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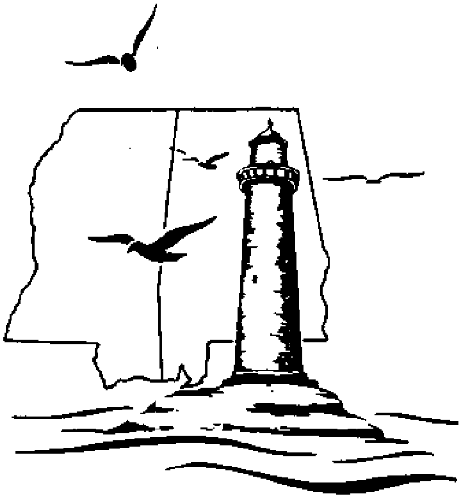

MISSISSIPPI-ALABAMA
SEA GRANT CONSORTIUM

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ABSTRACT

Primary production rates of four autotrophic components in _Halodule wrightii_ Aschers. beds off Horn Island in Mississippi Sound were measured over an annual cycle. The epiphytic algal assemblage on _Halodule_ leaves was dominated by the red alga _Acrochaetium_ _flexuosum_ Vickers and 12 taxa of araphid, monoraphid, and biraphid diatoms. The phytoplankton over the beds and microflora associated with the sandy sediments in which _Halodule_ was rooted were dominated by centric and small pennate diatoms, respectively. Hourly production rates varied from as little as 0.9 mg C/m^2 for _Halodule_ leaves in winter to as high as 1143 mg C/m^2 for epiphytic algae during summer.

Stepwise multiple regression showed that only 15% of the variation in hourly epiphytic algal production could be related to a single environmental variable (i.e. light energy). Variations in hourly production rates for the other three productivity components were best explained by light, water temperature, tidal range, and/or blade density; R^2 for these regressions ranged from 0.66 to 0.94. A single experiment conducted in August revealed that all productivity components exhibited photoinhibition, with the inhibition of the sand microflora and epiphytic algae being the most pronounced. Annual production rates were estimated (g C/m^2) as follows epiphytic algae (905), phytoplankton (468), sand microflora (337), and _Halodule_ (256). As far as the benthic components are concerned, system production is dominated by the microalgae with the contribution of _Halodule_ blades being only 17% of the total. The high standing crops and production rates of the epiphytic and benthic microalgae suggest they may be trophically important for consumers feeding in the beds.

INTRODUCTION

Seagrasses and their associated epiphytes are a unique component of the benthic communities of Mississippi Sound. Seagrass beds in the Sound occur primarily in shallow water (1-2 m) along the nearshore margins of the coastal barrier islands. They may also be found in semi-protected regions of coastal embayments and estuaries where substrate, salinity, and light requirements for the various seagrass species are met (Eleuterius, 1971; Eleuterius and Miller, 1976).

Seagrass beds are constitute extremely productive ecosystems in shallow coastal waters. Their complexity in both structure and function is due to the great diversity and abundance of organisms present. The dominant vascular plants are perennial marine angiosperms termed seagrasses, which are monocots but are not however members of the grass family Poaceae. Seagrasses are rooted in the sediments, which may be either sandy or muddy. Attached to the seagrass leaf blades is a diverse and highly productive epiphytic assemblage, comprised mainly of microscopic algae; this assemblage is dominated by various species of diatoms and red, brown, green, and blue-green algae (Humm, 1964; Ballantine and Humm, 1975; Sullivan, 1979; Thursby and Davis, 1984). Sediments beneath and adjacent to the seagrass beds are carpeted with a microfloral community populated primarily by species of small pennate diatoms. In addition to acting as a substrate for the epiphytic algal assemblage associated with the beds, seagrasses function as habitat for invertebrate and small vertebrate marine organisms. Resident fauna associated with seagrass beds includes copepods, amphipods, isopods, shrimp, crabs, other small crustaceans, gastropods, nematodes, polychaetes, echinoderms, and small fish

(Morgan and Kitting, 1984; Kitting, 1984; Kitting et al., 1984). Recent research indicates that the epiphytic algal assemblage may be the primary food source within this community, as opposed to the seagrasses and the detrital material they generate (Fry et al., 1982; Fry, 1984; Kitting et al., 1984; Nichols et al., 1985; Gleason, 1986; Fry et al., 1987; Dauby, 1989).

Studies of the primary production rates of seagrasses and their epiphytes indicate that the epiphytic component contributes significantly to both primary production and biomass. Reported productivity values for seagrass epiphytes range from 8% to 56% of the total leaf plus epiphyte production (Borum et al., 1984; Morgan and Kitting, 1984). Biomass ranged from as little as 1% to a maximum of 68% of the leaf plus epiphyte total (Borum and Wium-Andersen, 1980; Morgan and Kitting, 1984). The latter values in both cases are from studies done in a southern Texas bay in _Halodule wrightii_ Aschers. beds, where seagrass epiphyte contributions to primary production and to biomass averaged 50% of the total. Preliminary research for this project in _H. wrightii_ beds off Horn Island in Mississippi Sound showed that on a dry weight basis, the standing crop of algal epiphytes can equal or exceed that of the seagrass blades.

The dominant seagrasses in the Gulf of Mexico are _Halodule wrightii_ (shoal grass), _Thalassia testudinum_ König (turtle grass), and _Syringodium filiforme_ Kütz. (manatee grass). Studies of seagrasses conducted in Louisiana, Mississippi, and Alabama are summarized by Eleuterius (1987). Extensive beds of these seagrasses have developed off the northern shores of the offshore barrier islands in Mississippi Sound in the past (Eleuterius, 1971; Eleuterius and Miller, 1976). These beds are assumed to be trophically important to many consumer species in Mississippi Sound, particularly penaeid shrimp and fin fish. Our study was designed to quantitate the production of seagrasses, epiphytic algae, phytoplankton, and sand flora, with the ultimate goal being to evaluate the trophic importance of seagrass beds in Mississippi Sound.

Most research efforts have focused on the productivity and presumed trophic importance of the macroscopic seagrasses themselves; however, recent work has indicated that the epiphytic algae may be the primary basis of the food web in many seagrass ecosystems. Sand-associated microflora within seagrass beds have been virtually ignored. The primary production rates and trophic importance of epiphytic algae in Mississippi Sound's seagrass beds represent a completely unknown entity. Previous joint research on these two factors has been carried out in only one seagrass system in all the world's oceans.

The literature review that follows focuses mainly on marine seagrasses growing in offshore waters. Productivity of algae epiphytic on these seagrasses, possible negative effects of epiphytes on their hosts, and importance of epiphyte productivity in seagrass ecosystems are emphasized.

Epiphytic Algal Production.

The first bona fide study of epiphytic algal production in seagrass beds was carried out by Penhale (1977), who worked in a Zostera marina L. (eelgrass) bed in North Carolina. Utilizing a freeze-drying technique and ^{14}C uptake measurements she found that the epiphytes were responsible for 18% of the total epiphyte plus seagrass leaf production. Photosynthesis of both epiphytes and Zostera blades saturated at irradiances of 600-700 $\mu E/m^2/s$. Epiphyte production reached a maximum in late summer and fall. Of the total epiphyte plus seagrass biomass, 24% was contributed by epiphytic algae.

Borum and Wium-Andersen (1980) showed that the production of epiphytes and Zostera leaves were equal in the Øresund, Denmark. However, epiphyte biomass (36% of the total) was less than that of the macrophyte. The epiphytes greatly reduced light reaching the leaves, and their biomass increased with the age of the leaf and was concentrated on its oldest part (i.e., the upper part). In another Zostera bed in the Øresund, Borum et al. (1984) reported that annual epiphyte production was only 8% (70 g $C/m^2/yr$) of the combined epiphyte plus seagrass total (884 g $C/m^2/yr$). Both studies used the same methodology, but in the latter study, the beds were subject to nutrient limitation. Furthermore, a high grazing pressure limited the epiphyte biomass, which was only 1-5% of the epiphyte plus seagrass total on all sampling dates except one.

In the waters of the Pacific Ocean of Papua, New Guinea, Heijs (1984) studied three monospecific stands of Thalassia hemprichii (Ehr.) Aschers. He considered only epiphyte biomass but made measurements of its total dry weight (DW) and ash-free dry weight (AFDW). On a DW basis, epiphytes were responsible for 29-42% of the total biomass, but these figures dropped to 13-15% for the epiphytes on an AFDW basis. Inorganic carbonates and sediment incorporated in the epiphytic mat were responsible for the differences. Since virtually all workers have measured DW, it is likely that the epiphytic algae are even more productive than reported when such estimates are related to biomass.

Morgan and Kitting (1984) found that epiphytes in Halodule wrightii beds at two sites in a southern Texas bay were extremely productive. Epiphyte contribution to total production was 48 and 56% at the two sites; the algae were responsible for 19-68% (x = 50%) of the total biomass. The maximum contribution of epiphytes to biomass was correlated with reduced leaf growth. These findings led to the conclusion that epiphytes are a relatively more important productivity component in semi-tropical seagrass beds than in cooler temperate beds. Both epiphyte and Halodule photosynthesis saturated at 1100 $\mu E/m^2/s$. This value is greater than the 250-700 $\mu E/m^2/s$ range reported by Penhale (1977), Borum and Wium-Andersen (1980), and Mazzella and Alberte (1986) in more northerly seagrass beds. This difference may result from both warmer temperatures and higher insolation levels in the Texas beds, and could prove to be a general phenomenon in semi-tropical seagrass systems, but more data is needed to establish this conclusively.

Mazzella and Alberte (1986) studied the photosynthesis-irradiance (P-I) relationships for Zostera marina and its epiphytes along leaf blades. P_{max} increased nearly two-fold along the leaf axis from base to tip; age of the leaf tissue was found to be more important than light in determining P-I responses. Saturation occurred at 300 $\mu E/m^2/s$ and no photoinhibition was observed at irradiances up to 1400 $\mu E/m^2/s$. Even lower segments of the leaves, which never experienced light levels greater than 500 $\mu E/m^2/s$, exhibited no photoinhibition. On an areal basis, epiphytes contributed 27-50% of the total epiphyte plus Zostera production.

In summary, studies of epiphyte production in seagrass beds are limited in number, concentrating on only a few seagrass species, mainly Zostera marina. Production and biomass of the epiphytes associated with these seagrasses may exceed that of their seagrass hosts, representing a productivity component that may be highly underrated. Knowledge of the production rates of epiphytes and their contribution to total epiphyte plus seagrass production is extremely limited for semi-tropical seagrass beds such as those found in the northern Gulf of Mexico.

Effects of Epiphytes on Seagrasses.

Epiphytes are generally considered to have negative effects on their hosts. A comprehensive summary of the literature dealing with the effect of epiphytes on seagrasses can be found in Table 1 of a publication written by van Montfrans et al. (1984). The most often cited effect is a reduction in the photosynthetic rate of the seagrass leaves. Epiphytes may decrease seagrass photosynthesis by reducing light intensity (shading effect) and/or acting as a barrier to inorganic carbon uptake by the leaves (diffusion barrier). In experimental studies of a Zostera marina bed, Sand-Jensen (1977) showed that epiphytes reduced Zostera photosynthesis by up to 31% at optimum light conditions and ambient bicarbonate concentrations. Under conditions of constant light, Zostera photosynthesis was reduced by 45% when bicarbonate concentrations were lowered from 1.7 meq/l (ambient level) to 0.2 meq/l. However, epiphyte photosynthesis on the Zostera blades was unaffected by varying carbonate levels. Epiphytes reduced both optimum photosynthesis and the initial slope of the P-I curve when intact leaves and those with their epiphytes removed were compared. Epiphyte photosynthesis saturated at lower light levels than did that of the Zostera blades.

Morgan and Kitting (1984) found that epiphytes were nearly twice as productive as Halodule wrightii at irradiance values ranging from 300-800 $\mu E/m^2/s$, and suggested that epiphyte contributions to community production are likely even more important in deeper or turbid water or during cloudy weather. Such data suggest that epiphytes are more efficient than macrophytes in capturing light energy at levels characteristic of the submerged habitats in which the beds are found.

Epiphytes have been shown to decrease both vegetative and reproductive growth in seagrasses. Bulthuis and Woelkerling (1983) demonstrated that epiphytes decrease biomass accumulation by the leaves of the Australian seagrass Heterozostera tasmanica (Aschers.) den Hartog. Epiphyte biomass accumulated at a sufficient rate to significantly reduce the time in which positive net photosynthesis by the leaf was possible to less than one-half of the leaf life span.

Howard and Short (1986) grew Halodule wrightii in experimental tanks with and without invertebrate grazers. Epiphytes flourished in tanks free of grazers, but were greatly reduced when grazers were present. After three months, growth of ungrazed Halodule, measured as above- and below-ground biomass and shoot density, was significantly less in the presence of abundant epiphytes than in the presence of reduced epiphytes in the grazed treatment.

In some instances, epiphytes have caused a severe decline or even elimination of seagrasses from a locality. Such incidents are apparently the result of nutrient enrichment. Silberstein et al. (1986) provided evidence that loss of the seagrass Posidonia australis Hook. f. in Cockburn Sound, Western Australia, was caused by sewage enrichment, this effect being mediated through the epiphytes. Epiphyte loads, expressed as dry weight per unit leaf area, were two to eight times higher at the impacted site than at a site exposed to clean oceanic water. Shoot growth was 33% lower and the beds were 29% less dense at the impacted site. Light attenuation by the epiphytes was 63 and 15% at the impacted and "clean" sites, respectively. The data of Neverauskas (1987) are similar for declining seagrass beds near Port Adelaide, South Australia. Seagrasses were completely lost from an area of 365 ha four years after sewage dumping began; effects were discernible over an area of

1900 ha. All impacted seagrass beds were characterized by unusually heavy growths of epiphytes.

In a freshwater habitat, thick coatings of epiphytic diatoms on the pondweed Potamogeton crispus L. were as productive as their macrophyte hosts, based on oxygen microelectrode measurements (Sand-Jensen et al., 1985). The authors considered the epiphytes a severe stress to macrophyte metabolism because of their shading effect and their generation of anoxic conditions at the macrophyte surface under dark conditions and a combination of high O_2 and low CO_2 concentrations in the light. Epiphytes on the freshwater angiosperm Lobelia dortmanna L. decreased light levels by 67-82% at a depth of 0.5 m (Sand-Jensen and Borum, 1984). This attenuation was spectrally selective; percent transmittance of red light increased as epiphyte density increased. Epiphyte light attenuation and reduction of Lobelia photosynthesis were proportional at low light levels but independent in saturating light.

