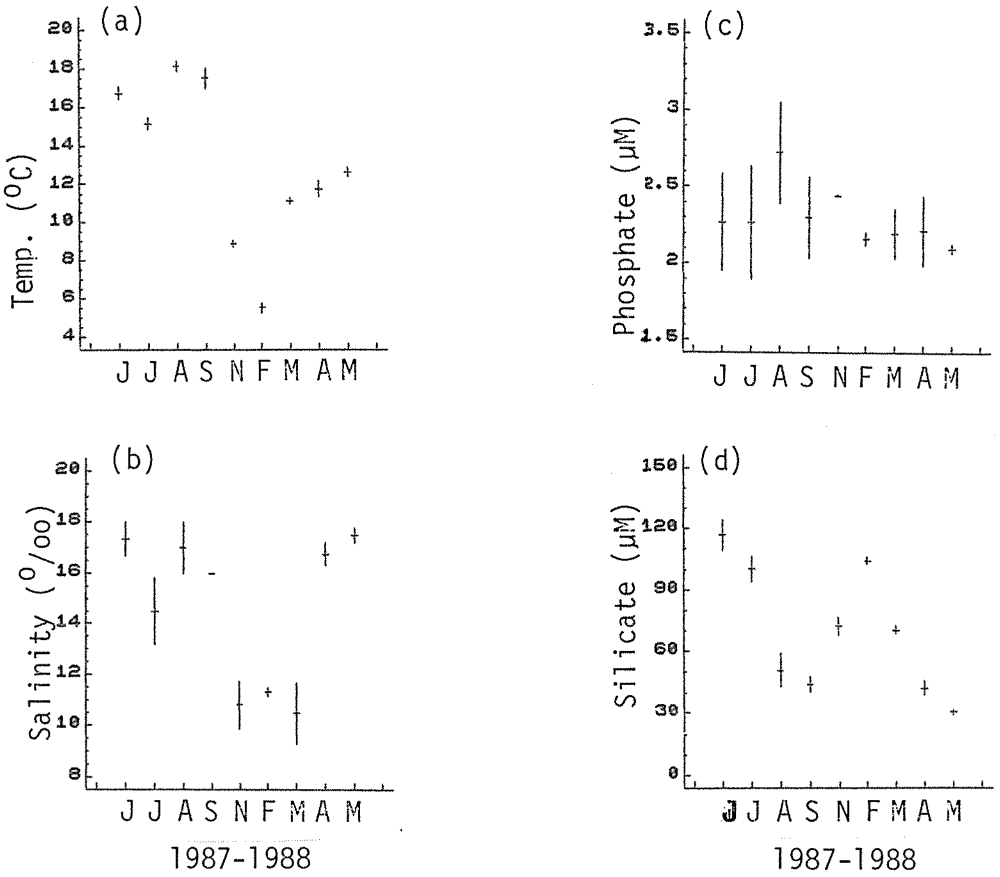

Figure 3. Mean (± 1SE) water property values: (a) water temperature; (b) salinity; (c) phosphate concentration; (d) silicate concentration; (e) nitrate concentration; (f) nitrite concentration; (g) ammonia concentration; (h) total inorganic nitrogen to phosphate ratio (N:P).

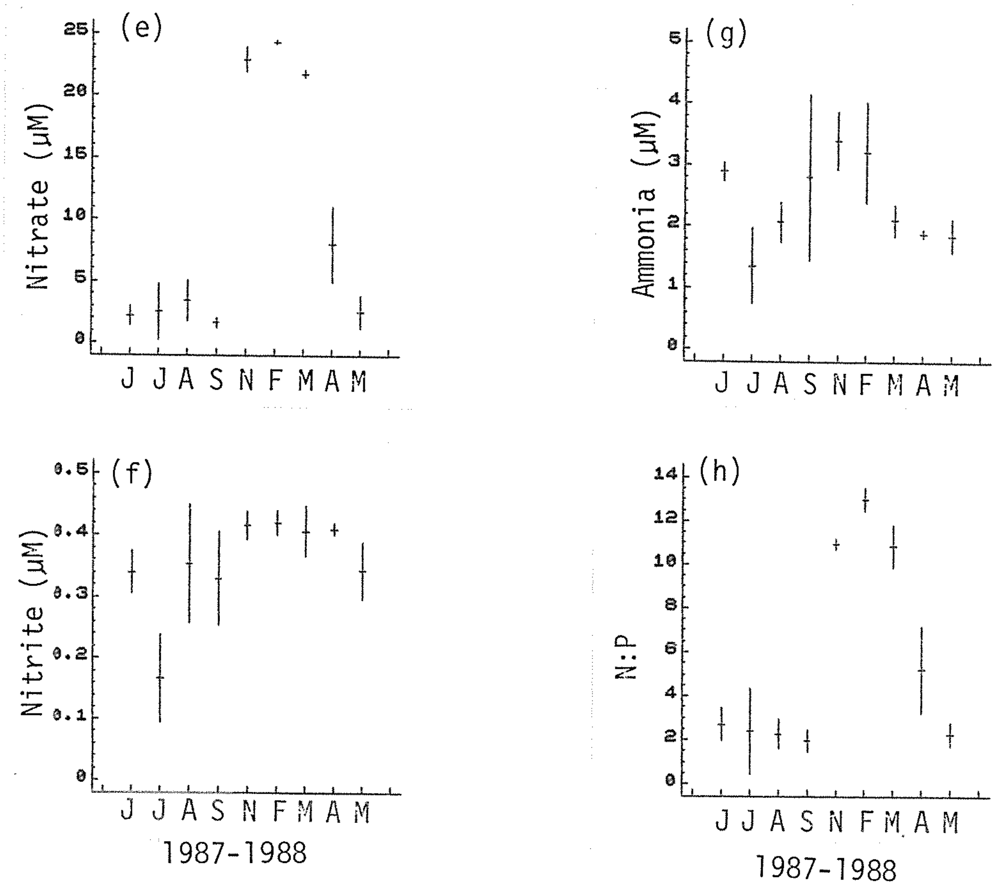

Figure 3 - continued.

Table 2. Correlation coefficients for water properties. Absolute values greater than 0.36 are significant at P = 0.05.

	Salinity	Phosphate	Silicate	Nitrate	Nitrite	Ammonia	N:P
Temp.	0.61	0.23	-0.25	-0.78	-0.35	-0.10	-0.76
Salinity	1.00	0.25	0.06	-0.86	-0.23	-0.27	-0.84
Phosphate	0.25	1.00	0.06	-0.23	-0.15	0.13	-0.34
Silicate	-0.35	0.06	1.00	0.21	-0.17	0.27	0.25
Nitrate	-0.86	-0.23	0.21	1.00	0.49	0.30	0.98
Nitrite	-0.23	-0.15	-0.17	0.49	1.00	0.44	0.50
Ammonia	-0.27	0.13	0.27	0.30	0.44	1.00	0.37
N:P	-0.84	-0.34	0.25	0.98	0.50	0.37	1.00