Epiphyte effects on photosynthesis appear to determine the depth distribution of freshwater macrophytes. Sand-Jensen and colleagues worked with two aquatic angiosperms (Lobelia dortmanna and Litorella uniflora (L.) Aschers.) that take up inorganic carbon from the sediment through their roots; hence, epiphytes interfere mainly with light conditions (Sand-Jensen and Borum, 1984; Sand-Jensen and Søndergaard, 1981). In both cases, the epiphytes severely shaded the macrophyte and limited its depth distribution. The depth limit for Lobelia was 1.0 m in a Danish lake but was calculated to 3.5 m in the absence of epiphytes, based on light compensation point data for the macrophyte (Sand-Jensen and Borum, 1984). It was also concluded that light attenuation by epiphytes was important in the seasonal growth of macrophytes.

In marine environments, it has been demonstrated that seagrasses are not completely at the mercy of their epiphytes. Their defensive strategy involves a rapid production and turnover of new photosynthetic tissue (Orth and van Montfrans, 1984). Heavily epiphytized leaves are sloughed off and replaced by young, rapidly growing leaves which are at least initially free of epiphyte fouling. Some representative life spans for seagrass leaves are 50 (summer) and 200 (winter) days for *Zostera marina* (Borum et al., 1984) and 37 days for *Halodule wrightii* (Morgan and Kitting, 1984). The shorter the life span of the leaf, the less time available for epiphyte colonization and growth.

Several studies did not find detrimental effects of epiphytes on marine macrophyte photosynthesis (Morgan and Kitting, 1984; Borum et al., 1984; Mazzella and Alberte, 1986). In two of these studies, epiphyte and seagrass production were approximately equal. Epiphytes would then greatly enhance the overall production of seagrass bed systems in such cases.

The presence of a heavy coating of epiphytes generally has negative effects on the photosynthetic rate and growth of seagrasses. Such effects are most pronounced under low light conditions (deeper water or turbidity) since epiphytes tend to saturate at lower irradiances than their hosts, are more photosynthetically efficient, and are apparently not limited by inorganic carbon supplies.

Grazing of Seagrass Epiphytes.

Grazing of epiphytes by a wide variety of organisms is a universal phenomenon in seagrass beds from widely separated localities (van Montfrans et al., 1984). Van Montfrans et al. (1984) summarized relevant studies conducted up to 1984. The major groups of grazers are gastropods, amphipods, isopods, decapods, polychaetes, echinoderms, and fish.

In a novel approach in Texas seagrass beds, Kitting (1984) used remote time-lapse photographic sampling coupled with microacoustical monitoring and immediate, high-resolution gut content analysis to determine when, where, and often what each invertebrate species was eating. Feeding occurred most frequently at night while various invertebrates were among the epiphytic algae, not while they were on the bottom detritus. Particular ephemeral algal taxa (i.e., the early successional forms on the leaf blades) were generally selected over all other foods, including seagrass leaves.

Morgan and Kitting (1984) found that epiphytes accounted for the major fraction of recognizable stomach contents of common seagrass bed invertebrates in southern Texas. Invertebrates monitored included grass shrimp (Palaemonetes), crabs (Callinectes), snails (Anachis, Bittium), and amphipods (Cymadusa). Diatoms and filamentous and coralline red algae were the most abundant stomach contents. Little seagrass appeared in stomachs, although intact seagrass was readily available. Night photography revealed that grazers were all found primarily among epiphytes on the middle or tips of seagrass blades where diatoms and red algae were most common; this was also where most feeding motions were observed.

Photographic sampling was also used by Dirnberger and Kitting (1988) in a Halophila decipiens Ostenfeld meadow to further demonstrate that grazing in seagrasses is primarily on epiphytes, even at depths greater than 20 m. In open Halophila meadows, only approximately 2% of leaf blade tissue was ever eaten by grazers.

Highest densities of motile epifauna on Halodule wrightii blades were observed by Howard (1987) at night. He did find, however, that the structural similarity of day and night epifaunal assemblages in the seagrass canopy ranged from 95 to 98%.

Further evidence supporting the concept that detrital material is little-used by organisms inhabiting seagrass beds was collected by Blum et al. (1988). Microbial biomass was present on seagrass detritus at very low levels, making it unlikely that detritovores can rely solely on microorganisms as an energy source.

The removal of epiphytes through grazing activities has beneficial effects on their seagrass hosts. As previously mentioned, Howard and Short (1986) showed that a rapid and heavy buildup of epiphytes occurred on Halodule wrightii blades grown in experimental tanks devoid of invertebrate grazers. They hypothesized that reduction of epiphytic biomass by grazing results in enhanced vigor of the host seagrass and furthermore that grazing is an important factor in the maintenance of seagrass production, growth, and depth distribution, particularly in environments in which seagrasses are light- and nutrient-stressed.

Invertebrate grazing increased with age of Zostera marina leaves and the epiphyte biomass they supported in Roskilde Fjord, Denmark (Borum, 1987). Zostera leaves were monitored for 40 days; exclusion of grazing species significantly increased epiphyte biomass. It was estimated that epiphytes contributed four to five times more to total aboveground production in the Zostera bed than was indicated by their biomass contribution because of their constant removal by grazers. In the absence of grazing, Borum calculated that, with all other factors held constant, epiphyte biomass would have been 10 times higher than was actually measured in unprotected Zostera beds. Grazing was the major factor accounting for algal biomass loss and was much more important than sloughing of seagrass leaves.

As discussed above, epiphyte biomass reduction through grazing increases the amount of light energy available to seagrasses and lessens any effect epiphytes might have in acting as a barrier to diffusion of inorganic carbon into the leaf tissue. In general, seagrasses depend upon epiphyte removal through grazing to maximize their production, growth, and reproductive success (van Montfrans et al., 1984). As Orth and van Montfrans (1984) have stated, the ultimate success of seagrasses is determined by the quality and quantity of light reaching the leaf surface; therefore, epiphyton grazers may represent a crucial element for determining light penetration in those areas where they are abundant. One might hypothesize that any structural or biochemical adaptations present in seagrasses that might serve to attract potential grazers would be highly selected traits. This aspect of seagrass biology has not yet been investigated to the authors' knowledge.

Superimposed on all these patterns are seasonal changes in environmental conditions and the densities and types of epiphytes and grazers present. Furthermore, these factors are coupled with seasonal cycles of growth and reproduction in the seagrasses themselves. This is yet another area that has received little study to date.

Sand Microflora Within Seagrass Beds.

The role of benthic microalgal production in seagrass bed sediments has been largely overlooked. The seagrasses themselves have often been examined as the major component of primary production, when in fact the benthic microalgae are more easily incorporated by consumers as a direct source of energy (Murray and Wetzel 1987). The few studies which have examined their production dynamics have found that their contribution to total system production varies greatly. Invertebrates depend on the resident algae for much of their carbon (Kitting et al. 1984). Thayer and LaCroix (1971) found that the epibenthic invertebrates assimilated 12.3 % of the estimated daily net production of benthic algae, phytoplankton, and eelgrass (Zostera) in a northeastern embayment.

Pomeroy (1960) found that the contributions of Thalassia, phytoplankton, and sediment-associated microalgae were equal in water depths less than 2 m in Boca Ciega Bay, Florida. The mean gross primary production of the benthic microalgae and Thalassia was 130 and 80 mg O_2/hr, respectively. At a 3-5 m depth, phytoplankton were the dominant primary producers, followed by benthic microalgae and then Thalassia. Surprisingly, Pomeroy found production rates were equal for Thalassia leaves with intact epiphytes and those that had their epiphytes removed. This, however, could indicate that seagrass production was reduced by the covering of epiphytes, as discussed previously.

Heffernan and Gibson (1983) studied seagrass, epiphyte, benthic microalgal, and phytoplankton production at three sites during spring and summer in the Indian River, Florida. In general, seagrasses and sediment microalgae were the most important productivity components. The contribution of the latter to total system production ranged from 3 to 85%.

Jensen and Gibson (1986) compared the production rates of seagrasses, epiphytic algae, sediment microalgae, and phytoplankton from two Florida sites and one in the Bahamas. The seagrasses Halodule wrightii, Syringodium filiforme, and Thalassia testudinum were present in varying proportions at all three study sites. In general, production rates of the first three autotrophic components were similar in each location; contributions of the phytoplankton varied greatly. In the two Florida sites, which had high nutrient concentrations, the contribution of the phytoplankton was 58 and 72%. In the pristine ocean waters off the Bahamas, the phytoplankton were responsible for only 8% of the total community production. Epiphytes and their seagrass hosts were equally productive when comparisons were made on a dry weight basis, irrespective of the specific identity of the seagrass or location.

In a Virginia Zostera bed, Murray and Wetzel (1987) determined that 14% of total annual production (seagrass, epiphyte, phytoplankton, and benthic microflora) was attributable to sediment-associated microalgae. In a Ruppia maritima L. bed in this same locale, the benthic microflora was responsible for 10% of the total production. Annual production rates for benthic microflora in the Zostera and Ruppia beds were 225 and 106 g C/m^2, respectively. It should be noted that in this study the productivity rates of seagrass and epiphytes were not separated but rather estimated together by subtracting sediment and phytoplankton rates from those measured for the total community beneath large plexiglass chambers.

The major objective of the present study was to begin to assess the importance of seagrass communities in Mississippi Sound. To accomplish this, we attempted to quantitate the temporal and spatial production of epiphytic algae and their macrophyte hosts in a representative seagrass bed system in the Sound. Environmental factors potentially most important in regulating seagrass and epiphyte production were monitored during in situ experiments for development of hypotheses and predictive models. Functional importance of epiphytic algae in seagrass bed energetics was assessed by comparing their production rates to those of the host seagrasses. Finally, the relative contributions of epiphytic algae, seagrasses, phytoplankton, and sand-associated microflora to total community primary production were determined.

DESCRIPTION OF STUDY AREA

Climate.

The Gulf Coast region is characterized by high humidity, long warm summers and short mild winters; it is classified as being semi-tropical. Other than brief winter intrusions of polar continental air, moist tropical air predominates over the area. Air temperatures generally range from 50.6 to 81.9°F (10.3 to 27.7°C), with extremes ranging from -1 to 106°F (-18.3 to 41.1° C). Mean annual air temperature is 66.7°F (19.3°C); mean humidity is 78%. Mean annual precipitation averages about 60 inches (154.2 cm), resulting primarily from a typical number of 75.7 days with thunderstorms. Winds are generally from the SSE with a mean velocity of 6.5 mph (10.4 kph). October is usually the driest month of the year; July is the wettest (ONWI, 1983).

The occurrence of tropical storms and hurricanes is a major feature of Gulf Coast weather, with an average of one tropical cyclone event impacting the state every two years, of which one every four years is a hurricane (Simpson and Lawrence, 1971).

Geographic Setting.

Horn Island is one of the five islands comprising the barrier island chain off the Mississippi coast. The island extends roughly 14 miles (22 km) from Dog Keys Pass at its western extremity (N 30°15 , W 88°45) to Horn Island Pass at its eastern end (N 30°13 , W 88°32). From the coastline south of Ocean Springs, the island lies 7 miles (11 km) offshore in Mississippi Sound, separating the waters of the Sound from the Gulf of Mexico. At its widest point, the island is 1 mile (1.6 km) across; it measures less than a tenth of a mile across (0.16 km) at its narrowest point.

Horn Island is hydrologically affected by drainage from the Biloxi Back

Bay, the Biloxi River, and the Pascagoula River; degrees of influence are a function of discharge rates and prevailing winds. Upland drainage from the island proper is a very minor factor, as the island is a sand formation and all rainfall tends to percolate into the local water table or accumulates as runoff in a series of island lagoons and marshes.

Astronomical tidal range is 2 feet (0.6 m); the effects of wind on local hydrodynamics generally overrides this and tends to determine local water depth and surface level fluctuations.

Soils.

Horn Island's soils are dominated by sands of varying grain size at its margins and out into the surrounding waters along the northern shore where the island adjoins Mississippi Sound. This sand contains varying amounts of plant detritus and debris of both plant and animal origins resulting from mechanical action of the surf and bioperturbation by various organisms. Degree of sorting of sand material is a function of these physical and biological activities. The sand is characterized by an upper oxygenated layer, the thickness of which depends on wave action, ambient water temperature and oxygen concentration, salinity, and biological activity. Beneath this oxygenated layer is a gray to black layer of anoxic sand and silt, rich in material of biological origin. Dramatic shifts in salinity can result in a die-off of the organisms "cementing" the microlayer of surface sand together, resulting in rearrangement of the sand surface and a marked increase in the depth of the oxygenated layer.

Flora.

Horn Island's vegetation features salt-tolerant plants common on beach fronts, marsh plant associations, and stands of slash pine (Pinus elliotii

Englmn.). On the side of the island bordering Mississippi Sound, sand flats adjacent to the shoreline are sparsely populated by beds of the marine angiosperm *Halodule wrightii*. More protected sand flat regions of the shoreline feature denser, larger, and more closely spaced seagrass beds. In addition to this vascular vegetation, a diverse aquatic flora exists throughout the water column in the form of phytoplankton, epiphytes on the seagrasses, and a microscopic plant community associated with the sand surface, dominated by diatoms.

Fauna.

The island proper is inhabited by seasonal and resident bird populations, re-introduced populations of red wolves and rabbits, and other small mammals. Alligators, snakes, nutria, and muskrats inhabit the marshes of the island. Large populations of insects and other invertebrates are found throughout the island's several habitats.

Waters surrounding the island are home to a variety of invertebrates; the most visible of these are several species of snails, crabs such as the hermit crab (*Clibanarius vittatus*), sand dollars, and starfish. Vertebrate species in the water include a number of commercial and non-commercial finfish species, small sharks, and porpoises.

Utilization.

Horn Island is part of the Gulf Shores National Seashore and is thus a protected resource area. The Department of Wildlife and Fisheries maintains a Ranger's outpost on the island. It is also used as a site for research on the red wolf (the island population is an experiment in reestablishment). Primary use of the island is recreational; it is a favorite location for birding, fishing, boating, beachcombing, and camping.

METHODS AND MATERIALS

Sampling Strategy.

Representative seagrass beds were chosen along the western end of Horn Island where the presence of seagrass communities was observed during preliminary studies in 1988 (Fig. 1). These beds are composed exclusively of *Halodule wrightii* and are extremely persistent, having survived both extended periods of low salinity and hurricanes. All three seagrass species dominant in the northern Gulf of Mexico have been documented in the past in this area, occurring in distinct zones or colonies (Eleuterius and Miller, 1976). Only *H. wrightii* occurs in this region at present; occurrence of hurricanes can decimate seagrass beds, as can poor water quality (Larkum et al., 1989). Disappearance of two historically present seagrass species from the study area limited the scope of the research.

Extensive development of the epiphytic flora was observed on seagrass blades; collections of *Halodule*, *Syringodium*, and *Thalassia* leaves made by Sullivan (1979) in July 1977, plus those of *Halodule* made in preliminary studies during 1988, yielded blades so overgrown with epiphytic algae that the green color of the seagrass leaves was essentially undetectable.

Sampling was attempted on a monthly basis, beginning in May 1989 and concluding in August 1990. Vagaries of the environment and equipment breakdown (i.e., lack of a suitable boat) prevented sampling during months for which no data is presented. Three adjacent beds were selected for productivity measurements during each month samples were collected; different set of beds were used on consecutive trips. Beds were selected on the basis of visual estimates of size, stem density, and degree of epiphytization, relative to all beds visually inspected in the area.

Recreational use of the study area prohibited the placement of permanent markers in beds used in the study; prominent vegetation and geographic features on the island proper were used as visual markers to avoid repeated samplings in the same seagrass beds. This approach allowed for measurements to be made in the same area, eliminating possible perturbation effects due to use of seagrass beds for two successive sampling dates.

Seagrass and Epiphyte Biomass Measurements.

Aboveground live biomass for each of the three *Halodule wrightii* beds was estimated by the method of Morgan and Kitting (1984). Two 10 x 10 cm quadrats were randomly selected in each bed. All seagrass blades from each quadrat were clipped at the sediment surface. Samples were stored on ice for transport from the study area to the laboratory. Upon return to the laboratory, the leaves were rinsed with fresh water for salt removal and dried at 60°C to a constant weight, yielding a total combined dry weight for seagrass leaves and their associated epiphytes on an areal basis. Ten or more blades were selected at random from these samples to determine the relative contribution of each component. Epiphytes were scraped from these blades and the dry weights of epiphytes and seagrass blades determined separately. Their ratio was used to estimate g dry wt/m^2 for the seagrass and the epiphyte component from the total biomass determinations.

Epiphytic Algal Primary Production.

The protocol employed for measurement of epiphytic algal production used selected aspects of the methods of Penhale (1977), Penhale and Smith (1977), Morgan and Kitting (1984), and Jensen and Gibson (1986), with certain modifications. Primary production as ^{14}C uptake was measured simultaneously for both seagrass leaves and their epiphytes in the field. This eliminated the problems associated with simulation of field conditions in the laboratory and those involved with measurements made on scraped seagrass blades and suspensions of epiphytes. Individual leaves with their attached epiphytes were clipped near their bases and incubated in clear 70 ml glass test tubes containing 5 μCi of $NaH^{14}CO_3$ for 3 hr. The number of blades incubated per jar and their degree of epiphytization were chosen on each sampling date so as to approximate existing conditions in the beds (Morgan and Kitting, 1984). A total of six incubations was carried out in each of the three beds. Five of these were incubated with isotope only; the sixth received isotope plus 10^{-5} M dichlorophenyl dimethyl urea (DCMU) dissolved in distilled water. Addition of DCMU to ^{14}C incubations allows estimation of inactive uptake of the isotope (Legendre et al., 1983). Values for the DCMU treatments were subtracted from those for isotope only when calculating uptake rates. All samples were incubated _in situ_, placing them back in the seagrass bed under ambient conditions of light and temperature. Uptake of ^{14}C at the end of each incubation period was stopped by the addition of buffered 4% formalin. Samples were transported to the laboratory on ice.

Upon return to the laboratory, samples were held at 4°C until processing (within less than one week after collection). Seagrass leaves and attached epiphytes were removed from the test tubes and washed with 10% HCl onto 0.45 μm nitrocellulose filters to remove unincorporated adsorbed label and to trap loosely attached epiphytes. Seagrass blades were removed from the filtration apparatus and the epiphytes scraped off the blades with a dissecting knife; the epiphytic material thus obtained was rinsed onto the filters containing the loosely attached epiphytes, combining them for the epiphyte sample.

Penhale (1977) and Morgan and Kitting (1984) reported high removal efficiencies (>90%) using scraping techniques for Zostera marina and Halodule wrightii epiphytes, respectively. Microscopic examination of similarly treated unlabelled seagrass blades and epiphytes indicated similar efficiencies of removal. Epiphyte samples were subjected to cold HNO_3 digestion for a minimum of 48 h to homogenize the labelled organic matter, using a modification of the technique outlined by Van Raalte et al. (1974). Prepared samples were counted using a Beckman LS 3801 liquid scintillation counter programmed for "wide-window" counting (color and chemical quench correction). Counts (disintegrations per minute) were converted to uptake rates expressed as mg C/seagrass blade/hr and mg C/g dry wt seagrass/hr for epiphytes using modifications of the formulas of Penhale (1977). These rates were used to estimate areal rates for epiphyte production (mg C/m^2/hr) by multiplying the weight specific hourly rates by the biomass determinations for each bed (Jensen and Gibson, 1986).

Seagrass Blade Primary Production.

The protocol used for seagrass blade production estimates was identical to that used for the epiphytes, as samples were incubated intact. Individual leaves were incubated with their attached epiphytes as described above. Morgan and Kitting (1984) found that clipped Halodule blades continued to grow for a week in the lab and concluded that clipping effects on production were negligible for the short incubation times used. Blades incubated per jar were selected to mimic existing conditions in the beds (Morgan and Kitting, 1984). As stated above, a total of six incubations was carried out in each of the three beds; five of these received the isotope only. The sixth chamber received isotope plus 10^{-5} M DCMU (Legendre et al., 1983). As with the epiphyte samples, values for the DCMU treatments were subtracted from those containing isotope to account for inactive uptake.

Processing of seagrass leaves has been described in detail in the section on epiphytic algal primary production. Seagrass blade samples were subjected to cold HNO_3 digestion ($\geq$ 48 h) to homogenize the labelled plant tissue (Van Raalte et al., 1974). Prepared samples were counted as described for the epiphyte samples. Counts (dpm) were converted to uptake rates expressed as mg C/seagrass blade/hr and mg C/g dry wt seagrass/hr for the seagrass leaves. These rates were converted to areal rates for seagrass production (mg C/m^2/hr) by multiplying the weight specific hourly rates by the biomass determinations for each bed (Jensen and Gibson, 1986).

Sand Microflora Primary Production.

Primary production of the sand microflora was measured by a ^{14}C uptake technique described by Van Raalte et al. (1974) for edaphic salt marsh algae, with certain modifications. Six sediment cores were randomly taken within each bed on each collection date with a modified 2.1 cm diameter disposable syringe. It is important to note here that the cores were taken below the canopy of Halodule wrightii leaves and not immediately adjacent to the beds. Each core was taken to a depth in excess of 1 cm. The excess (i.e. that amount over 1 cm) was extruded and discarded. The upper 1 cm of each core was placed directly into a clear glass incubation chamber to which 1 ml of labeled $NaH^{14}CO_3$ (5 μCi/ml) and 9 ml of unfiltered Mississippi Sound water were added. Five of the cores received the isotope only while the sixth received dichlorophenyl dimethyl urea (DCMU) at a concentration of 10^{-5} M prior to isotope addition (Legendre et al., 1983). DCMU is a herbicide which inhibits the operation of Photosystem II and thus active carbon uptake, generating a "blank" for determination of absolute active uptake of ^{14}C. DCMU values were subtracted from those values measured in cores that received the isotope only. The incubation chamber was sealed and returned to the site of collection and secured to the sand substrate for an <u>in situ</u> incubation period of 3 hr. At the end of the incubation period, buffered formalin was added at a concentration of 4% to stop isotope uptake. Cores were then sealed, transferred on ice back to the laboratory, and stored under refrigeration until processing. All samples were processed within one week of their collection.

In the laboratory, cores were removed from the incubation chambers by washing them onto 0.45 μm nitrocellulose filters. Each sample was then washed with a minimum of 50 ml of 2% HCl under a fume hood to remove the surface adsorbed and unincorporated $NaH^{14}CO_3$. The filter containing all core material was placed in a 125 ml wide mouth Erlenmeyer flask for digestion. Digestion was accomplished by adding 10 ml of concentrated HNO_3 and allowing the mixture to stand for 4 hr under a fume hood. The digested samples were decanted into 15 ml polyethylene tubes and centrifuged for 10 min at 1000 rpm. A 1 ml subsample of the supernate was added to 9 ml of 0.75 M tris buffer. One ml of this preparation was combined with 10 ml of a scintillation cocktail (3a70 LS Cocktail, Isolab). As with all other ^{14}C samples, these samples were also counted using a Beckman LS 3801 liquid scintillation counter programmed for "wide window" counting. Count rates were then converted to hourly rates of carbon uptake via a combination of formulas given by Strickland and Parsons (1972) and Leach (1970); a factor of 1.064 was employed to correct for differential uptake of ^{14}C. Since unfiltered Mississippi Sound seawater was used in the incubations, phytoplankton production was subtracted from the total measured uptake in the incubation chambers.

Sand Flora Chlorophyll Determinations.

Biomass of the sand microalgae was estimated as chlorophyll (chl) *a* concentrations. Five sediment cores were taken within each seagrass bed immediately adjacent to the exact sites where the production cores receiving the isotope only were taken. Biomass samples were collected using sharpened aluminum corers (1.6 cm inside diam x 5 cm length). The cores were sealed in aluminum foil and transported back to the laboratory on ice and immediately frozen. Determination of chl *a* in the top 1 cm of each core consisted of a standard acetone (100%) extraction followed by spectrophotometric readings before and after acidification with concentrated HCl to correct for any pheopigments that may be present (American Public Health Association, 1985).

Phytoplankton Primary Production.

Protocol for determination of phytoplankton production was primarily based on the methods of Strickland and Parsons (1972), with modifications for use of DCMU to compensate for inactive uptake (Legendre et al., 1983). Water samples, collected from immediately above the seagrass beds, were incubated *in situ* in clear 300 ml borosilicate glass BOD bottles, to which 5 μCi of $NaH^{14}CO_3$ had been added, for a period of 3 hr. A total of three incubations was carried out in each of the three beds. Two of these were incubated with isotope only; the third received isotope plus 10^{-5} M dichlorophenyl dimethyl urea (DCMU) dissolved in distilled water. Values for the DCMU treatments were subtracted from those for isotope only when calculating uptake rates. All samples were incubated *in situ*, placing them back in the seagrass bed under ambient conditions of light and temperature. Uptake of ^{14}C at the end of each incubation period was stopped by the addition of buffered 4% formalin.

Samples were transported to the laboratory on ice.

Upon return to the laboratory, samples were held at 4°C until processing (within less than one week after collection). Samples were drawn down onto 0.45 μm nitrocellulose filters and washed with 10% HCl onto to remove unincorporated adsorbed label. The filters were allowed to dry completely prior to addition of an LSC cocktail for counting. Prepared samples were counted using a Beckman LS 3801 liquid scintillation counter programmed for "wide-window" counting (color and chemical quench correction). Counts (dpm) were converted to uptake rates expressed as mg C/m^3/hr. These rates were used to generate correction factors to account for uptake of ^{14}C by phytoplankton present in seagrass and microalgal samples, and as estimates of phytoplankton production.

Microalgal Floristics.

On all collection dates, samples were procured for taxonomic examination to determine the dominant algal taxa present in each productivity component. Phytoplankton were sampled using a 26 μm mesh Nitex plankton net towed by hand over the seagrass beds for 2 min.; care was taken to keep the net below the surface yet sufficiently above the seagrass beds to avoid the introduction of loosely attached epiphytes from the seagrass beds themselves. Epiphyte samples were obtained as subsamples of the material clipped from the beds for the ^{14}C incubations. On each sampling date, the dominant non-diatom algal taxa within each of the three seagrass beds were determined from the examination of both fresh material and material preserved with 4% formalin. This data indicated which algal taxa made the major contributions to epiphytic biomass and production. Additionally, subsamples of seagrass blades from each bed were processed with hot HNO_3 as described by Sullivan (1979) to obtain cleaned diatom frustules for taxonomic identification and enumeration.

Sand microflora were sampled as described in the following subsection; the collection method is identical to that described for the chlorophyll samples. However, the cleaning technique employed differs from that used for preparation of diatom samples from epiphyte subsamples. An additional sediment sample was collected and fixed immediately in the field with 2% glutaraldehyde to allow for determination of the presence of any non-diatom algae.

Collection and Processing of Diatom Cores.

Three sediment cores were randomly taken within each seagrass bed with an aluminum corer (1.6 cm inside diam x 5 cm length). In the laboratory, diatom frustules were harvested from these cores by taking the upper 1 cm of each core and placing it in a beaker containing 25 ml of 30% H_2O_2 and 0.5 ml concentrated HNO_3 and allowing it to sit overnight. Rao and Lewin (1976), Round (1979) and Lukatelich and McComb (1986) found this to be a sufficient depth to adequately sample sand diatoms.

During preliminary tests, an H_2O_2 solution was found to clean the diatoms as effectively as boiling in dilute or concentrated HNO_3. The immersed sample was agitated gently until gas was no longer evolved. At this point the solution was again agitated until both sand grains and diatom frustules were suspended in solution and the sand grains were then allowed to settle. The supernate was quickly poured off and saved. The sand grains were rinsed with 5 ml of distilled water and the supernate added to the first solution. This procedure was repeated 5 times. The sand grains were saved to determine the effectiveness of the cleaning process. The supernate (now 50 ml) containing the diatom frustules was allowed to settle for a period of not less than 4 hr; at this point the supernate was decanted gently up to the point where the diatom frustules could be seen moving towards the edge of the beaker (ca. 5 ml solution remains). Then 50 ml of distilled water was added to the beaker and the contents allowed to settle again. This step is used to limit the oxidizing effect of H_2O_2 on the diatom frustules and was repeated 5 times.

The diatom frustules were mounted on glass slides by removing an aliquot of sample (the amount varied with the abundance of diatoms) from the beaker and placing it on a cover slip which was placed over a low heat source. A drop of acetone was added to the sample prior to evaporation to reduce clumping of the frustules. Once all the water was evaporated, the cover slip was inverted and placed on a slide containing sufficient Hyrax (Custom Research and Development, Inc., Auburn, CA) to mount the sample. The slide was then placed on a separate heat source to drive off the solvent (toluene). The cleaned and mounted sample was then ready for microscopic examination.

Photoinhibition Study.

A preliminary estimate of the effects of light levels on primary productivity rates for the four production components was made on 7 August 1990. Techniques used for this study were identical to those previously described. A total of three samples for each autotrophic component was employed for *in situ* incubations at six illumination levels. Samples were incubated for 1 hr. Samples were incubated at the bottom, at 2/3 and 1/3 of the water column depth, and at the surface. One set, covered with shade cloth and placed on the bottom, experienced the lowest light levels. A final set was incubated in a shipboard compartment for the highest light level.

Environmental Factors.