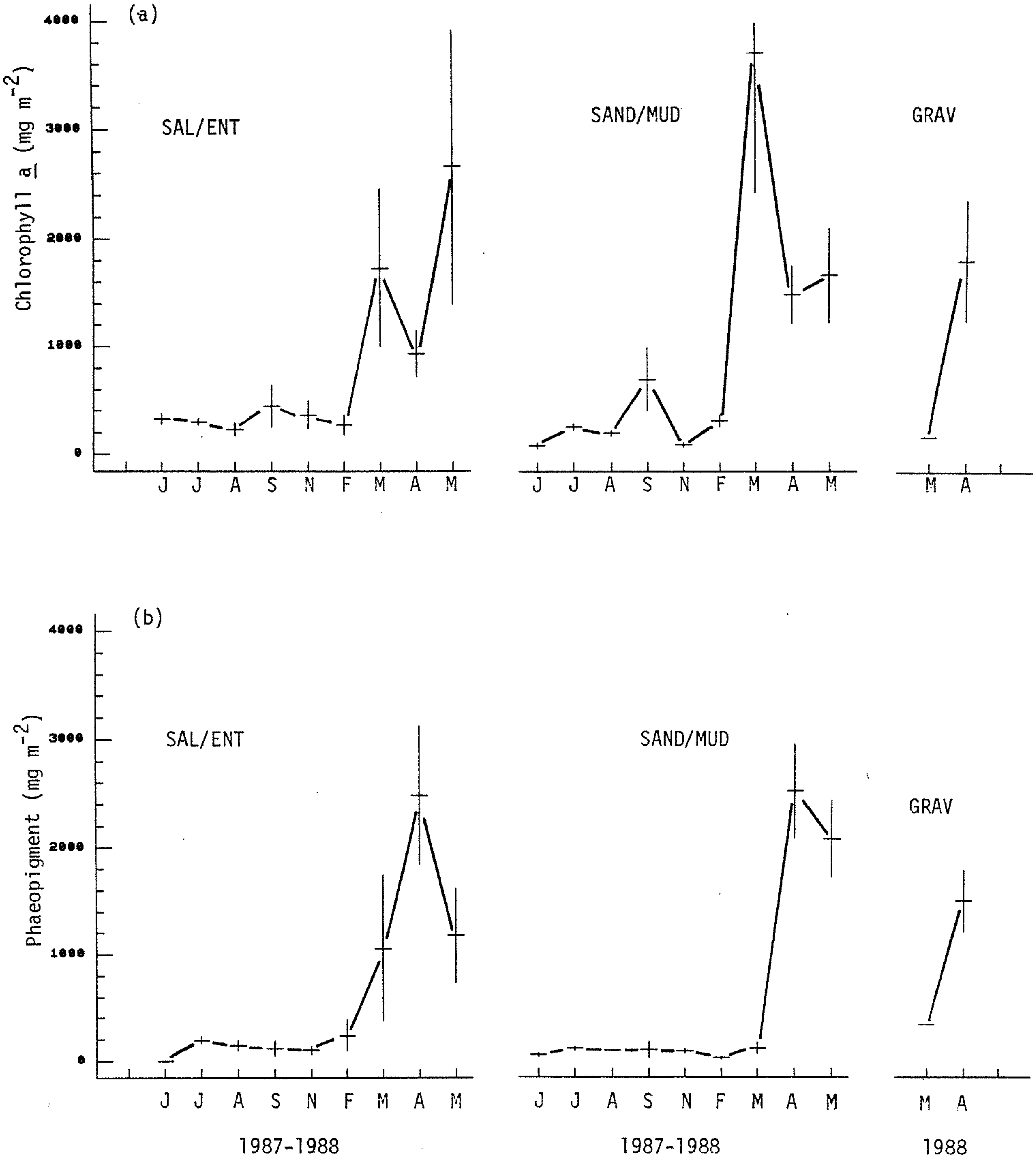

Figure 4. Mean (± 1SE) chlorophyll *a* (a) and phaeopigment (b) concentration in sediments at sites within the three habitats.

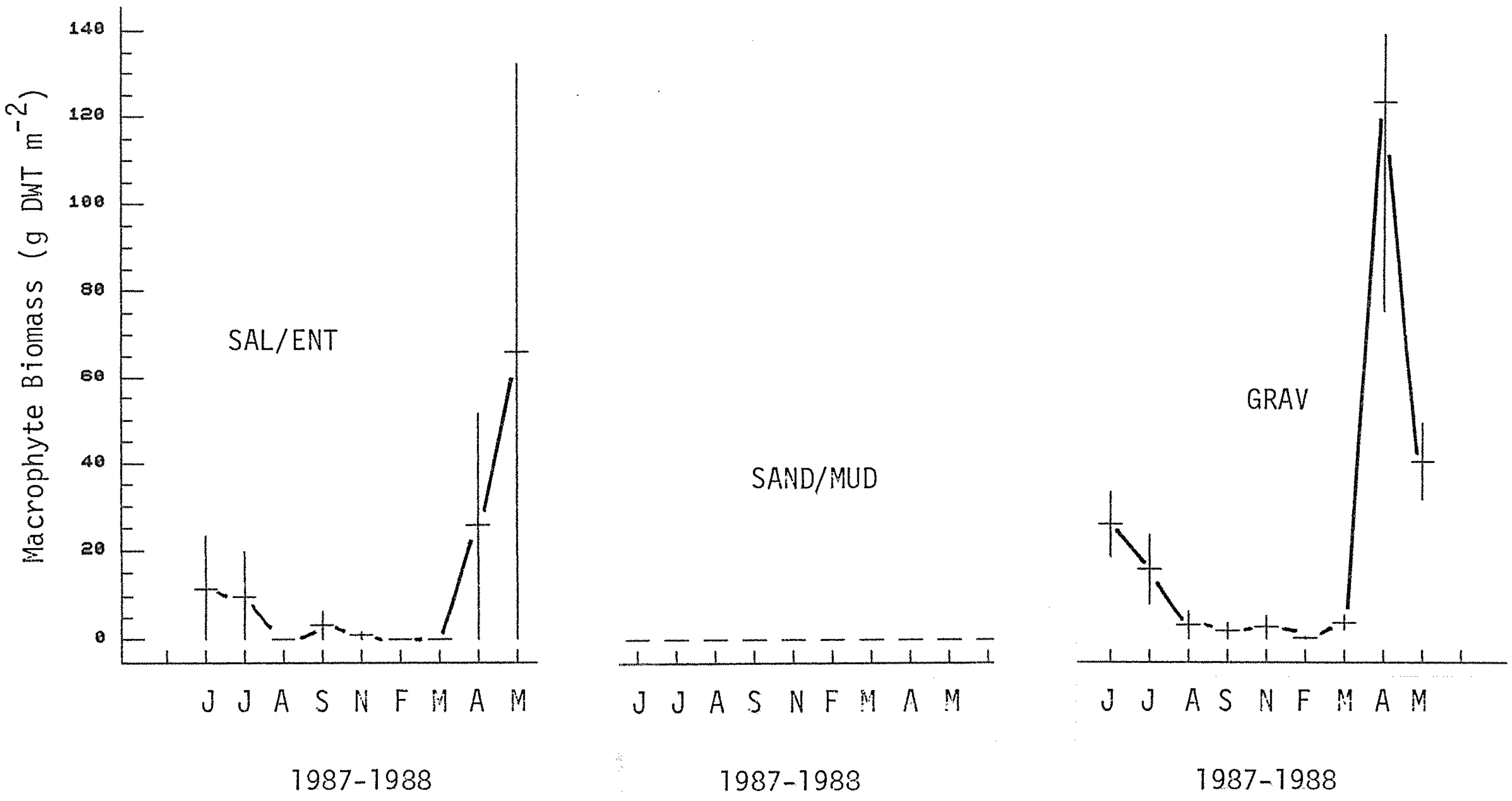

Figure 5. Mean (± 1SE) total macroalgal biomass within the three habitats.

Table 3. Mean (SD) dry weight biomass of macroscopic vegetation within the SAL/ENT and GRAV habitats. N = 4 for SAL/ENT; n = 6 for GRAV. Values are in g DWT m^{-2}.

	June '87		July '87		Aug. '87		Sep. '87		Nov. '87		Feb. '88		Mar. '88		Apr. '88		May '88	
Taxon	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV	SAL/ENT	GRAV
Ceramium pacificum																0.002 (0.004)		
Chaetomorpha sp.						0.013 (0.033)				< .001 (< .001)				<.001 (<.001)				0.153 (0.376)
Diatoms																100.522 (110.248)		
Enteromorpha linza																22.173 (14.112)		
E. intestinalis	11.625 (23.250)	0.578 (0.606)	4.132 (8.265)	0.700 (0.598)										<.001 (<.001)	13.908 (27.815)		40.582 (81.165)	0.062 (0.151)
E. prolifera		9.937 (24.085)	1.358 (2.715)	0.047 (0.064)														
Fucus gardneri			0.678 (1.355)				3.361 (6.722)		0.862 (1.725)						11.935 (23.870)		25.625 (51.250)	
Gracilaria pacifica		0.087 (0.212)		0.080 (0.136)		0.320 (0.784)		1.318 (3.229)		1.130 (2.768)		0.243 (0.596)		1.422 (3.482)		0.990 (2.425)		0.797 (1.951)
Monostroma sp.														0.858 (0.864)		0.017 (0.041)		
Petalonia fascia																0.152 (0.256)		
Sargassum muticam																0.020 (0.049)		
Scytosiphon lomentaria																0.333 (0.708)		
Spongomorpha sp.														0.028 (0.069)				
Ulva fenestrata		20.500 (10.563)	3.670 (7.340)	15.003 (18.382)		0.015 (0.037)												39.638 (21.170)
Zostera japonica		0.015 (0.037)		0.052 (0.127)		0.183 (0.449)		0.605 (1.482)		1.660 (4.066)				0.038 (0.094)				0.002 (0.004)
TOTAL	11.625 (23.250)	25.980 (18.135)	9.838 (19.675)	15.882 (18.617)		3.412 (8.357)	3.361 (6.722)	1.923 (4.711)	0.862 (1.725)	2.825 (6.920)		0.243 (0.596)		3.960 (4.603)	25.842 (51.685)	124.208 (118.034)	66.208 (132.415)	40.652 (22.054)

this patch. *Enteromorpha intestinalis* had the highest mean biomass among all species occurring in the SAL/ENT habitat in spring and early summer, was most abundant in May, and was not collected in August 1987-March 1988 (Table 3). The fucoid brown alga *Fucus gardneri* was collected during all seasons in the SAL/ENT habitat (Table 3).