During the course of ^{14}C incubations within each seagrass bed, the following environmental factors were monitored: photosynthetically active radiation (PAR) reaching the leaves and epiphytes, water temperature, salinity, sea state, turbidity, and current speed. These factors were chosen as being most likely to affect spatial and temporal variations in seagrass and epiphyte production rates and biomass. Additionally, predicted tidal range was recorded for each sampling date from published tide tables (MS-AL Sea Grant, 1989). Sediment samples were collected from within each seagrass bed on the majority of the collection dates for determination of sand grain sizes (sediment particle analysis) as an additional factor that could have potential effects on sand microfloral production rates.

PAR was measured using a Li-Cor Quantum Radiometer Photometer Model No. LI-185B (Li-Cor,Inc., Lincoln, NE), equipped with an underwater sensor. This instrument detects the visible wavelengths of light that are most critical in primary production. Measurements were made both at the surface (full sunlight) and immediately above the seagrass bed canopy; the latter measurement was used in all regression analyses.

Water temperature within the seagrass beds was measured using a YSI Model 33 CST meter (Yellow Springs Instrument Co., Yellow Springs, OH). Salinity was determined using a refractometer. Sea state was visually assessed and recorded at the beginning and end of each trip, with any major changes and their time of occurrence being noted. Turbidity was measured as Secchi depth and was recorded to the nearest 5 cm. Current speed was measured using a General Oceanics Model 2030 digital current meter, equipped with a low-speed rotor (General Oceanics, Inc., Miami, FL).

Sand grain sizes were estimated as proportions of the total sample on a dry weight basis; sizes selected for separation ranged from 0.5 mm to 63 μm. Samples for sediment particle analysis (upper 4 cm of sediment) were collected within each of the three seagrass beds on most collection dates. The three samples for each date were combined and oven-dried at 60°C to a constant weight, then stored in a moisture-proof container until further analysis. A 50 g subsample from each composite sample was sifted through 5 sieves stacked in order of decreasing mesh size (500, 250, 180, 125, and 63 μm from top to bottom). The stack of sieves and 50 g sediment sample was placed in a Burrell Wrist Action Shaker (Model 75) and agitated for 20 min. Blatt et al. (1972) recommended 10-15 min of agitation for a 30 g sample. Following separation, the sediment particles retained within each sieve were weighed. Sediment size classes were defined according to the Udden-Wentworth scale for sand grain size (Blatt et al., 1972).

Data Analysis.

Hourly production rates for the four productivity components were related to environmental factors and biomass via stepwise multiple regression analyses (SAS/STAT, Release 6.03, SAS Institute Inc.). These analyses identified those factors potentially important in regulating phytoplankton, seagrass blade, epiphyte, and sand microflora production. The seagrass and epiphyte production values were combined and used as the dependent variable, in addition to treating each productivity component separately. Factors which were employed in the models included sampling date (a temporal indicator), light (PAR), water temperature, current speed, tidal range, salinity, seagrass blade density, and a sand grain size ratio. Two models were run for each autotrophic component: (1) an 8-variable model using light (PAR), water temperature (TEMP), seagrass blade density (STEMS), sand chlorophyll a content (CHLA), current speed (CURRENT), tidal range (TIDE), average salinity (SAL), and seagrass bed (BED); and (2) a 9-variable model containing the same variables as the 8-variable model, plus a sand grain size ratio (GRAINSIZ).

To assess the potential effects of one biotic component on another, two additional stepwise regression models were employed using seagrass blade productivity as an independent factor in the epiphyte productivity model, while the epiphytes were entered as an independent variable in the model for seagrass blade production.

A one-way ANOVA (SAS/STAT, Release 6.03, SAS Institute Inc.) was run on the hourly phytoplankton, seagrass blade, epiphyte, and sand microflora production data to test for significant temporal differences in production over the growth cycle of the seagrass beds. Additionally, differences among samples within the individual seagrass beds, plus differences among the seagrass beds themselves, were examined within each month.

Evaluation of the relative importance of seagrasses, their epiphytes, sand-associated microflora, and phytoplankton as primary producers in the beds was based on the areal productivity rates for each component.

RESULTS AND DISCUSSION

Environmental Factors. Environmental factors were strongly related to observed productivity rates. Phytoplankton productivity rates exhibited the strongest relationship to a single environmental factor, temperature; epiphyte productivity appeared to be least influenced by the environmental factors. In general, temperature, light, and tidal fluctuations were the most important environmental factors in explaining observed variations.

Temperature. Average water temperature ranged from 15.6 to 30.5°C during the course of the study, with the maximum temperature being observed on 15 September 1989 and the minimum during the 18 January 1990 collection (Table 1). Mean water temperature for the study period was 26.3 ± 4.8°C. Fluctuations in water temperature on collection dates were generally ± 2°C of the reported value. Water temperature is shown graphically in Figure 2.

Salinity. Recorded salinities ranged from 11.1 to 29.1 ppt on the average, with a mean of 21.5 ± 4.9 ppt over the entire study (Table 1). Highest average salinity was observed during the October 1989 collection; the low average occurred on the February 1990 sampling trip. Movement of water masses across the study site during sampling periods was observed on several of the trips. Changes in salinity accompanied these events, with drops or rises averaging 5 ppt being measured in conjunction with these events. Little to no difference between surface and bottom water salinities were measured at the study site; therefore, only one average value is reported for each collection. Fluctuations in salinity are illustrated in Figure 2.

Light Energy. Photosynthetically active radiation (PAR) reaching the tips of the seagrass leaves varied on average from 81.1 to 900.0 $\mu E/m^2/sec$, with the minimum occurring on 18 January 1990 and the maximum on 1 June 1989 (Table 1). Mean PAR for the entire study was 434.4 ± 229.3 $\mu E/m^2/sec$. Recorded values for PAR fluctuated widely on sampling dates as a function of both seasonal changes in irradiance and the daily light regime resulting from the progression of the sun across the sky and the degree of light penetrance below the water surface associated with this. Averages of observed values are shown in Figure 2. Wave action and turbidity also strongly affected the reported measurements.

Current Speeds. Current speeds, reported in m/hr, were extremely variable, both on sampling dates and over the course of the study (Table 1). These measurements were affected by daily fluctuations in wind speed and direction, time of sampling in relation to daily and monthly tidal cycles, local hydrologic events, and effects of barometric pressure on rate and direction of movement of water masses. Calculated average speeds ranged from 7.8 to 580.2 m/hr, with a mean of 166.1 ± 196.8 m/hr for the study.

Tidal Range. Daily tidal fluctuation in cm, predicted for the study area on the collection date on the basis of astronomical data, is shown in Table 1. This value ranged from 18.3 cm on 15 September 1989 to 79.2 on 18 January and 16 February 1990, with a mean predicted range of 58.5 ± 20.0 cm. Actual tidal fluctuations at the study site were affected by the same factors listed above for current speed.

Sand Grain Size. Relative proportions of the selected grain sizes analyzed are shown in Table 2. The sediments on all dates were dominated by medium size (>0.25 mm) particles. An intermediate grain size (fine) of ≥ 180 μm was selected for use in the regression model employing all environmental variables; this proportion ranged from 14.2 to 24% of the total sample dry weight (Table 3). Shifts in relative proportions of grain sizes most likely are a result of seasonal changes in wave patterns and action, plus daily changes in water movement and degree of sediment resuspension in response to prevailing winds and accompanying changes in wave form and height. Relative location of the seagrass beds sampled in the surf zone could also be a factor contributing to the observed results. Of interest is the lack of sediment below the 63 μm size grade; there is an apparent deficit of silt to clay-sized particles at the sediment surface as sampled. All grain size classes were used in stepwise regression analyses (SAS) to determine the variation in observed values for sand microflora productivity rates and chlorophyll a levels and phytoplankton productivity. Once again, the factors listed above in controlling grain size distribution may be responsible for the observed relationships between the variables analyzed and grain size class. Phytoplankton productivity can be tied to changes in the proportion of medium-graded sediment. Sand microflora production was most closely associated with fine and very fine grain size classes; sand flora chlorophyll a levels were very weakly associated with the coarse grain size class. These results are summarized in Table 4.

Seagrass-Algal Community Composition.

General Comments.

Seagrasses were viable over an annual cycle at the study site. Degrees of epiphytization changed dramatically from month to month, with the most extensive development being observed in July of 1989 and in January of 1990. Degree of development of the sand microflora also varied, with a thick "crust" of microflora observed within the seagrass beds on some dates. Occasionally, a noticeable golden-brown color was apparent on the sediment surface beneath the seagrass blades.

During the sampling trip attempted for the month of March 1990, the seagrass beds virtually "disappeared" at the location on the northeast end of Horn Island. Bottom sediments were extremely unconsolidated, and on closer inspection, it was determined that the seagrass beds had been buried by shifting sand. One isolated bed was found that was only partially buried; however, it was at an extremely shallow depth and not of sufficient extent to allow the productivity studies to be conducted as designed.

Seagrass Species.

Shoal areas of Horn Island monitored during the course of the productivity studies were populated exclusively by *Halodule wrightii* (shoal grass). No other seagrasses were observed along the northern shore of this island through August of 1990. The presence of *Thalassia* was reported in an isolated location at the eastern tip of the island at approximately that same time (G. M. Armistead, pers. comm.). During the summer and fall of 1988 and the spring of 1989, prior to the initiation of this series of productivity studies, the nearshore regions of East and West Ship Islands, Horn Island, and Petit Bois Island were searched for the presence of viable beds of seagrasses. The only species observed along the northern island margins was *H. wrightii*, with the most extensive and persistent beds occurring along the northeastern end of Horn Island.

In a follow-up survey of the islands at the conclusion of this study, beds of *Syringodium filiforme*, plus mixed beds of *S. filiforme* and *H. wrightii*, were documented along the northern margin of Petit Bois Island. Further monitoring and study of the seagrasses in this area are planned.

Non-Diatom Epiphytic Algal Flora.

The most remarkable aspects of the non-diatom algal flora are the paucity of species and the virtual absence of green and blue-green algal epiphytes. A very occasional blue-green algal filament was encountered, but their abundance was so insignificant they were not included in Table 5. The red alga *Acrochaetium flexuosum* was the dominant filamentous alga on all dates except 18 January. It formed a very dense canopy of entangled filaments that covered the *Halodule* leaves but these were by far most abundant around the blade edges. This alga frequently supported a dense covering of epiphytic diatoms either attached directly to the filaments (e.g. Rhopalodia, Tabularia) or as chains of cells entangled amongst its filaments (e.g. Grammatophora, Fragilaria). Asexual monosporangia were observed on Acrochaetium frequently thought the year. Edwards (1976) recorded A. flexuosum as a common year-round epiphyte in Aransas Bay, Texas. The red alga Polysiphonia sp. was present on Halodule in June and July. It was much less abundant than Acrochaetium. Sterile, antheridial, cystocarpic, and tetrasporic plants of Polysiphonia were observed.

Hummia onusta was the most abundant brown alga; its occurrence was restricted to late fall and winter. This alga has a strongly heteromorphic life cycle. In fact, its gametophyte and sporophyte are so dissimilar that they were formerly classified in different genera and even higher level taxa. Its gametophyte and sporophyte are known as Myriotrichia subcorymbosa (Holden) Blomquist and Stictyosiphon subsimplex Holden, respectively, in the literature. The gametophyte was recorded only on 27 October and plurilocular organs were present. The sporophyte was the only filamentous alga on Halodule on 18 January, forming a dense covering over the entire blade surfaces. It declined to a subdominant status on 16 February. Humm (1964), Dawes (1974), Ballantine and Humm (1975), and Edwards (1976) have all recorded the gametophytic phase of H. onusta as an abundant year-round epiphyte on Halodule. These same authors report the sporophytic phase as abundant on Halodule but only during winter and spring. Small populations of the brown alga Giffordia mitchelliae were observed from 16 February to 25 June 1990. Plurilocular organs were always present. The same four authors listed above also report this alga as a common epiphyte on seagrass leaves.

The most common non-algal epiphytes on Halodule blades were calcareous bryozoans, a hydroid, and a vorticellan type of protozoan. The hydroid was typically covered by the diatom *Cocconeis* and the protozoan supported large numbers of the diatoms *Licmophora* and *Tabularia*.

Epiphytic Diatom Flora.

Along with the filamentous red alga *Acrochaetium*, the epiphytic flora of *Halodule* was dominated by araphid and raphid pennate diatoms. Diatoms utilized all available surfaces for attachment; they were abundant over the entire leaf blade, on the red and brown filamentous algal epiphytes, and on the hydroid and *Vorticella*-like protozoan epiphytes. Microscopic examination of field-collected material revealed that few of the epiphytic diatom cells were dead. Most appeared to be quite "healthy" as evidenced by their deep golden-brown chloroplasts. These observations also revealed dichotomously branched colonies of *Licmophora* cells with their mucus stipes, the tubes of *Berkeleya*, and needle-like clusters of *Tabularia*. Zig-zag colonies of *Grammatophora* and *Fragilaria hyalina* were also apparent, as well as the attachment of *Cocconeis* by its raphid valve and of *Rhopalodia* along its ventral margin. *Navicula*, *Nitzschia*, *Amphora*, and *Mastogloia* exhibited low profiles in their attachment to a suitable surface.

A total of 61 diatom taxa representing 19 genera were encountered in the samples (Table 6). Of these, 10 could not be ascribed with certainty to a species and in 3 cases to a genus. However, with the exception of *Fragilaria* sp. 1 which formed short ribbon-like colonies, all were minor components of the flora, in some cases being represented by a single valve in the combined samples. As expected, the epiphytic diatom flora was completely dominated by pennate taxa. Only 9 centric taxa were recorded: 4 belonged to *Cyclotella*, 2 to *Thalassiosira*, and the remaining 3 could not be assigned to a genus using light microscopy. Although the genus *Navicula* was best represented in terms of recorded taxa (16), these taxa accounted for only 259 (2.9%) of a grand total of 9,000 valves counted.

The 12 most abundant diatom taxa are listed in Table 7. Each had an overall relative abundance ≥ 1% (i.e. 90 valves) and collectively these 12 taxa accounted for 8,485 (94.3%) of the 9,000 valves counted. The 3 most abundant epiphytic diatoms were *Fragilaria hyalina*, *Amphora tenuissima*, and *Mastogloia pumila*, and these accounted for slightly more than 1 out of every 2 valves counted in the combined samples. Other taxa with total valve counts ≥ 600 were *Rhopalodia acuminata*, *Berkeleya hyalina*, and *Cocconeis scutellum*. Collectively, these 6 taxa accounted for 3 out of every 4 valves counted. Most of the dominant taxa exhibited a moderately to highly pronounced seasonality. Table 8 represents an attempt to express this observation in quantitative terms. Five taxa had their greatest relative abundances in summer-fall (29 June-27 October) and spring (15 May-25 June) but were relatively rare during winter (18 January-16 February). These taxa were *Amphora tenuissima*, *Cocconeis placentula* var. *euglypta*, *C. scutellum*, *Navicula perminuta*, and *Rhopalodia acuminata*. Conversely, *Berkeleya hyalina* and *Tabularia fasciculata* were only abundant in the winter communities. *Fragilaria hyalina* and *Nitzschia fontifuga* had their greatest development during summer-fall, with their relative abundances being approximately equal in winter and spring. *Mastogloia pumila* showed an opposite pattern as its populations were poorly developed in summer-fall but were well developed in winter and spring. *Grammatophora oceanica* and *Navicula duerrenbergiana* did not appear to exhibit any pronounced seasonality.

Two diatom taxa not listed above are worthy of special mention.

Protoraphis atlantica was collected only on 27 October. On this date it represented 3 and 10 of the valves counted in two replicates; it was not recorded in the count for the remaining replicate bed. This diatom was originally described by Gibson (1979) as epizoic on various copepod species collected from the Florida Current. As far as is known, species of the closely related diatom genera Protoraphis and Pseudohimantidium occur exclusively on marine pelagic copepods (Hallegraeff and McWilliam 1990). Therefore, it is unlikely that P. atlantica was present as an epiphyte on Halodule. A more likely explanation is that copepods infested with this diatom somehow were deposited on Halodule blades via tidal currents. The small centric diatom Thalassiosira minima was abundant only in the 29 June samples where it represented 7, 20, and 23 valves in the three replicate counts of 300 valves each. On other dates, it was either absent or accounted for ≤ 5 valves in a replicate sample. All other centric taxa were rare, a single taxon never accounting for more than 5 valves in a replicate sample. T. minima is a coastal form with a world-wide distribution; an excellent description of its morphological features and taxonomy can be found in Hasle (1980).

Sullivan (1979) identified epiphytic diatoms from a sample of Halodule collected on 20 July 1977 in the same locality off Horn Island as that of the present study. The 5 most abundant taxa were in order of decreasing abundance: Fragilaria hyalina, Mastogloia pusilla, Opephora pacifica, Licmophora cf. debilis, and Cocconeis placentula var. euglypta. Other abundant diatoms were Nitzschia fontifuga (identified as Nitz. paleacea Grun.), Rhopalodia acuminata (identified as R. gibberula (Ehr.) Müll.), Grammatophora oceanica, Amphora tenuissima, Tabularia fasciculata (identified as Synedra affinis var. intermedia Grun.), Mastogloia exigua Lewis, and Cocconeis scutellum. Of these, 8 were among the 12 most abundant diatoms of the present study and F. hyalina was the single most abundant taxon in both studies. Of the remaining taxa in the 1977 collection, M. pusilla, O. pacifica, and L. cf. debilis were minor components of the epiphytic diatom flora in the present study but M. exigua was not encountered in 1989-90. Apparently, M. pumila has replaced M. pusilla as the dominant Mastogloia species on Halodule. The available evidence indicates a high degree of similarity in the two floras separated in time by more than a decade.

Monthly means for indices of community diversity are presented in Table 7. The Shannon-Wiener information index (H' in bits/ind) typically exhibited values between 2 and 3 with a grand mean of 2.575. Of the 30 replicate samples, only 3 possessed H' values less than 2 and 6 had values greater than 3. The number of diatom taxa (S) in a sample of 300 valves varied from 11 to 24 with a grand mean of 16.8. In general, diversity (H' and S) tended to be lowest in the winter samples (Tables 8). H' and S values for the single sample examined by Sullivan (1979) were 3.473 and 29, respectively. It should be pointed out, however, that 1,064 valves were counted from Halodule in July 1977 instead of the 300 here, which should of course result in a higher value for S. The H' value recorded by Sullivan (1979) was matched in the present study on 25 June as two of the replicates had values of 3.361 and 3.614.

Sand Microflora.

The benthic microflora is typically dominated by pennate diatoms less than 15 μm in length. These diatoms comprise 2 major groups: (1) epipelic forms which are motile and inhabit the interstitial spaces of the sandy substrate and (2) epipsammic forms which are the smaller of the two and inhabit the flat surfaces, crevices, and fissures of the sand grains. The latter adhere to sand grains by means of a mucilaginous stalk or pad. The diatom species present are extremely diverse and taxonomically difficult; attempts are presently underway to begin to identify this flora.

Phytoplankton.

With the exception of two collections, diatoms completely dominated the phytoplankton flowing over the Halodule beds. Although many genera were encountered, the following were most abundant: Chaetoceros, Rhizosolenia, Thalassiosira, Coscinodiscus, Hemiaulus, Guinardia, and Leptocylindrus. Benthic forms were sometimes observed but their numbers were small and they were members of the sediment flora rather than the epiphytic one. Dinoflagellates dominated the phytoplankton on 15 September 1989 and 5 June 1990; otherwise, their numbers were small. Virtually all cells belonged to the dinoflagellate genera Prorocentrum and Ceratium. The virtual absence of other flagellate groups may have been due to the net size (28 μm) or disintegration during the one or two day period from collection to microscopic observation, or may reflect the true nature of the flora.

Epiphytic Algal Production.

Hourly Production Rates. Monthly productivity rates, by bed, are shown in Table 9. Averages of the monthly values are shown in Figure 4. Values for individual beds ranged from a high of 1143 mg C/m^2/h in August 1989 to a low of 33 mg C/m^2/h on 5 June 1990. The mean hourly value for the entire study was 290 mg C/m^2/h. Large differences between beds occurred on 29 June and 20 July 1989 and 16 February 1990, as evidenced by standard deviations, shown in Figure 4. This variation was likely due to the condition of the epiphyte population, with higher values being associated with newer algal growth and lower values observed with senescent populations. Variability on all other sampling dates was relatively low (Fig. 4).

Stepwise regression analyses of environmental factors potentially affecting productivity rates observed for epiphytic algae yielded a minimum of information; only 14.6% of the observed variation in the data could be explained by the 8-variable model (Table 12). Inclusion of sand grain size to assess variability using a 9-variable model resulted in no independent variables entering the model for epiphyte production at α=0.05 (Table 13).

Annual Production Estimates. For purposes of comparison of this study with research on similar systems in other geographic locations, annual values were calculated on a m^2 basis for all components of this system (Table 10). These values were calculated by averaging the hourly rates for each month during which data was collected with estimates for those months not represented. This hourly rate was multiplied by the average day length for the region (12 hr) and by 365 for an estimate for the year. Annual epiphytic algal production was estimated to be 905 mg C/m^2. Results from studies conducted in other seagrass communities are shown in Table 11; eiphytes in the Horn Island seagrass community studied, on average, were more productive than those in other studies, as Murray and Wetzel (1987) stated that epiphytes accounted for less than 7% of seagrass blade plus epiphyte biomass.

Seagrass Blade Production.

Hourly Production Rates. Monthly productivity rates, by bed, are shown in Table 9, with averages of the monthly values shown graphically in Figure 5. Lowest seagrass blade production was measured in January 1990 with a value of 0.9 mg $C/m^2/h$; a high of 149 mg $C/m^2/h$ was observed in May 1990. The mean hourly value for seagrass blades for the entire study was 60 mg $C/m^2/h$.

Values were generally in close agreement, with the exception of 15 May 1990 (Fig. 5). The higher variation observed on this date was probably due to the increase in number of blades per unit area, indicating the presence of new rapidly growing seagrass blades (see Table 3 and Fig. 6).

Stepwise regression analyses indicated that light (PAR) was the single most important factor in explaining observed variation in blade production, accounting for 53% and 55% of the variation observed in the 8- and 9-variable models, respectively (Tables 12 and 13). Other factors did enter into the models, but their partial R^2 values were much smaller. These additional factors produced an overall R^2 0.80 and 0.94, respectively (Tables 12 and 13). Of particular interest is the negative association with tidal fluctuation (TIDE) in both models.

Annual Production Estimates. Halodule beds in the present study were less productive than their counterparts in Texas (Morgan and Kitting, 1984), with an average hourly production rate of 106 mg $C/^2$ (Tables 10 and 11). The annual production rate of 256 g C/m^2 is also lower than other seagrass species (Table 11). Freshwater outflow from the Pascagoula River system regularly passes through the study area, subjecting the seagrass beds to high levels of turbidity and low light levels. This would appear to have a negative effect on the seagrasses themselves.

Sand Microflora Production.

Hourly Production Rates. Monthly productivity rates, by bed, are shown in Table 9. Monthly averages calculated from these values are plotted in Figure 7. Values ranged from a high of 276 mg $C/m^2/h$ in September 1989 to a low of 9 mg $C/m^2/h$ in February 1990. Hourly values, when averaged for the entire study, yielded a mean of 78 mg $C/m^2/h$. Ranges in values for a given month were relatively small (Fig. 7). An extremely narrow range of values was measured in August and October 1989. A one-way ANOVA showed that date was significant; however 10 dates exhibited statistically equal productivity rates and production of the sand microflora on 15 September 1989 was higher than on 7 of the remaining 10 dates. A two-way ANOVA resulted in a significant date x bed interaction but on most dates production was not significantly different in the three beds sampled and on only one date were all three beds different.

Stepwise regression analyses of environmental variables yielded a strong positive association between sand microflora productivity rates and water temperature and tidal range for both the 8- and 9-variable models (Tables 12 and 13). Tide was negatively associated with productivity in both cases. Light energy was the final variable to enter the 8-variable model; and grain size the final variable to enter the 9-variable model, resulting in final R^2 values of 0.72 and 0.77, respectively.

Annual Production Estimates. Limited measurements exist from previous studies for purposes of comparison with this study. An annual estimate of 337 g C/yr was calculated from the hourly measurements on a m^2 basis for the sand microflora in this system. Jensen and Gibson (1986) measured seagrass benthic microfloral production rates of 5 and 18 mg $C/m^2/h$ in two different locales in seagrass beds, which can be extrapolated to annual estimates of 22 and 78 g C/m^2, respectively; Murray and Wetzel (1987) estimated annual rates of 106 and 225 g C/m^2 for sand microflora. Thus the sand microflora in this study were more productive, on average, than their counterparts in other seagrass systems.

Chlorophyll a Estimates. Analysis of sediment subsamples for chlorophyll a concentration resulted in measurements ranging from 14 to 125 mg/m^2 chl a (Table 3), with a grand mean of 41 mg/m^2. Monthly averages are shown in Figure 8; variation within any given month was generally high. This could be due to microscale changes in the environment, such as degree of shading by overlying seagrass blades and their attached epiphytes, or the feeding actions of sand-dwelling invertebrates.

A two-way ANOVA showed a significant date x bed interaction; however, only two months showed differences in chlorophyll a concentrations and in both cases two of the beds did not differ significantly from each other.

Stepwise regression analyses of environmental and biological (productivity) variables potentially affecting sediment chlorophyll a are summarized in Table 14. Water temperature and density of seagrass blades were the key factors "explaining" observed variation, for a total of 38% and 48% in the 8- and 9-variable models, respectively. Temperature entered in regression models for microflora production (Tables 12 and 13). The addition of phytoplankton production as an independent variable in the 9-variable model resulted in temperature being replaced by phytoplankton productivity rates (Table 14). This could be a result of an increase in chlorophyll a in surface sediments due to "raining" of phytoplankton cells onto the sediment surface as suggested by the positive sign of its regression coefficient.

Phytoplankton Production.

Hourly Production Rates. Productivity rates (m^3), by bed, are shown for each date during each month in Table 9, with averages of monthly values shown graphically in Figure 9. Phytoplankton production was lowest in January 1990 with a minimum value of 16 mg C/m^2/h being measured. Highest phytoplankton productivity (231 mg C/m^2/h) was observed in August 1989. Phytoplankton mean hourly production for the entire study was 130 mg C/m^2/h. Values for a given month were generally in close agreement, with the greatest variation being observed on 25 June 1990, the last date of the study (Fig. 9).

Stepwise regression analysis models with either 8 or 9 variables showed temperature to be the overriding factor in "explaining" rates of phytoplankton production, accounting for 66% and 75% of the observed variation, respectively. No other variables entered either model for phytoplankton production.

Annual Production Estimates. Comparisons of the phytoplankton productivity rates with those from research in other geographic locations showed the Horn Island study area phytoplankton population to be less productive than their counterparts elsewhere, with an annual production rate of 468 g C/m^2 (Tables 10 and 11). Pascagoula River outflow into the study area, resulting in high levels of turbidity, low light levels, and possible nutrient loading could strongly affect observed productivity rates. Apparently, the phytoplankton assemblage present in the Mississippi Sound waters along the northern shore of Horn Island are not adapted to these conditions, as measured productivity rates are in general lower than those observed in other studies.

The relative contributions of the four productivity components in this system are shown in Figure 10. System production appears to be dominated by *Halodule*'s epiphytes; on 7 of the 11 sampling dates, epiphyte productivity rates exceeded those of all other components. Phytoplankton production was the dominant component on 2 of the 4 dates when epiphytes were not the major producers (15 August 1989 and 5 June 1990); rates were essentially equal for all producers on 27 October 1989 and 15 May 1990. Table 10 lists relative contributions on an average hourly basis over the course of an annual cycle and on an annual basis for the four productivity components. Epiphytes are the dominant component; Halodule blades contributed the least.

Photoinhibition Study.

On 7 August 1990, a preliminary study was undertaken to assess the potential effects of levels of insolation on primary production rates. High levels of turbidity in the water column over the seagrass beds could potentially lead to the development of a seagrass community with primary producers that are most efficient at converting relatively low levels of light energy to carbohydrates and thus energy for plant growth and reproduction. A possible outcome of this type of strategy for growth is photoinhibition, or reduced rates of primary productivity, at higher levels of light than are usually encountered at the depths at which seagrass beds occur. The latter was in fact observed at the study site on 7 August 1990.

Light energy (PAR) ranged from 280 to 1483 μE at the depths selected for incubations of the samples of the four primary productivity components. PAR increased in a somewhat logarithmic manner with decreasing depth (Fig.11), but was sufficiently close to linear to allow data analysis without transformation of the data. Measurements for the +0.5 m depth area from a set of shipboard incubations in a water-cooled system, featuring higher levels of insolation than possible with the surface samples.

Epiphytes present on the seagrass blades exhibited highest productivity rates at the lowest light level (Fig 12). Productivity rates ranged from 205 mg C m^2/h at the highest light level to a maximum of 725 mg C/m^2/h at the lowest light level. Higher rates of primary production may have occurred at lower light levels, as a decrease in productivity rate that would be associated with a minimum level of irradiance was not observed.