NET PRIMARY PRODUCTIVITY, RESPIRATION AND GROSS PRIMARY PRODUCTIVITY

NEP was generally low, and at times negative, in the SAND/MUD habitat (Figure 6). NEP peaked in March. In comparison, NP was always positive in the SAL/ENT habitat, and showed peaks in late summer and late spring (April-May). The temporal pattern was similar between these two habitats in NP. However, mean NP in SAL/ENT habitat exceeded NEP in the SAND/MUD habitat in eight of the nine samplings. The lowest NPP measured occurred in July in both habitats. The SAL/ENT samples in the incubation chambers frequently contained attached macroscopic algae (e.g., *E. intestinalis, F. gardneri*), particularly in spring and summer. In contrast, the SAND/MUD habitat samples consisted only of sediments. Total NPP in the gravel patch was greatest in April. NPP in late spring through early summer (i.e., indicated by the May 1988 and June-July 1987 data; Figure 6) was substantially less. NPP in the gravel patch exceeded NEP in the SAND/MUD on four of the nine samplings, and exceeded NP in the SAL/ENT habitat on three of nine samplings.

Respiration rates varied seasonally and between habitats (Figure 7). Summer rates were lowest in the GRAV habitat, intermediate in the SAL/ENT habitat and greatest in the mud habitat. There was a decline in respiration in autumn and winter to the lowest values for the year in all habitats. April rates were the greatest in all habitats, with the GRAV habitat exceeding the other habitats during this sampling. Respiration dropped dramatically in the GRAV habitat by May but remained relatively high in the other two habitats.

GPP generally followed the same temporal patterns and between-habitat relationships as did NP (Figure 8). However, respiration was proportionally greater than NEP in the SAND/MUD habitat as compared to the other habitats during all samplings. The GPP:R ratio within the SAL/ENT habitat ranged between ca. 2 (July 1987) and 19 (March 1988). Heterotrophic conditions occurred in the SAND/MUD habitat in July 1987 and March 1988. The GPP:CR ratio ranged between ca. -0.5 and 1.5 during the study period in the SAND/MUD habitat. GPP:AR for macrophytes were always much greater than 1.0 owing to very low AR values (Table 4).

NPP, AR and GPP for the 11 macrophyte taxa tested are given in Table 4. Greatest mean rates for any sampling were recorded for macroscopically evident diatom tufts, *Z. japonica, E. intestinalis* and *E. linza.* Experiments were conducted on *F. gardneri* and *G. pacifica* most often owing to their year-round occurrence at the sites. Only *Gracilaria* showed seasonal rate changes, with

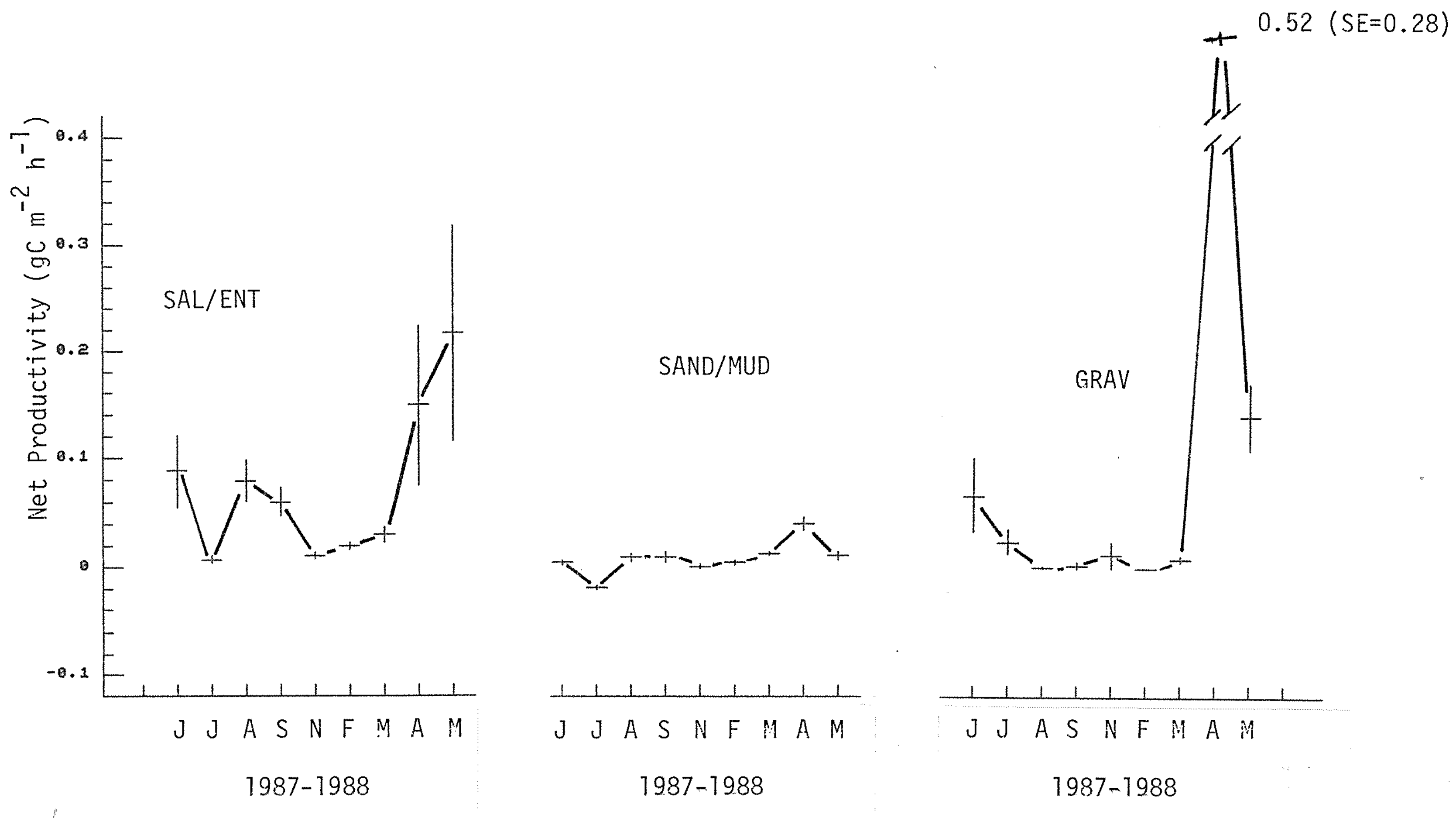

Figure 6. Mean (± 1SE) total net primary productivity (NP) within the three habitats.

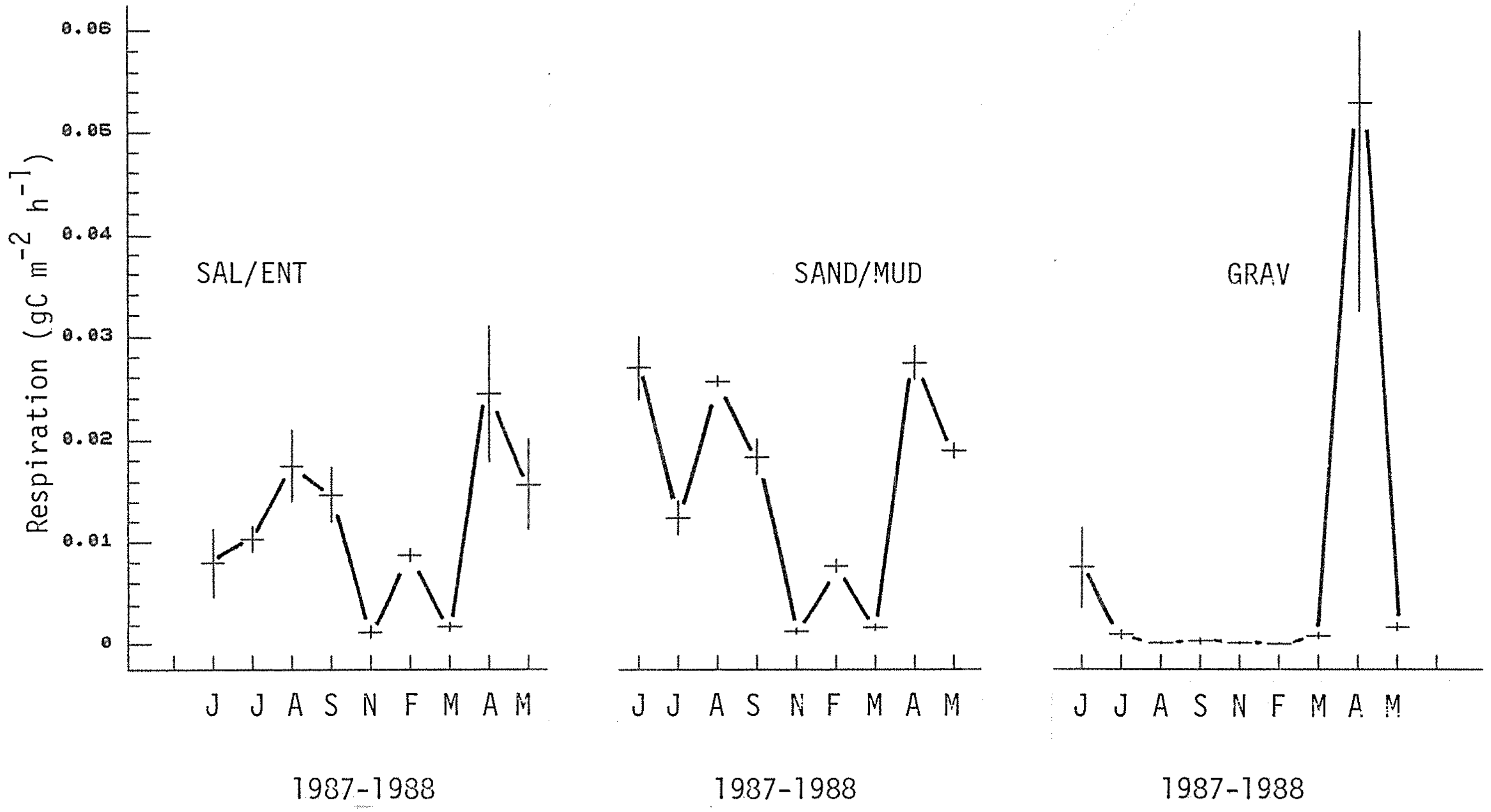

Figure 7. Mean (± 1SE) total respiration (R) within the three habitats.

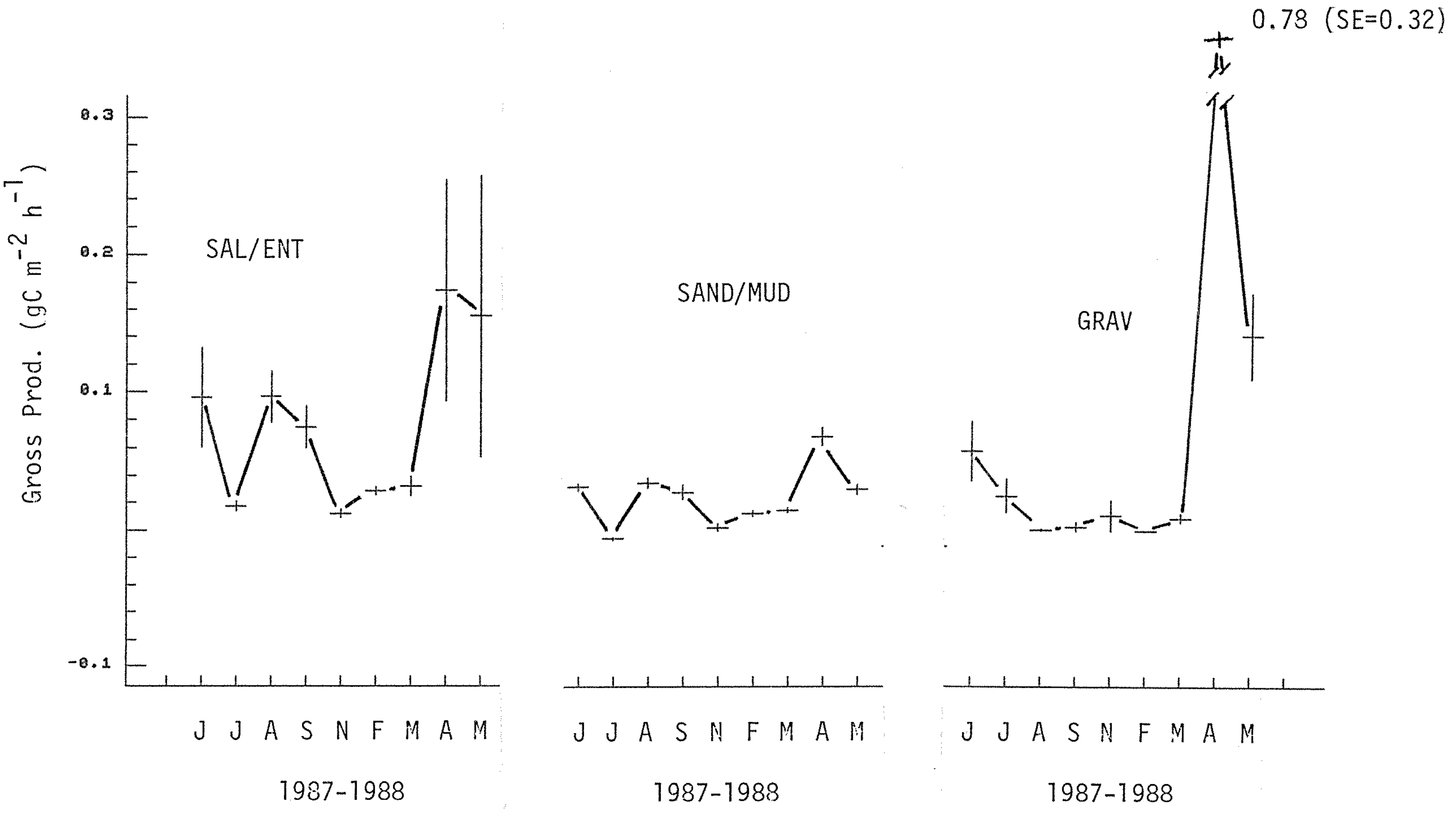

Figure 8. Mean (± 1SE) total gross primary productivity (GPP) within the three habitats.

Table 4. Mean (SD) productivity (NPP, GPP) and respiration (R) rates for seaweed taxa and eelgrass. Values are mg C g DWT^{-1} hr^{-1}.

Month and year	Parameter	N	Ceramium pacificum	Diatom	Taxon								
					Enteromorpha linza	Enteromorpha intestinalis	Enteromorpha prolifera	Fucus gardneri	Gracilaria pacifica	Monostroma sp.	Petalonia fascia	Ulva fenestrata	Zostera japonica
Jun 87	NPP	6				4.34(0.78)	3.18(0.99)					1.62(0.37)	
	R	3				0.28(0.12)	0.36(0.19)					0.19(0.16)	
	GPP					4.62	3.54					1.81	
Jul 87	NPP	6				1.72(0.37)	3.70(1.78)					1.53(0.32)	
	R	3				0.09(0.10)	0.18(0.05)					0.08(0.09)	
	GPP					1.81	3.88					1.61	
Aug 87	NPP	6							2.56(0.71)				
	R	3							0.21(0.03)				
	GPP								2.77				
Sep 87	NPP	6							2.20(0.69)				
	R	3							0.22(0.02)				
	GPP								2.42				
Nov 87	NPP	6						0.82(0.37)	1.75(0.99)				5.42(2.02)
	R	3						0.03(0.01)	0.01(0.02)				0.12(0.07)
	GPP							0.85	1.76				5.54
Feb 88	NPP	6							0.59(0.11)				
	R	3							0.08(0.01)				
	GPP								0.67				
Mar 88	NPP	6						0.50(0.15)	0.78(0.13)	8.44(1.85)			2.42(0.77)
	R	3						0.12(0.04)	0.11(0.10)	0.92(0.23)			0.53(0.07)
	GPP							0.62	0.89	9.36			2.95
Apr 88	NPP	4	2.21(1.20)	6.32(4.83)	4.14(0.78)			0.75(0.12)	1.49(0.76)		3.45(1.24)		
	R	2	0.23(0.07)	0.42(0.15)	0.47(0.30)			0.12(0.03)	0.18(0.03)		0.31(0.08)		
	GPP		2.44	6.74	4.61			0.87	1.67		3.76		
May 88	NPP	6				3.45(1.46)		0.99(0.21)	1.80(0.56)			3.48(1.05)	2.15(0.76)
	R	3				0.10(0.07)		0.07(0.01)	0.05(0.05)			0.11(0.11)	0.12(0.03)
	GPP					3.53		1.06	1.85			3.59	2.27

a winter minimum, spring increase and summer maximum. The rates in Table 4 were multiplied by mean biomass values for appropriate taxa in Table 3 to yield productivity and respiration rates per m^2.

Enteromorpha intestinalis and *U. fenestrata* dominated NP (and GPP) within the SAL/ENT and GRAV habitats, respectively, during spring and summer. Rates for *E. intestinalis* appeared to be greatest in June 1987 (Figure 9a). However, high spatial variability (due to high within-habitat biomass variance, Table 3) made the June sampling not significantly different from the other months. The greatest mean rate for *U. fenestrata* occurred in May 1988 (Figure 9b).

Elevation correlated significantly with sediment NEP ($r = 0.48$) and sediment GPP ($r = 0.50$) ($n = 161$). Neither NEP nor GPP correlated significantly with sediment chlorophyll *a* concentration. The linear model relationships are:

sediment NEP (g C m^{-2} hr^{-1}) = -0.036 + 0.056 x elevation (m)
sediment GPP (g C m^{-2} hr^{-1}) = -0.035 + 0.066 x elevation (m).