Seagrass blades were most productive at an intermediate light level of 630 $\mu E/m^2/s$, with rates ranging from 127 to 276 mg $C/m^2/h$. Both decreases from the maximal rate due to insufficient light and to photoinhibition were observed (Fig. 13). Productivity most likely would have continued to decrease with additional decreases in insolation reaching the Halodule blades.

Maximum productivity rates were observed for the sand microflora at the lowest light level, which parallels results for the epiphytic algae (Fig. 14). Productivity rates ranged from 116 to 572 mg $C/m^2/h$ for this component. A marked decrease in productivity occurred with further increases in light levels, indicating that the sand microflora were strongly photoinhibited. As for the epiphytes, a decrease in productivity rate that would be associated with a minimum level of irradiance was not observed.

Phytoplankton productivity also appeared to be photoinhibited at the higher light levels (Fig. 15), with productivity rates ranging from 108 to 275 mg $C/m^2/h$. Productivity most likely would have continued to decrease with additional decreases in insolation reaching the algal flora comprising the phytoplankton on that date.

Results of the photoinhibition study are summarized in Figure 16. All components of primary production in this seagrass bed system exhibited photoinhibition to some degree, with the inhibition of sand microflora productivity rates being the most pronounced. Whether or not production rates for the epiphytes and sand microflora would have been higher at lower irradiances than 280 $\mu E/m^2/s$ is unknown; however, phytoplankton and Halodule blades underwent a decline in productivity rates with a decrease in PAR from 630 to 280 $\mu E/m^2/s$. Morgan and Kitting (1984) found that both epiphyte and

Halodule photosynthesis saturated at 1100 $\mu E/m^2/s$, a value much higher than that observed in the present study. Penhale (1977) observed that photosynthesis of Zostera and its epiphytes saturated at 600-700 $\mu E/m^2/s$. Mazzella and Alberte (1986) examined P-I relationships for Zostera and its epiphytes; saturation occurred at 300 $\mu E/m^2/s$ and no photoinhibition was observed at irradiances up to 1400 $\mu E/m^2/s$. Borum and Wium-Andersen (1980) showed that epiphyte photosynthesis on Zostera saturated at ca. 280 $\mu E/m^2/s$, which is very close to the lowest irradiance value used in our study.

Biomass-Based productivity Estimates. To avoid potential pitfalls inherent in areal-based productivity estimates, many researchers have expressed primary production rates on a dry weight basis (Morgan and Kitting, 1984; Jensen and Gibson, 1986). For this study, such measurements were calculated for the primary producers epiphytic on Halodule and for the seagrass itself. This allows a degree of compensation for changes in seagrass blade length and age and the degree of epiphytization of seagrass blades that is not possible when relying strictly on stem densities for areal estimates.

Halodule blades and their associated epiphytes contributed differing amounts of biomass over the course of the study (Fig. 17). Relative proportions of each component are a good indicator of degree of epiphytization. Halodule blades were most heavily epiphytized during June and July of 1989, with % contribution to biomass by epiphytes reaching nearly 80%. Epiphyte coverage of the seagrass blades decreased during fall and winter months, followed by a spring increase (Fig. 17).

Seagrass blade production rates per g dry wt of epiphyte-free Halodule blades is shown in Figure 18 (epiphyte removal was accomplished via scraping of epiphytic material from intact blades). Values ranged from 0.4 to 41.2 mg C/g dry wt/h, with a mean of 13.6 mg C/g dry weight.

Stepwise regression using a 9- or 10-variable model showed light (PAR), tide, and sand grain size to be most critical in "explaining" observed variations in seagrass blade productivity rates (Table 15). Stem densities and temperature are no longer as important as they were for regressions employing production on an areal basis as the dependent variable (see Tables 12 and 13).

Epiphyte productivity rates ranged from 5.3 to 81.7 mg C/g dry wt _Halodule_/h, with a mean of 27.4 mg C/g dry wt _Halodule_/h (Fig. 19). Weights for epiphytes were determined from the material removed from the _Halodule_ blades as described previously.

Stepwise regression using a 9-variable model showed stem densities to be the only factor entering the model but R^2 was low (0.21; Table 15). In the stepwise regressions utilizing epiphyte production rates on an areal basis only light entered the model (see Table 12). There was a small improvement in the weight-based model over the areal-based model; "explained" variation increased from 14.6% to 21.5%, an improvement of 32% in the overall model.

Figure 20 shows both epiphyte and blade production on a dry weight basis. Epiphyte productivity exceeded seagrass blade production rates on all but two sampling dates. Rates were virtually equal on two dates (18 January and 5 June 1990). Seagrass blade productivity was greater than epiphyte productivity on 15 August and 27 October 1989. These dates concur with three of four dates on which epiphyte productivity rates equalled or were less than other primary production components on an areal basis.

SUMMARY

1. Seasonal patterns of seagrass community production were determined over an annual cycle for four components of primary production: (1) Halodule blades, (2) algae epiphytic on Halodule, (3) sand microflora within the seagrass beds, and (4) phytoplankton in the water column overlying the seagrass blades. This is the first study of its type in a coastal Mississippi seagrass bed system.

2. A suite of environmental factors were monitored in conjunction with productivity measurements for purposes of relating these variables to observed productivity rates. Light and current speed were the most variable factors. Stepwise multiple regression analyses were used to determine the relative importance of each of these and other factors. Water temperature, light (PAR), and range of tidal fluctuation were the factors most often entering the models for productivity.

3. Biological factors investigated included density of seagrass blades within the beds and the floristic composition of the productivity components. Stepwise regression analyses indicated that seagrass blade density was an important constituent in some models of component production.

4. Sand grain size could be used to account for roughly 30% of the observed variation in productivity rates for the phytoplankton and up to 50% of the variation in sand microflora production. In the latter case, there was a negative correlation with the sediment fraction 0.125-0.18 mm and a positive correlation with the 0.063-0.124 mm size fraction. Phytoplankton production

was positively correlated with the medium sediment fraction (0.25-0.5 mm). Resuspension may play a role in these observations (Shaffer and Sullivan, 1988).

5. The only seagrass species studied was *Halodule wrightii* (shoal grass). Although other seagrass species had been documented as occurring in the Horn Island study area in the past (Sullivan, 1979), no other species were observed in the immediate locale during the course of the study. Beds were relatively small in size in comparison to the extent of beds observed in the region previously.

6. The non-diatom algal flora epiphytic on *Halodule* was dominated by the filamentous red alga *Acrochaetium flexuosum*, which was present and abundant on virtually all sampling dates. Brown algae were sometimes sub-dominant; blue-green algae were an insignificant part of the flora.

7. The epiphytic diatom flora was dominated by a total of 12 taxa. *Fragilaria hyalina*, *Amphora tenuissima*, and *Mastogloia pumila* were the most abundant species, and were present throughout the course of the study. *Cocconeis scutellum*, *Grammatophora oceanica*, and *Rhopalodia acuminata* were also present on all sampling dates. Seasonal peaks in abundance occurred for all of these species.

8. Hourly production rates were highest during most months for the epiphytes. Phytoplankton, sand microflora, and seagrass blades generally followed in decreasing order of production rates. The lowest production rate

of 0.9 mg C/m^2/h was observed on 18 January 1990 for seagrass blades. The highest rate was observed on 1 June 1989 for the epiphytes (1143 mg C/m^2/h).

9. Conversion of hourly production rates to annual estimates for the four productivity components yielded the following rates in g C/m^2: epiphytes, 905; Halodule blades, 256; sand microflora, 337; phytoplankton, 468. Annual values for epiphyte and phytoplankton production were lower than other reported rates. Seagrass blade production rates observed were intermediate in comparison to other studies. These observed differences may be a function of latitude, tidal regime, water quality, or a combination of these parameters.

10. The preliminary photoinhibition study showed that epiphytes present on the seagrass blades exhibited highest productivity rates at the lowest light level, as did the sand microflora; both the epiphytes and the sand microflora were strongly photoinhibited. Seagrass blades were most productive at an intermediate light level. Phytoplankton productivity also appeared to be photoinhibited at higher light levels. Thus all components of primary production in this study exhibited photoinhibition to some degree.

11. Production rates on a dry weight basis for seagrass blades and epiphytes yielded relatively similar seasonal patterns overall. Differences were observed between production values on an areal basis and those on a dry wt basis in the stepwise regression analyses. Stepwise regressions employing dry weights eliminated stem density from the models for blade productivity, while this same variable entered the models for epiphyte production with the exclusion of all others.

CONCLUSIONS

Seagrass communities in Mississippi Sound possess significant primary production rates. Monthly estimates show that individual components approximate or exceed local marsh plant aboveground production rates; a combined system production estimate of 1966 g C/m^2/yr is equivalent to annual aboveground production in Mississippi salt marshes (Cruz, 1974).

Seagrass blade, sand microflora, and phytoplankton, taken as a whole, are basically comparable to the epiphytes alone in production rates. All components are productive on a year-round basis, although rates decrease markedly during winter months.

Water temperature and light energy were key factors affecting observed rates of primary production. Tidal range and density of seagrass blades were also important. The positive correlation between productivity and light energy, as determined by stepwise multiple regression analyses, taken in conjunction with the results of the photoinhibition study, suggests that the Halodule community located along the northeast shore of Horn Island may be uniquely adapted to lower light levels associated with the highly turbid water that seemed to predominate in the area on most study dates. This concept of possible physiological and genetic uniqueness has been previously proposed by Eleuterius (1987).

All of the productivity components are potentially important food resources; the algal components are likely of greater importance, as they have been reported as a preferred food item (Morgan and Kitting, 1984; Gleason, 1986). The seagrass blades themselves may function primarily as substrate and habitat. There is some disagreement as to whether seagrass beds function primarily as a refuge or as a food source. Research is underway to address this specific question in our current Sea Grant project (R/LR-23). Hopefully, the issue of seagrass communities and their function as nursery grounds for commercial and non-commercial species of invertebrates and fishes will begin to be properly addressed.

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Table 1. Average values for recorded environmental data at the Horn Island study site from 1 June 1989 to 25 June 1990. Units are as follows: PAR (E/m^2/s), water temp. (°C), current (m/h), tidal range (cm), salinity (ppt).

Date	Light (PAR)	Water Temp.	Current	Tidal Range	Salinity
1/6/89	900.0	29.50	7.8	79.2	23.00
29/6/89	427.8	30.00	45.6	79.2	19.00
20/7/89	219.4	29.50	339.4	67.1	27.00
15/8/89	458.3	29.50	17.1	73.2	22.17
15/9/89	373.0	30.50	21.0	18.3	25.20
27/10/89	546.5	21.00	65.6	39.6	29.10
18/1/90	81.1	15.89	496.8	33.5	22.80
16/2/90	153.8	20.09	580.2	42.7	11.10
5/5/90	736.1	25.10	102.6	70.1	21.00
15/6/90	399.2	29.80	44.3	67.1	14.64
25/6/90	483.3	28.70	106.9	73.2	21.78

Table 2. Grain size classes for single sediment samples collected on each date at the Horn Island study site expressed as percentages of 50 g subsamples (n.a.=not available).

Date	Coarse (>.5 mm)	Medium (>.25 mm)	Fine (>.18 mm)	Fine (>.125 mm)	Very fine (>.063 mm)	Silt (<.063 mm)
1/6/89	n.a.	n.a.	n.a.	n.a.	n.a.	0.0
29/6/89	3.6	72.6	19.1	4.3	0.4	0.0
20/7/89	n.a.	n.a.	n.a.	n.a.	n.a.	0.0
15/8/89	5.7	66.1	22.3	5.3	0.5	0.0
15/9/89	7.7	75.7	14.2	2.2	0.2	0.0
7/10/89	8.0	63.3	22.1	6.0	0.6	0.0
18/1/90	8.5	65.4	20.9	4.9	0.3	0.0
16/2/90	8.6	67.4	19.3	4.4	0.3	0.0
15/5/90	5.5	64.7	24.0	5.1	0.5	0.0
5/6/90	8.7	71.7	16.5	2.9	0.2	0.0
25/6/90	5.2	75.3	16.0	3.2	0.3	0.0

Table 3. Average values for seagrass blade densities, sand microflora chl a (mg/m^2), and intermediate (0.18-0.25 mm) sand grain size percentages in each bed at the Horn Island study site from 1 June 1989 to 25 June 1990.

Date	Bed	Seagrass blades per 10 cm^2	Chl a	Grain size
1/6/89	1	143.0	32.1	.
	2	163.0	19.6	
	3	183.0	44.6	
29/6/89	1	96.0	41.9	19.1
	2	43.5	74.0	
	3	63.5	80.0	
20/7/89	1	104.5	39.3	.
	2	67.0	33.5	
	3	53.5	59.2	
15/8/89	1	58.0	70.0	22.3
	2	57.5	125.2	
	3	55.0	62.2	
15/9/89	1	123.0	91.4	14.2
	2	152.0	14.1	
	3	124.0	62.4	
27/10/89	1	98.0	36.2	22.1
	2	58.5	23.9	
	3	72.0	28.8	
18/1/90	1	18.0	26.2	20.9
	2	61.5	52.6	
	3	68.0	26.6	
16/2/90	1	76.0	20.7	19.3
	2	99.0	43.8	
	3	47.0	32.9	
15/5/90	1	215.0	27.4	24.0
	2	167.5	35.6	24.0
	3	265.0	16.5	24.0
5/6/90	1	236.0	19.9	16.5
	2	202.0	23.4	16.5
	3	213.5	53.1	16.5
25/6/90	1	148.0	59.8	16.0
	2	143.0	34.5	16.0
	3	149.0	66.0	16.0

Table 4. R^2 values and F-values for each variable entering the stepwise regression model and the sign of its regression coefficient for sand grain size analysis (fractions listed in Table 2) for the dependent variable specified and the sign of its regression coefficient (significance level=0.05).

Summary of Stepwise Procedure for Dependent Variable SANDPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	FINES (-)	1	0.2616	0.2616	25.5007	8.8587	0.0064
2	VERYFINE (+)	2	0.2461	0.5077	11.3367	11.9968	0.0020

Summary of Stepwise Procedure for Dependent Variable CHLA

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	COARSE (-)	1	0.1761	0.1761	12.1961	5.3428	0.0293

Summary of Stepwise Procedure for Dependent Variable PHYTPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	MEDIUM (+)	1	0.2878	0.2878	98.6718	10.1010	0.0039

Table 5. A list of non-diatom filamentous algae epiphytic on *Halodule* (29 June 1989-25 June 1990) and a relative indictation of their abudance on each collection date.

	6/29	7/20	8/15	9/15	10/27	1/18	2/16	5/15	6/5	6/25
Acrochaetium flexuosum Vickers	+++	+++	+++	+++	++		+++	+++	+++	+++
Polysiphonia sp.	++	++	+						+	+
Hummia onusta (Kutz.) Fiore										
Gametophyte					++					
Sporophyte						+++	++			
Giffordia mitchelliae (Harvey) Hamel							+	+	+	+

Table 6. An alphabetical list of diatom taxa epiphytic on *Halodule*.