Macrophyte biomass in the GRAV habitat correlated significantly ($N = 53$) with macrophyte NPP ($R = 0.98$), respiration ($ar = 0.96$) and GPP ($r = 0.98$), as would be expected because biomass was used to weight the productivity measurements to unit areas. However, the linear models are useful for predicting NPP, AR and GPP using biomass data. The models are:

NPP (g C m^{-2} hr^{-1}) = -0.034 + 0.006 x biomass (g DWT m^{-2})
AR (g C m^{-2} hr^{-1}) = -0.003 + 0.0004 x biomass (g DWT m^{-2})
GPP (g C m^{-2} hr^{-1}) = -0.038 + 0.006 x biomass (g DWT m^{-2}).

SEDIMENT GRAIN SIZE EFFECTS

The July 1987 sampling showed that chlorophyll *a* concentration exhibited two peaks relative to sediment grain size (Figure 10). The greatest concentrations occurred in very coarse sand (phi = 0.0 to -1.0) and medium to fine sand (phi = 2.0 to 3.0). Lowest concentrations were recorded in very fine sand (phi = 3.5 to 4.5). Sediment NEP decreased as sediment grain size decreased (i.e., increasing phi size) (Figure 11). For this July data set, coarse to very coarse sands (i.e., phi sizes 1.0 to -0.8) had either zero or positive NEP. Finer grained sediments had negative NEPs. Simple linear regression models show that NEP had the strongest relationship to sediment grain size followed by GPP and CR (Table 5). In contrast to NEP and GPP, AR increased with decreased grain size.

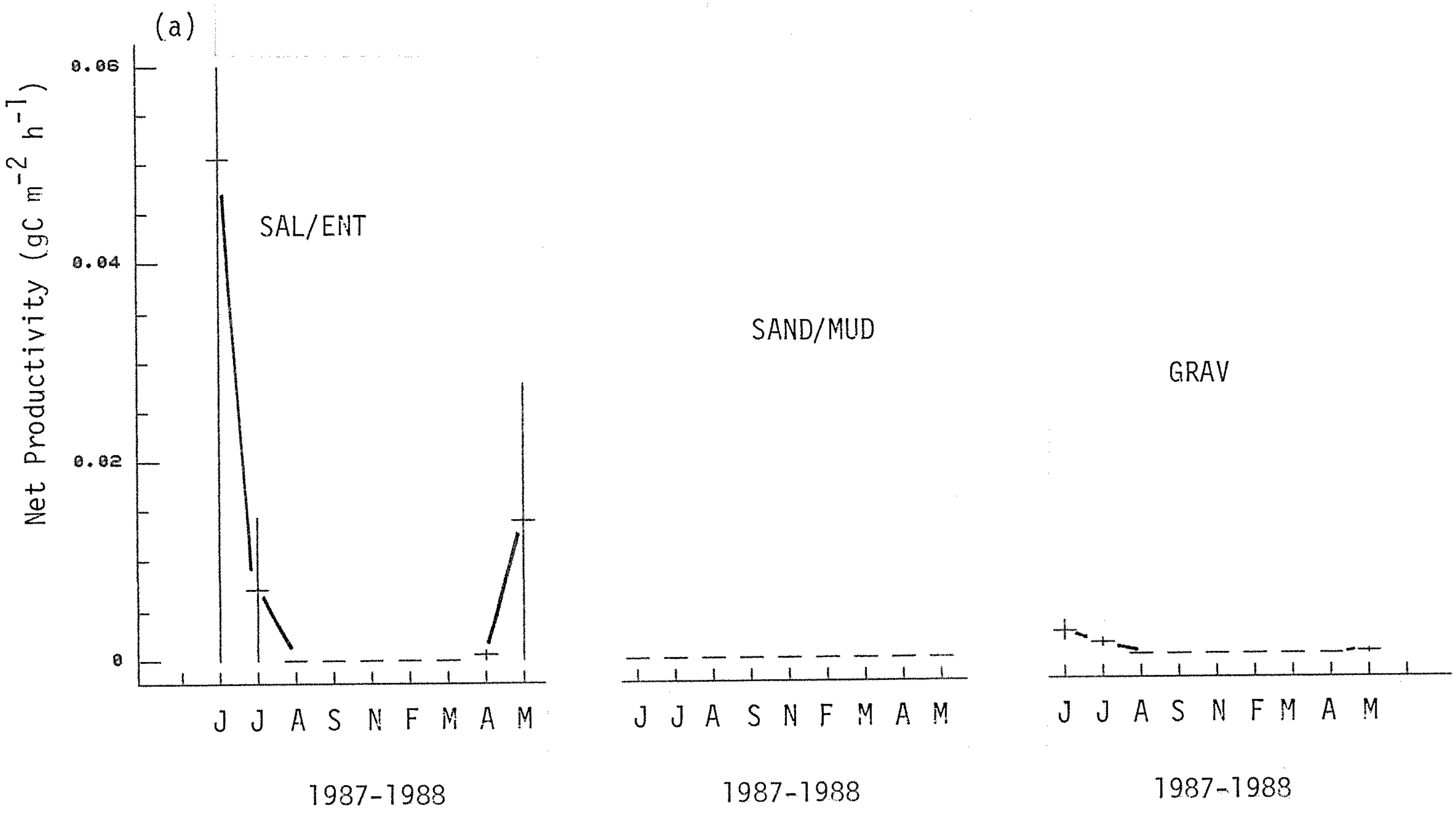

Figure 9. Mean (± 1SE) net primary productivity (NPP) by (a) *Enteromorpha intestinalis* and (b) *Ulva fenestrata* within the three habitats.

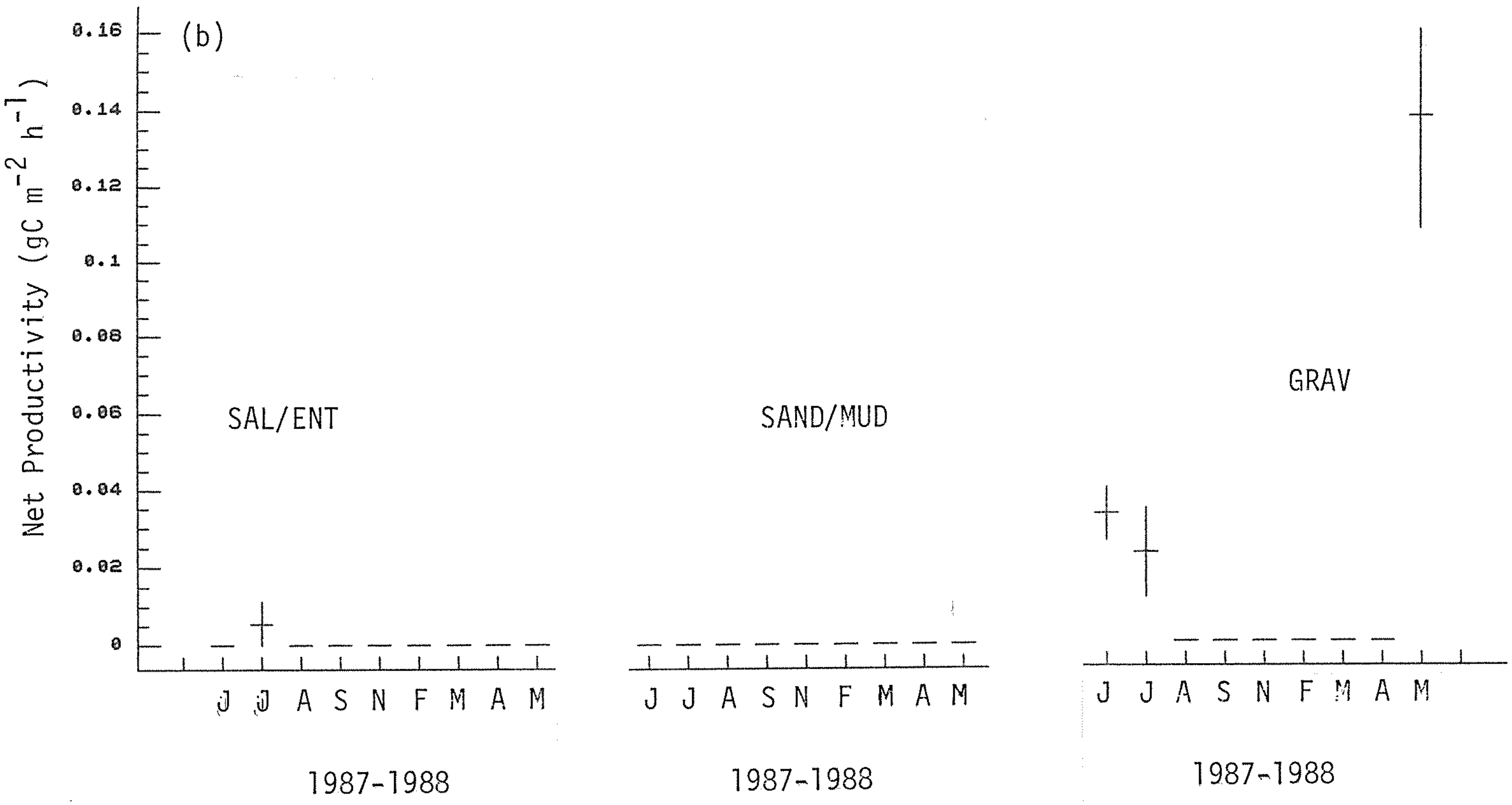

Figure 9 - continued.

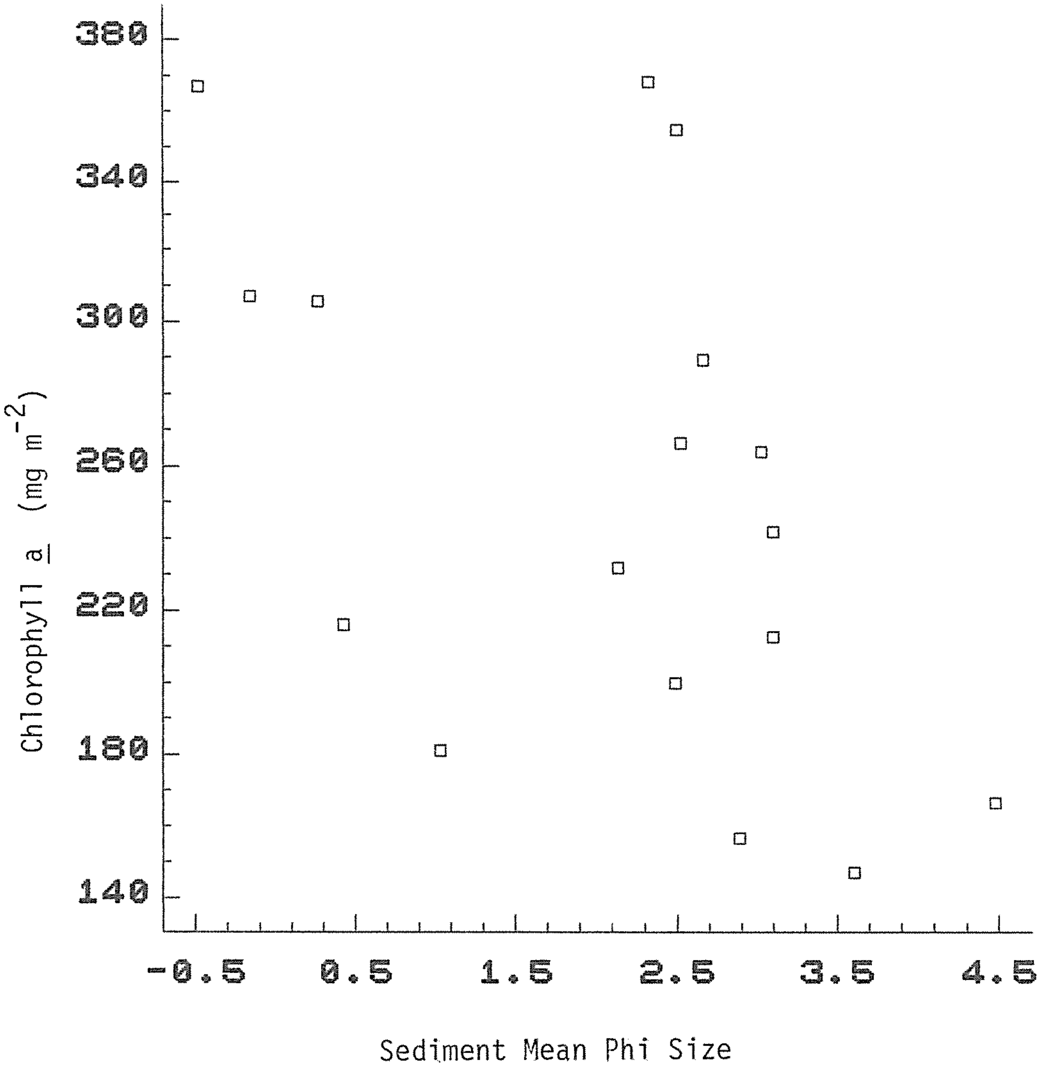

Figure 10. Chlorophyll *a* concentration in sediments versus mean phi size for July 1987 sampling. Curve fitted by hand.

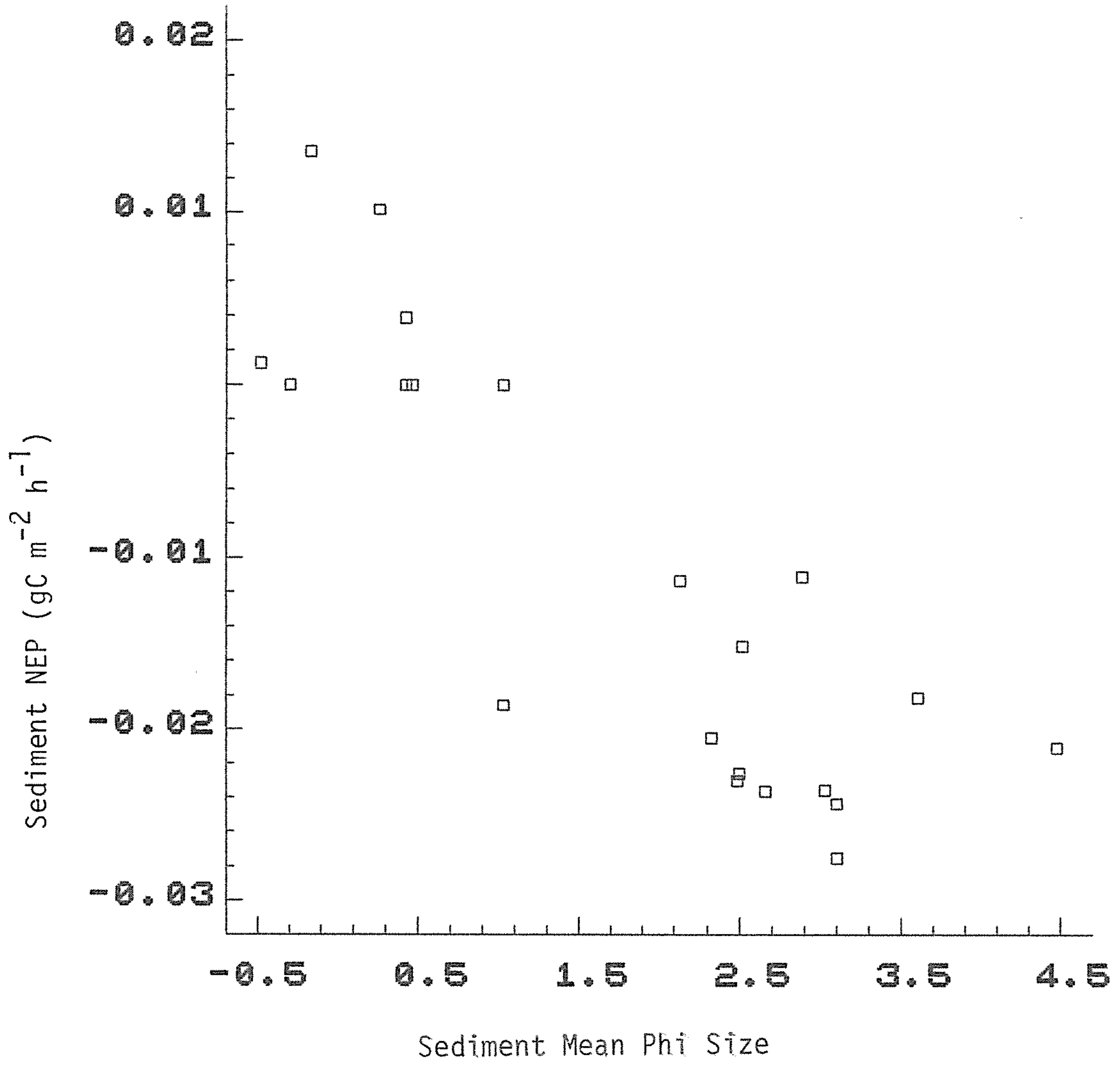

Figure 11. Sediment net productivity (NEP) versus mean phi size for July 1987 sampling.

Table 5. Linear regression results for sediment phi size (X) on dependent variables (Y) sediment NEP, CR and GPP for sampling in July 1987. The model is Y = a + bX. r = correlation coefficient; r^2 = coefficient of concordance.