Amphora angusta Greg.
A. *coffeaeformis* (Ag.) Kütz.
A. *exigua* Greg.
A. *exilitata* Giffen
A. *helenensis* Giffen
A. *proteus* Greg.
A. *pusio* Cl.
A. *tenuissima* Hust.

Berkeleya hyalina (Round & Brooks) Cox

Cocconeis deperdita Giffen
C. aff. *dirupta* Greg.
C. *placentula* var. *euglypta* (Ehr.) Cl.
C. *scutellum* Ehr.

Cyclotella atomus Hust.
C. *caspia* Grun.
C. *litoralis* Lange & Syvertsen
C. *meneghiniana* Kütz.

Cymbellonitzschia sp. 1

Diploneis oblongella (Naeg.) Ross
D. *weissflogii* (A.S.) Cl.

Fragilaria hyalina (Kütz.) Grun.
Fragilaria sp. 1

Grammatophora oceanica (Ehr.) Grun.

Licmophora abbreviata Ag.
L. cf. *debilis* (Kütz.) Grun.

Mastogloia binotata (Grun.) Cl.
M. *pumila* (Grun.) Cl.
M. *pusilla* Grun.

Navicula abunda Hust.
N. *aequorea* Hust.
N. *clamans* Hust.
N. *consentanea* Hust.
N. *duerrenbergiana* Hust.
N. *fenestrella* Hust.
N. *hudsonis* Grun.
N. *hyalinula* De Toni
N. *litoricola* Hust.
N. *patrickae* Hust.
N. *perminuta* Grun.
N. *pseudony* Hust.
N. *salinarum* Grun.
N. aff. *iranensis* Hust./*nolens* Simonsen

Table 6. An alphabetical list of diatom taxa epiphytic on *Halodule* (concl.).

N. aff. *rogallii* Hust.
Navicula sp. 1

Neodelphineis pelagica Takano

Nitzschia capitellata Hust.
N. *constricta* (Greg.) Grun.
N. cf. *dissipata* (Kütz.) Grun.
N. *fontifuga* Cholnoky
N. *quadrangula* (Kütz.) Lange-Bertalot

Opephora pacifica (Grun.) Petit
O. cf. *parva* (Grun.) Krasske

Plagiogramma sp. 1

Protoraphis oceanica Gibson

Rhopalodia acuminata Krammer

Tabularia fasciculata (Ag.) Williams & Round

Thalassiosira decipiens (Grun.) Jørgensen
T. *minima* Gaarder

Small centric diatom no. 1
Small centric diatom no. 2
Small centric diatom no. 3

Table 7. A list of the 12 most abundant diatoms epiphytic on *Halodule* and the number of valves present in the counts (29 June 1989-25 June 1990). The three replicates were pooled on each date to yield a composite sample of 900 valves. Values of H′ and S are means of three replicates for each date.

Diatom Taxon	6/29	7/20	8/15	9/15	10/27	1/18	2/16	5/15	6/5	6/25	TOTAL
Amphora tenuissima	542	183	106	209	33	28	4	96	281	127	1,609
Berkeleya hyalina	---	---	---	---	---	311	324	22	4	25	686
Cocconeis placentula vas. *euglypta*	26	22	50	44	34	3	---	55	92	52	378
C. scutellum	12	17	29	57	75	7	4	232	145	26	604
Fragilaria hyalina	30	268	283	155	600	43	190	264	14	159	2,006
Grammatophora oceanica	12	88	21	1	2	33	47	19	13	65	301
Mastogloia pumila	1	3	44	23	36	350	175	118	276	143	1,169
Navicula duerrenbergiana	5	24	31	11	---	8	---	---	5	9	93
Nav. perminuta	20	6	10	18	---	1	4	18	20	19	116
Nitzschia fontifuga	114	178	126	35	2	---	1	---	1	40	497
Rhopalodia acuminata	26	57	164	238	36	2	3	13	35	159	733
Tabularia fasciculata	---	4	4	68	24	78	110	5	---	---	293
H′ (bits/ind)	2.229	2.773	2.928	2.978	1.902	2.235	2.370	2.577	2.403	3.356	
S (no. taxa/sample)	20.3	17.0	17.7	17.7	15.3	15.3	12.7	17.7	13.7	20.3	

Table 8. Seasonality of the 12 most abundant diatoms epiphytic on *Halodule*. Values represt % of total valve count for each time period and in all combined samples. Mean H′ and S values also shown for time periods and combined samples.

Diatom Taxon	29 Jun-27 Oct	18 Jan-16 Feb	15 May-25 Jun	Total
Amphora tenuissima	23.8	1.7	18.7	17.9
Berkeleya hyalina	0.0	35.3	1.9	7.6
Cocconeis placentula vas. *euglypta*	3.9	0.2	7.4	4.2
C. scutellum	4.2	0.6	14.9	6.7
Fragilaria hyalina	29.7	12.9	16.2	22.3
Grammatophora oceanica	2.8	4.4	3.6	3.3
Mastogloia pumila	2.4	29.2	19.9	13.0
Navicula duerrenbergiana	1.6	0.4	0.5	1.0
Nav. perminuta	1.2	0.3	2.1	1.3
Nitzschia fontifuga	10.1	0.1	1.5	5.5
Rhopalodia acuminata	11.6	0.3	7.7	8.1
Tabularia fasciculata	2.2	10.4	0.2	3.3
H′ (bits/ind)	2.562	2.302	2.779	2.575
S (no. taxa/sample)	17.6	14.0	17.2	16.8

Table 9. Average values for productivity data, by bed, at the Horn Island study site from 1 June 1989 to 25 June 1990 (n=5). Phytoplankton rates are reported in mg $C/m^3/h$; all other values are reported in mg $C/m^2/h$.

Date	Bed	Phytoplankton	Seagrass blades	Epiphytes	Sand microflora
1/6/89	1	196.0	79.5	1001.6	82.7
	2	193.0	88.9	894.5	108.1
	3	194.9	116.6	1143.4	121.9
29/6/89	1	176.5	61.3	914.9	72.3
	2	115.0	24.5	267.3	49.4
	3	118.0	31.5	245.7	29.5
20/7/89	1	155.0	50.7	645.6	39.7
	2	85.0	22.8	227.6	114.5
	3	80.0	29.8	190.1	113.9
15/8/89	1	218.3	53.6	86.1	118.9
	2	230.6	56.2	167.1	110.2
	3	215.0	58.6	114.6	121.3
15/9/89	1	184.7	86.8	276.9	180.9
	2	196.5	137.0	417.3	275.8
	3	182.3	97.4	314.4	209.8
27/10/89	1	57.4	81.2	88.2	31.9
	2	60.3	33.5	39.4	35.1
	3	52.0	44.7	50.6	32.9
18/1/90	1	18.1	0.9	60.5	19.1
	2	15.5	6.0	83.8	12.7
	3	17.6	5.8	91.1	21.0
16/2/90	1	115.0	17.0	274.3	20.7
	2	95.2	22.8	702.8	8.6
	3	90.2	11.3	192.7	34.1
15/5/90	1	101.5	149.4	68.1	83.6
	2	104.6	105.5	86.6	113.1
	3	81.6	142.5	167.4	87.1
5/6/90	1	162.7	54.5	100.6	72.0
	2	181.4	57.2	33.0	54.2
	3	161.5	59.3	88.3	36.8
25/6/90	1	103.3	68.5	426.4	84.8
	2	154.8	54.8	243.0	66.4
	3	167.7	53.4	278.4	91.7

Table 10. Average hourly production rates and annual estimates calculated from productivity data at the Horn Island study site from 1 June 1989 to 25 June 1990.

Phytoplankton	Seagrass blades	Epiphytes	Sand microflora
107 mg $C/m^2/h$	58 mg $C/m^2/h$	206 mg $C/m^2/h$	77 mg $C/m^2/h$
468 g $C/m^2/yr$	256 g $C/m^2/yr$	905 g $C/m^2/yr$	337 g $C/m^2/yr$

Table 11. Productivity rates for the four autotrophic components of seagrass bed systems. All rates are expressed as C production/m^2 unless otherwise indicated; H=Halodule, S=Syringodium, T=Thalassia, R=Ruppia (ND=not determined).

Epiphytes	Seagrass blades	Sand microflora	Phytoplankton	Units	Reference
905	256 (H)	337	256	g/yr	This study
ND	80 mg O_2(T)	130 mg O_2	0-400 mg O_2	mg/hr	Pomeroy (1960)
69	310 (Z)	ND	ND	g/yr	Penhale (1977)
48	69 (Z)	ND	ND	g/5 mo	Borum & Wium-Andersen (1980)
70	814 (Z)	ND	ND	g/yr	Borum et al. (1984)
18	18 (H,S,T)	ND	ND	mg/hr	Jensen & Gibson (1986)
Seagrass blades + epiphytes					
409 (H, Location 1)		ND	ND	mg/hr	Morgan & Kitting (1984)
239 (H, Location 2)		ND	ND	mg/hr	Morgan & Kitting (1984)
1100 (R)		106	495	g/yr	Murray & Wetzel (1987)
1600 (Z)		225	720	g/yr	Murray & Wetzel (1987)

Table 12. R^2 values and F-values for each variable entering the stepwise regression model employing 8 independent variables for the dependent variables indicated and the sign of their regression coefficients (significance level=0.05).

Models With 8 Independent Variables

Summary of Stepwise Procedure for Dependent Variable PHYTPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.6590	0.6590	8.1549	59.9089	0.0001

Summary of Stepwise Procedure for Dependent Variable BLADPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PAR (+)	1	0.5320	0.5320	33.4441	35.2346	0.0001
2	STEMS (+)	2	0.1501	0.6821	15.4176	14.1639	0.0007
3	TIDE (-)	3	0.0711	0.7532	7.9334	8.3515	0.0072
4	TEMP (+)	4	0.0483	0.8015	3.4894	6.8115	0.0144

Summary of Stepwise Procedure for Dependent Variable EPIPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PAR (+)	1	0.1460	0.1460	12.1366	5.2977	0.0282

Summary of Stepwise Procedure for Dependent Variable SANDPROD

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.3632	0.3632	32.6880	17.6819	0.0002
2	TIDE (-)	2	0.2935	0.6567	6.2533	25.6529	0.0001
3	PAR (+)	3	0.0596	0.7164	2.4774	6.0959	0.0197

Table 13. R^2 values and F-values for each variable entering the stepwise regression model employing 9 independent variables for the dependent variables indicated and the sign of their regression coefficients (significance level=0.05).

Models With 9 Independent Variables

Summary of Stepwise Procedure for Dependent Variable <u>PHYTPROD</u>

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.7535	0.7535	7.2335	76.4248	0.0001

Summary of Stepwise Procedure for Dependent Variable <u>BLADPROD</u>

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PAR (+)	1	0.5516	0.5516	125.9821	30.7572	0.0001
2	STEMS (+)	2	0.1294	0.6810	84.9866	9.7361	0.0047
3	TIDE (-)	3	0.1076	0.7887	51.2204	11.7149	0.0023
4	TEMP (+)	4	0.0346	0.8233	41.7203	4.3086	0.0498
5	GRAINSIZ (+)	5	0.0410	0.8642	30.1094	6.3364	0.0200
6	CURRENT (+)	6	0.0275	0.8917	22.9771	5.0767	0.0356
7	SAL (+)	7	0.0436	0.9353	10.4817	12.8208	0.0020

Summary of Stepwise Procedure for Dependent Variable <u>EPIPROD</u>

No variable met the 0.0500 significance level for entry into the model.

Summary of Stepwise Procedure for Dependent Variable <u>SANDPROD</u>

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.3715	0.3715	162.6085	14.7770	0.0007
2	TIDE (-)	2	0.3313	0.7027	66.7840	26.7451	0.0001
3	GRAINSIZ (+)	3	0.0708	0.7735	47.8806	7.1886	0.0133

Table 14. R^2 values and F-values for each variable entering the stepwise regression model for the dependent variable chlorophyll _a_ and the sign of its regression coefficient (significance level=0.05).

Summary of Stepwise Procedure for Dependent Variable _CHLA_
(Model Execution Without Independent Variable Grainsiz)

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.1311	0.1311	8.8098	4.6772	0.0384
2	STEMS (-)	2	0.2515	0.3826	-0.1345	12.2212	0.0015

Summary of Stepwise Procedure for Dependent Variable _CHLA_
(Model Execution With Independent Variable Grainsiz)

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	TEMP (+)	1	0.1912	0.1912	20.5694	5.9117	0.0225
2	STEMS (-)	2	0.2956	0.4869	6.6441	13.8260	0.0011

Summary of Stepwise Procedure for Dependent Variable _CHLA_
(Model Execution With Independent Variable Grainsiz And Phytprod)

Step	Variable Entered Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PHYTPROD (+)	1	0.2166	0.2166	17.2785	6.9131	0.0144
2	STEMS (-)	2	0.1942	0.4108	9.2954	7.9086	0.0097

Table 15. R^2 values and F-values for each variable entering the stepwise regression model for the dependent variables representing seagrass blade productivity on a dry weight basis (BLDWTPRD) and epiphyte productivity on a dry weight basis (EPIWTPRD) and the sign of their regression coefficients (significance level=0.05).