Y	a	b	r	r^2
NEP (mg C m^{-2} hr^{-1})	1.05×10^{-3}	-7.00×10^{-3}	-0.85	72%
AR (mg C m^{-2} hr^{-1})	4.93×10^{-3}	2.30×10^{-3}	0.58	33
GPP (mg C m^{-2} hr^{-1})	5.99×10^{-3}	-4.70×10^{-3}	-0.69	48

PRODUCTIVITY, RESPIRATION AND TURNOVER IN THE SYSTEM

Studies conducted in 1986-87 in the seagrass system (Thom 1988, and unpublished data) were combined with data from the present work to develop estimates of benthic metabolism in Padilla Bay (Table 6). Annual NP and GPP per m^2 were greatest among all habitat types in the GRAV habitat, followed closely by SAL/ENT habitat, *Z. marina* and *Z. marina* epiphytes. Annual NEP was low but positive in the SAND/MUD habitat in contrast to the negative NEP in the eelgrass bed sediments. R per m^2 was greatest in sediments. The vast majority of Padilla Bay system NP was attributed to *Z. marina* and its epiphytes, primarily owing to the large area covered by these components. Most of the annual R was attributed to sediments. Sediments in the eelgrass bed had GPP:R values below 1.0, indicating heterotrophic conditions on an annual basis. The major proportion of system annual GPP occurred in the *Z. marina* habitat. Turnover rates were greatest in habitats dominated by annual seaweeds. Total system GPP exceeded total system R on an annual basis (GPP:R = 1.8). Turnover rate (i.e., total system NPP/total system annual mean biomass = $7{,}414.2 \times 10^3$ kg C/$1{,}063.5 \times 10^3$ kg C) was 7.0 for the system. Average annual NP, R and GPP for the system were 166, 211 and 377 g C m^{-2}, respectively.

DISCUSSION

Season, grain size and elevation affected the biomass, structure, and primary productivity and respiration rates of the tidal flat assemblages. The seasonal patterns can be summarized as follows: (1) biomass, NP and R were low for all components in winter when light energy was lowest and nutrients were greatest; (2) increasing light in spring resulted in increased water temperatures coupled with peak NP and R, and lowered nutrient concentrations; (3) summer conditions were characterized by high light level, lowest nutrients, and intermediate and low biomass and

Table 6. Annual productivity and respiration rates for habitat components in Padilla Bay. Data for the *Zostera* habitat are from Thom (1988), except where noted otherwise. Areas in the system are from Webber et al. (1987) with modifications as given in footnote a.

Habitat	Elev. range (m)	Area in system[a] (ha)	Annual NP (gC/m^2)	Annual system NP ($10^3 kgC$)	Percent of total NP	Annual R (gC/m^2)	Annual system R ($10^3 kgC$)	Percent of total R	Annual GPP (gC/m^2)	Annual system GPP ($10^3 kgC$)	Percent of total GPP	GPP:R	Mean annual biomass		Turnover rate (NP :B)
													($gDWT/m^2$)	(gC/m^2)[f]	
SAL/ENT	2.0 to 1.3	9.1	185.2	16.9	0.2	91.4	8.3	0.1	276.6	25.2	0.1	3.0	23.1[d,e]	8.8	21.1
SAND/MUD	0.8	896.8	22.3	200.0	2.7	126.5	1134.5	12.0	148.8	1334.4	7.9	1.2	11.1[e]	4.2	5.3
GRAV	0.8 to 0.5	9.1	296.0	26.9	0.4	58.9	5.4	0.1	354.9	32.3	0.2	6.0	24.3	9.2	32.1
Zostera japonica	0.8 to 0.3	1427.5	44.7	638.1	8.6	3.2[c]	45.7	0.5	47.9	683.8	4.1	15.0	24.2	9.2	4.9
Z. japonica epiphytes	0.8 to 0.3	1427.5	21.3	304.1	4.1	1.6[b]	22.8	0.2	22.9	326.9	1.9	14.3	1.4	0.5	40.0
Z. japonica sediment	0.8 to 0.3	1427.5[b]	-13.8	-197.0	-2.7	216.1[b]	3084.8	32.6	202.3	2887.8	17.1	0.9	3.0[e]	1.1	-12.1
Zostera marina	0.3 to -0.4	2132.5	199.7	4258.6	57.4	69.0[b]	1471.4	15.6	268.7	5730.0	34.0	3.9	92.2	35.0	5.7
Z. marina epiphytes	0.3 to -0.4	2132.5	205.7	4386.6	59.2	8.5[b]	181.3	1.9	214.2	4567.8	27.1	25.2	13.2	5.0	41.0
Z. marina sediment	0.3 to -0.4	2132.5[b]	-104.1	-2219.9	-29.9	164.5[b]	3508.0	37.1	60.4	1288.0	7.6	0.4	2.1[e]	0.8	-130.5
TOTAL SYSTEM		4475.0		7414.2			9462.1			16876.3		1.8			7.0

[a] SAL/ENT = 1% bare flat area (915 ha); SAND/MUD = 98% of bare flat area; GRAV = 1% of bare flat area; *Z. japonica* habitat = very sparse eelgrass area + sparse eelgrass + 50% of complete seagrass (high intertidal); *Z. marina* habitat = 50% complete seagrass (high intertidal) + complete seagrass (low intertidal and subtidal).

[b] Thom, unpublished data from 1986-7 studies.

[c] From the present study.

[d] Includes seaweed + chlorophyll a data.

[e] 62.0 x chlorophyll a = wet wt biomass (Valiela 1984); 0.2 x wet wt = dry wt. (unpublished data).

[f] 0.38 x dry wt. = carbon (Westlake 1963).

productivity; and (4) decreasing light and water temperature in autumn was coupled with low biomass and productivity and increasing nutrient concentrations. This pattern is typical of temperate estuarine systems (Pamatmat 1968, Marshall et al. 1971, Pomeroy and Stockner 1976, Cadeé and Hegeman 1977, Davis and McIntire 1983, Colijn and de Jonge 1984, Nienhuis and De Bree 1984, Lukatelich and McComb 1986). Increased light energy in spring initiates an increase in photosynthetic rates. Temperature increases result in more rapid photosynthesis and cell division, and increased algal (Hartwig 1978, Admiraal and Peletier 1980, Davis and McIntire 1983) and animal respiration (Pamatmat 1968, Asmus and Asmus 1985). Nutrient limitation, along with photoinhibition, may result in low summer biomass and productivity rates in these types of ephemeral estuarine assemblages (Van Raalte et al. 1976). The small autumn increase in biomass in the SAND/MUD habitat I measured was also recorded by Davis and McIntire (1983) in Netarts Bay, Oregon. Nitrite and ammonia concentrations increased in autumn because of increased allochthonous input and autochthonous production or both (Boynton and Kemp 1985), and may have stimulated the autumn bloom (Van Raalte et al. 1976). Annual productivity rates for benthic components within the system imply that most of the nutrient depletion is due to the seagrass and its epiphytes. However, increased autotrophic productivity occurs 1-3 months earlier on the sand/ mud flats as compared to within the seagrass system (Thom 1988). Hence, nutrient depletion early in the spring may be largely due to sand/mud flat autotrophs. The reason for the earlier spring increase may be due to more light energy being received, on average, at the higher elevations during early spring (Admiraal and Peletier 1980).

Chlorophyll *a* peaked in concentration in the SAND/MUD and SAL/ENT habitats in March as compared to an April-May peak in macrophyte biomass. Peak productivity coincided with peak biomass for the macrophyte-dominated habitats, but not on the SAND/MUD. Peak GPP in this latter habitat was recorded 1 month after the peak biomass. This suggests that early spring sediment-associated algae have a low productivity to biomass ratio. Grazing by benthic copepods, gastropods and other herbivores conceivably could be cropping algal cells as quickly as they are produced. Harpacticoid copepods typically bloom in March-April in estuarine mudflats (Simenstad and Cordell 1985), and appear to potentially be linked to variations in the biomass of mudflat algae (Thom et al. 1988). Harpacticoids and other small crustacea are abundant on Padilla Bay tidal flats in spring (Simenstad et al. 1988). Asmus and Asmus (1985) found a synchrony between the seasonal development of plant biomass on a estuarine flat in the North Sea and monthly secondary productivity. Where macrofauna were in high densities, sediment-associated microalgal biomass decreased during the warmer months.

The coarsest sediments had the greatest productivity rates. In contrast, the finest sediments had the highest respiration rates. Coarser sediments were autotrophic or at least balanced with regard to NEP and CR. The SAND/MUD habitat typified a region of net organic matter deposition as evidenced by generally higher volatile solids concentrations. These same results have been documented in several estuarine systems (Davis and McIntire 1983, McIntire and Amspoker 1986, Grant and Hargrave 1987). I found that sediments were heterotrophic at a mean phi size of ca. 1.0 in the July experiments. However, I do not consider this latter phi size as a threshold between heterotrophy and autotrophy. The y-intercept, slope and strength of the grain size-productivity relationship probably changes throughout the year owing to variations in light, temperature, nutrients and sediment movement.

Macrophytes showed a major peak in productivity and biomass in April in the GRAV habitat. This short-lived assemblage included green-bladed algae and filamentous and tube-dwelling diatoms, which typically bloom during this period in Northwest estuaries (Thom 1980, Davis and McIntire 1983). The fact that chlorophyll *a* was found in relatively high concentrations by limited sampling in the soft sediments of the GRAV habitat suggests that sediment productivity may be significant. Sediment respiration was not measured and may be significant also. Therefore, I probably underestimated total productivity and respiration for this habitat. On the basis of annual productivity and respiration data for the SAND/MUD habitat and the GRAV habitat, NEP and respiration in the gravel patch were underestimated by about 7.5% and 215%, respectively. By comparison, the SAL/ENT estimates included both sediments and macrophytes.

Hourly sediment NEP and GPP were significantly correlated with elevation for the entire sampling period. However, the measure of algal biomass (i.e., chlorophyll *a*) in the sediments did not correlate with productivity or respiration. This is in contrast to significant correlations between these measures documented by Davis and McIntire (1983) in Netarts Bay, Oregon, in the Columbia River estuary by McIntire and Amspoker (1986), and in Balgzand in the North Sea by Cadeé and Hegeman (1977). In Padilla Bay, maximum chlorophyll *a* did not coincide in time with maximum productivity. As discussed above, possible explanations include temporal variations in productivity to biomass ratios and grazing pressure. This apparent uncoupling needs further study in Padilla Bay.

The rate of annual GPP for the sand/mud flats (149 g C m^{-2}) was on the order of estimates for other estuaries (Colijn and de Jonge 1984). Colijn and de Jonge state that tideflat annual productivity rates worldwide fall into a small range (i.e., 50-200 g C m^{-2}), which is surprising in view of the myriad methodologies employed in measuring and calculating these rates. The macrophyte NPP rates in Padilla Bay (185-296 g C m^{-2}) were near the low end of the range (200-700 g C m^{-2}, Thom 1984) reported for temperate estuarine systems. Nutrient limitation, due to probable low rates of nutrient input relative to a high proportion of area dominated by benthic vegetation, may partially explain the lower productivity rates in Padilla Bay.

Correll (1978) asked which primary producers are most important in an estuary, and based relative importance on two factors: productivity rate and availability of organic matter to the consumers. He concluded that phytoplankton are usually the most important primary producers. However, in shallow systems, benthic algae and submersed aquatic macrophytes are probably more important. Phytoplankton productivity data are unavailable for Padilla Bay. In the experiments I conducted, blank chambers containing plankton usually had undetectable changes in dissolved oxygen during the incubations. Limited data on chlorophyll *a* concentrations in the water column (my unpublished data) for 1986-87 over the seagrass system showed that water column values were less than 10% of sediment values. This information suggests that phytoplankton were not as important as benthic primary producers in the system. The fact that displacement of benthic diatoms into the water column is caused by tidal mixing in shallow systems complicates the interpretation of the relative importance of phytoplankton in a system such as Padilla Bay (Baillie and Welsh 1980, Shaffer and Sullivan 1988). Turnover rate may be a more important indicator of relative importance (Mann 1988). The higher the rate, the greater the availability to the system. Judging from the turnover rates in Padilla Bay and the area occupied by the benthic primary producers, algal epiphytes of eelgrass are most important, followed by *Z. marina*, SAND/MUD habitat microalgae and *Z. japonica*. Stable carbon isotope analyses of vegetation and animals in the nearshore systems of Hood Canal, an arm of Puget Sound, corroborate the importance of algal derived carbon to that system (Simenstad and Wissmar 1985). Factors such as seasonal peaks in productivity, energy content, grazing effects and spatial and temporal patterns in microbial breakdown ultimately determine the relative importance of the various components to the system. These factors need to be studied in Padilla Bay before we can assign final importance rankings.

It is interesting to compare my results with those of Murray and Wetzel (1987) in a seagrass system at Vaucluse Shores in Chesapeake Bay. In Padilla Bay, sediments contributed 33% of total annual GPP as compared to 10-25% in Vaucluse Shores. Annual GPP (seagrass + epiphytes + sediment) in Vaucluse for the seagrass meadow (1,092 g C m^{-2}) was twice the annual rate for Padilla Bay seagrass (543 g C m^{-2}, *Z. marina* system only). However, the GPP:R ratios were very similar between the two systems (2.0 in Vaucluse and 2.2 in Padilla Bay). Shallow water areas of Chesapeake Bay are nutrient enriched (Davis 1985), and rates of nutrient input probably significantly exceed that for Padilla Bay. The similarity between the GPP:R values suggests that productivity increases are proportionally offset by increased respiration. Tidal factors and water temperature, which were reported by Murray and Wetzel to be 30°C as compared to ca. 19°C in Padilla Bay, may also help explain the differences in productivity and respiration rates.

In Padilla Bay, sediments in the seagrass meadow were heterotrophic, but those on the tidal flats were not. Several factors, including heavier organic loading and greater sediment stability, may account for the lower GPP:R ratios in the seagrass meadow.

Forty-four percent (i.e., based on total system GPP:R = 1.8) of the organic matter produced in Padilla Bay benthic system is exported. For a mudflat-dominated intertidal system near Padilla

Bay (False Bay, San Juan Island), Pamatmat (1968) found that 32% of the annual GPP was exported. For Padilla Bay, roughly 19.5 x 10^6 kg DWT (total annual GPP as carbon x 2.63 g DWT g C^{-1}) of organic material not utilized within the system is available to support the food web adjacent to the system. Padilla Bay represents a dominant shallow nearshore system, with an open connection to deeper areas, in northern Puget Sound and the Straits of Juan De Fuca. Substantial fisheries resources, in particular Pacific herring and Dungeness crab, exist in this region (Evans-Hamilton, Inc. and D.R. Systems, Inc. 1987), and it is probable that the food web including these resources is receiving substantial support from productivity in the Padilla Bay system. The plants in the bay can be viewed as an integrated set of "pumps" that draw energy from the sun and nutrients from the water and sediments, and release organic matter. Some of the component pumps work faster than others, and the quality of material released and pumping rate vary with season. The flow of energy (e.g., Day et al. 1973) within the system and outside the system is in need of study.

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APPENDIX A

LOCATIONS OF SAMPLING TRANSECTS AND SITES

Two transects were established for sampling over the period from June 1987 through May 1988. One of the transects included the sparse *Salicornia* marsh habitat and the sand-mud habitat. The second transect covered the gravel patch. Five additional sites were sampled in July 1987 only. These latter sites were located in sand-mud habitat. The sites were numbered serially 1-23 (see below for distribution) for data management purposes.

Transect 1. The *Salicornia* sand-mud habitat transect was located near the beach access trail located approximately 1.45 km north of the Padilla Bay Interpretive Center. The shore base point (SBP) for the transect was positioned on the seaward face of the wood piling wall (122°28'58"W, 48°30'6"N), at a point 26 m north of the tallest pile in the wall. This latter pile was located almost directly seaward of the seaward end of the dike which runs perpendicular to the face of the cliff. The dike abuts the cliff at a point approximately 30 m north of the base of the beach access trail. The head of the transect (site 1) was positioned 57 m at an angle of 238° mag. from the SBP. Site 1 is in the approximate center of a small, sparse *Salicornia* marsh. The transect ran from site 1 toward the south tip of Hat Island at an angle of 268° mag. The sites were positioned along the this transect as follows:

Sites	Distance (m)
1	0
2	10.4
3	31.4
4	53.9
5	87.5
6	102.5
7	117.5
8	132.5
9	147.5
10	162.5
11	177.5
12	192.5

Transect 2. The first site (site 13) at the upper end of the gravel patch transect was located in the approximate center of a patch of gravel which measured 60 m wide and 105 m long. The patch was located at an angle of 212°mag from the SBP for transect 1, and at 210° mag. from site 1 on transect 1. The patch is approximately 560 m from the SBP.

ADDITIONAL SITES SAMPLED ONLY IN JULY 1987.

Isthmus Sites. Sites 19, 20 and 21 were located on the mudflat seaward of the largest residence on the Padilla Bay side of the isthmus separating the mainland from Samish Island (122°31'00", 48°33'50"). The sites were located along a transect that ran 248° mag. from the house. Sites 19, 20 and 21 were located 90, 202 and 288 m from the seaward face pf the wood piling wall located immediately seaward from the house.

South bay Sites. Sites 22 and 23 were located where the dike road intersects with Bay View-Edison road at a point approximately 0.8 km south (128°28'18", 48°28'44") of the Interpretive Center. Sites 22 and 23 were located 22 and 45 m directly seaward from the face of the dike at a point on the dike approximately 100 m south of the intersection of the dike road with Bay View-Edison Road.