Summary of Stepwise Procedure for Dependent Variable BLDWTPRD

Step	Variable Entered	Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PAR (+)		1	0.5436	0.5436	60.6196	29.7779	0.0001
2	TIDE (-)		2	0.1959	0.7395	26.7348	18.0421	0.0003
3	GRAINSIZ (+)		3	0.1464	0.8859	1.9070	29.5134	0.0001

Summary of Stepwise Procedure for Dependent Variable BLDWTPRD
(EPIWTPRD Included as an Independent Variable)

Step	Variable Entered	Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	PAR (+)		1	0.5436	0.5436	57.3557	29.7779	0.0001
2	TIDE (-)		2	0.1959	0.7395	24.8715	18.0421	0.0003
3	GRAINSIZ (+)		3	0.1464	0.8859	1.0910	29.5134	0.0001

Summary of Stepwise Procedure for Dependent Variable EPIWTPRD

Step	Variable Entered	Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	STEMS (+)		1	0.2149	0.2149	74.0458	6.8445	0.0149

Summary of Stepwise Procedure for Dependent Variable EPIWTPRD
(BLDWTPRD Included as an Independent Variable)

Step	Variable Entered	Removed	Number In	Partial R**2	Model R**2	C(p)	F	Prob>F
1	STEMS (+)		1	0.2149	0.2149	70.2578	6.8445	0.0149

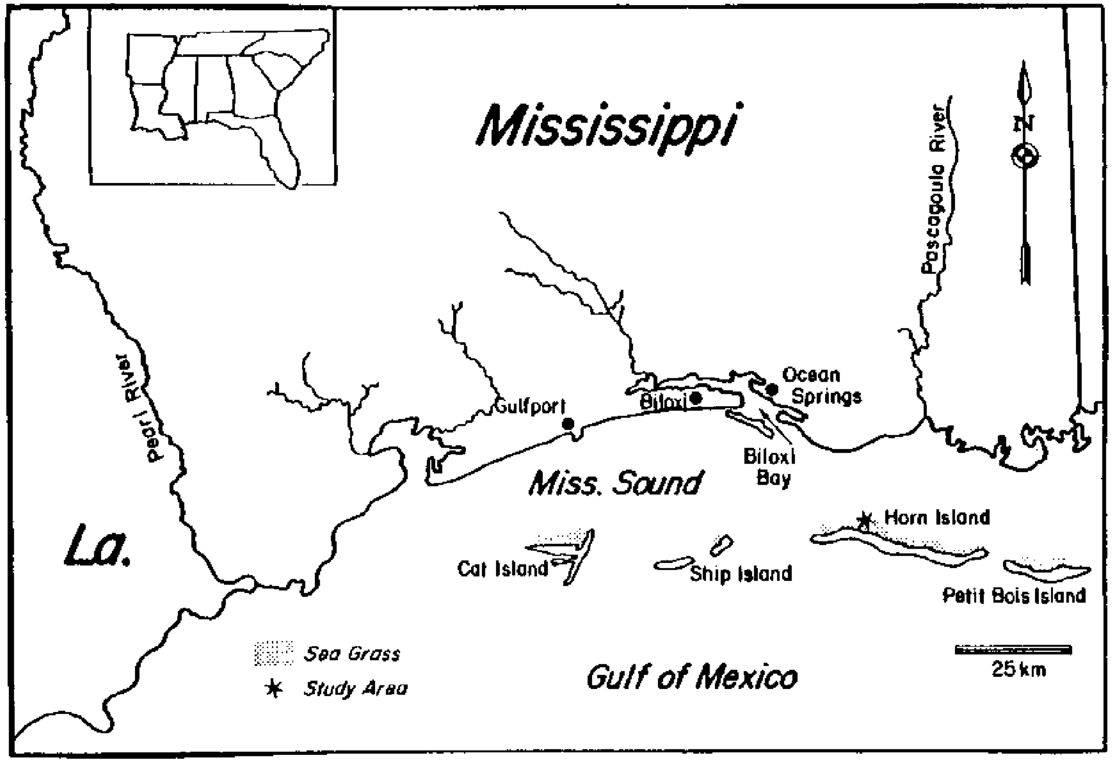


Figure 1. Map of study area.

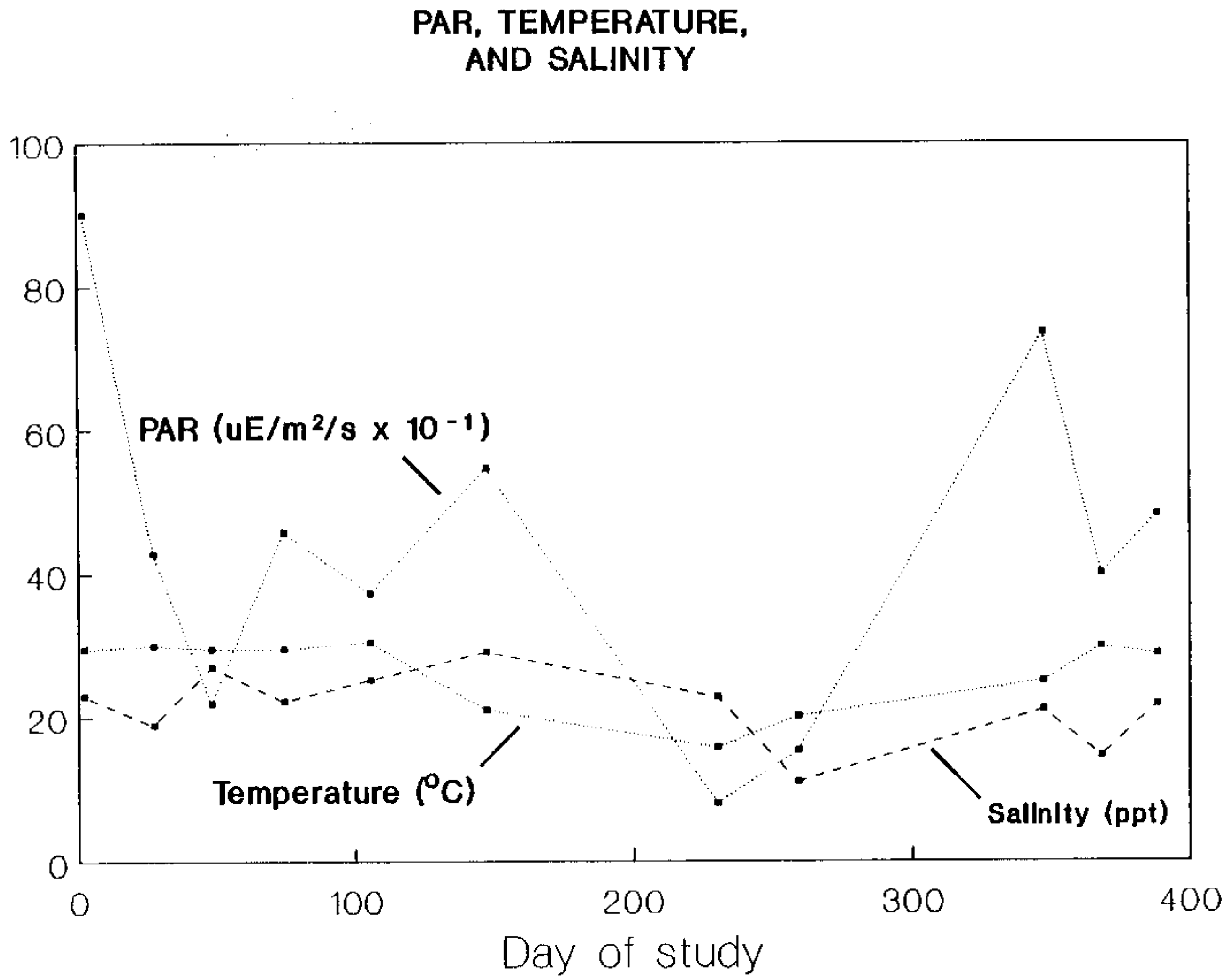

PAR, TEMPERATURE,
AND SALINITY
PAR (uE/m²/s x 10⁻¹)
Temperature (°C)
Salinity (ppt)
100
80
60
40
20
0
0
100
200
300
400
Day of study

Figure 2

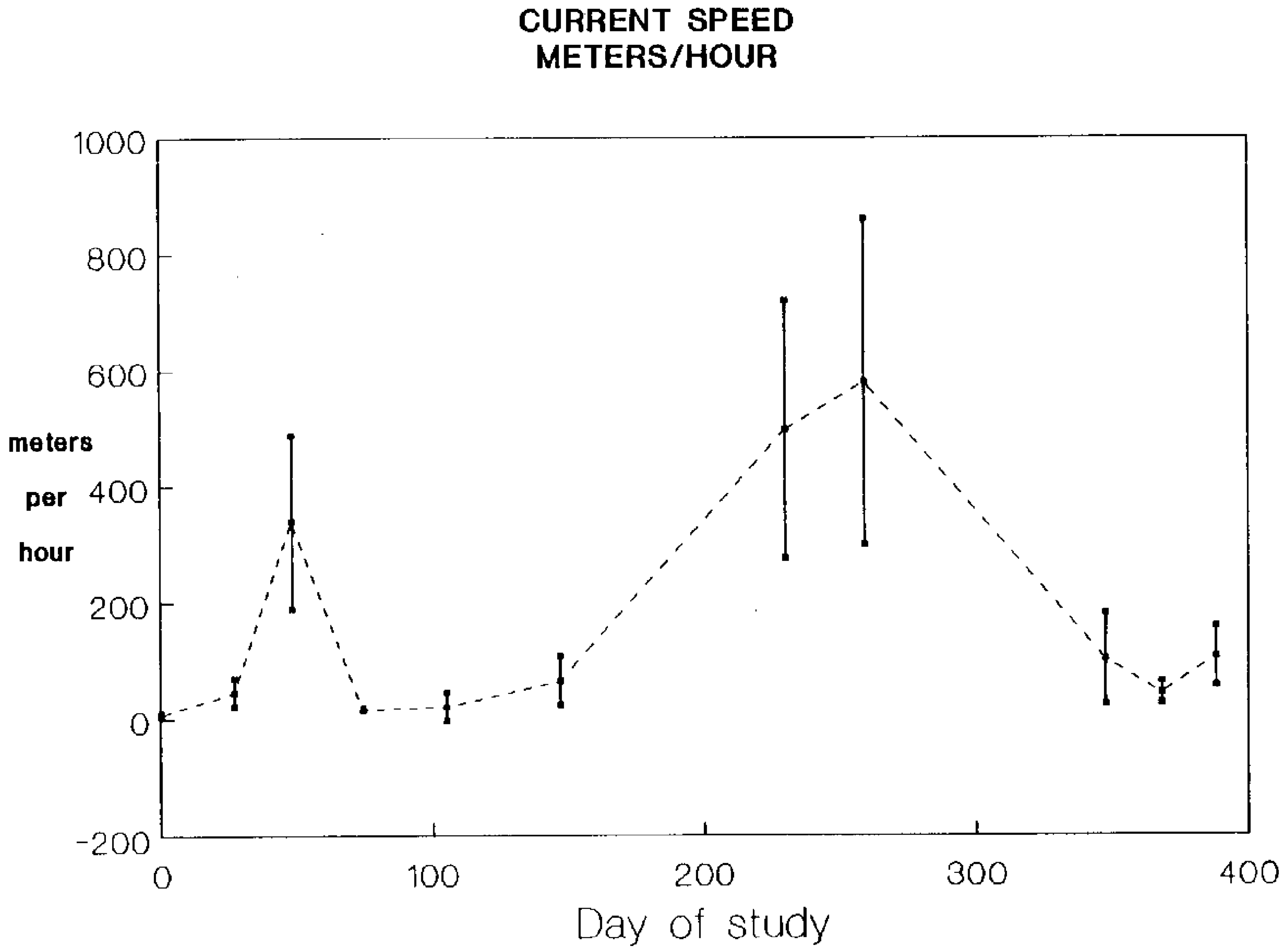

CURRENT SPEED
METERS/HOUR
1000
800
600
400
200
0
-200
meters
per
hour
0
100
200
300
400
Day of study

Figure 3

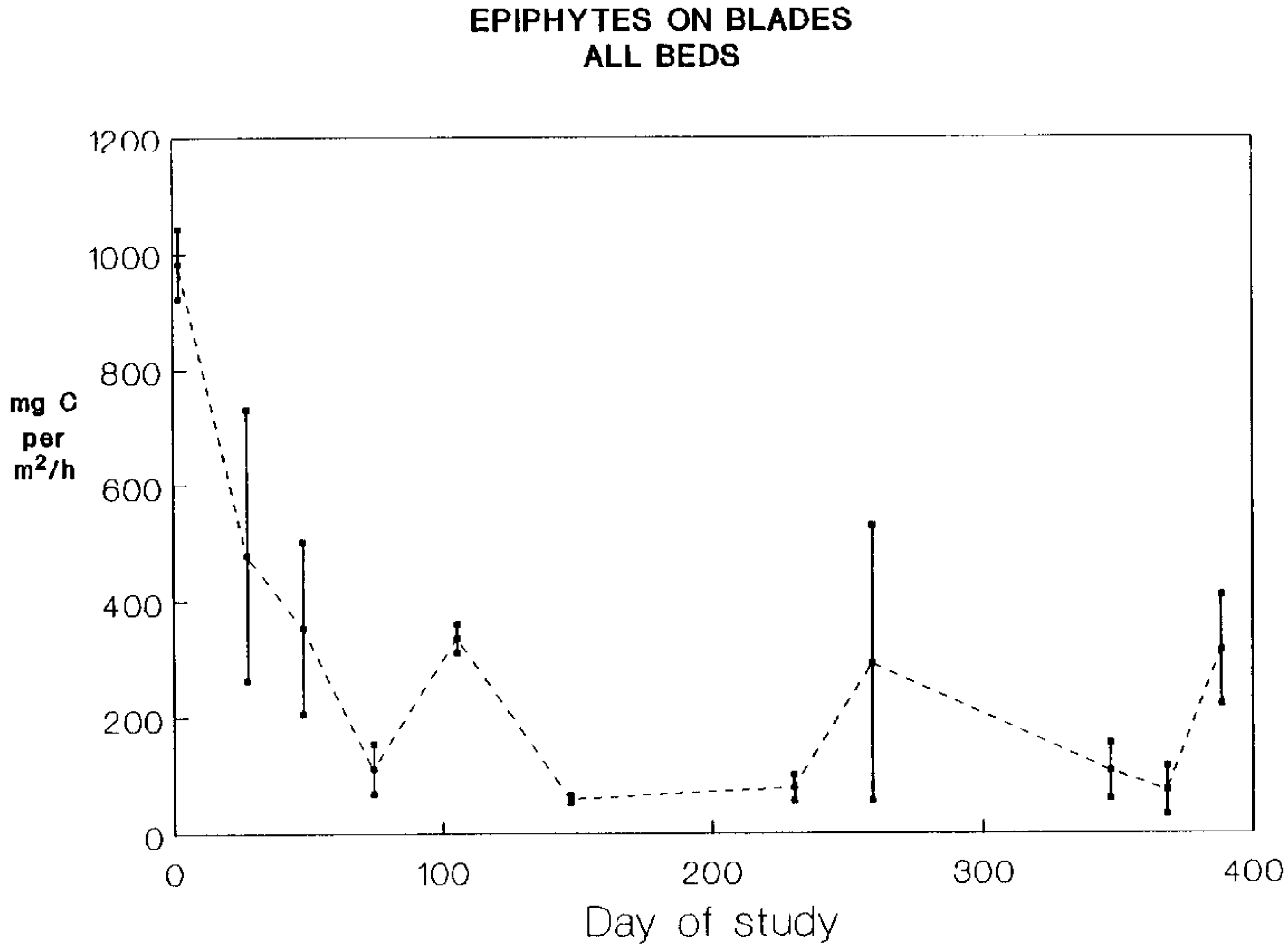

EPIPHYTES ON BLADES
ALL BEDS
mg C per m^2/h
1200
1000
800
600
400
200
0
0
100
200
300
400
Day of study

Figure 4

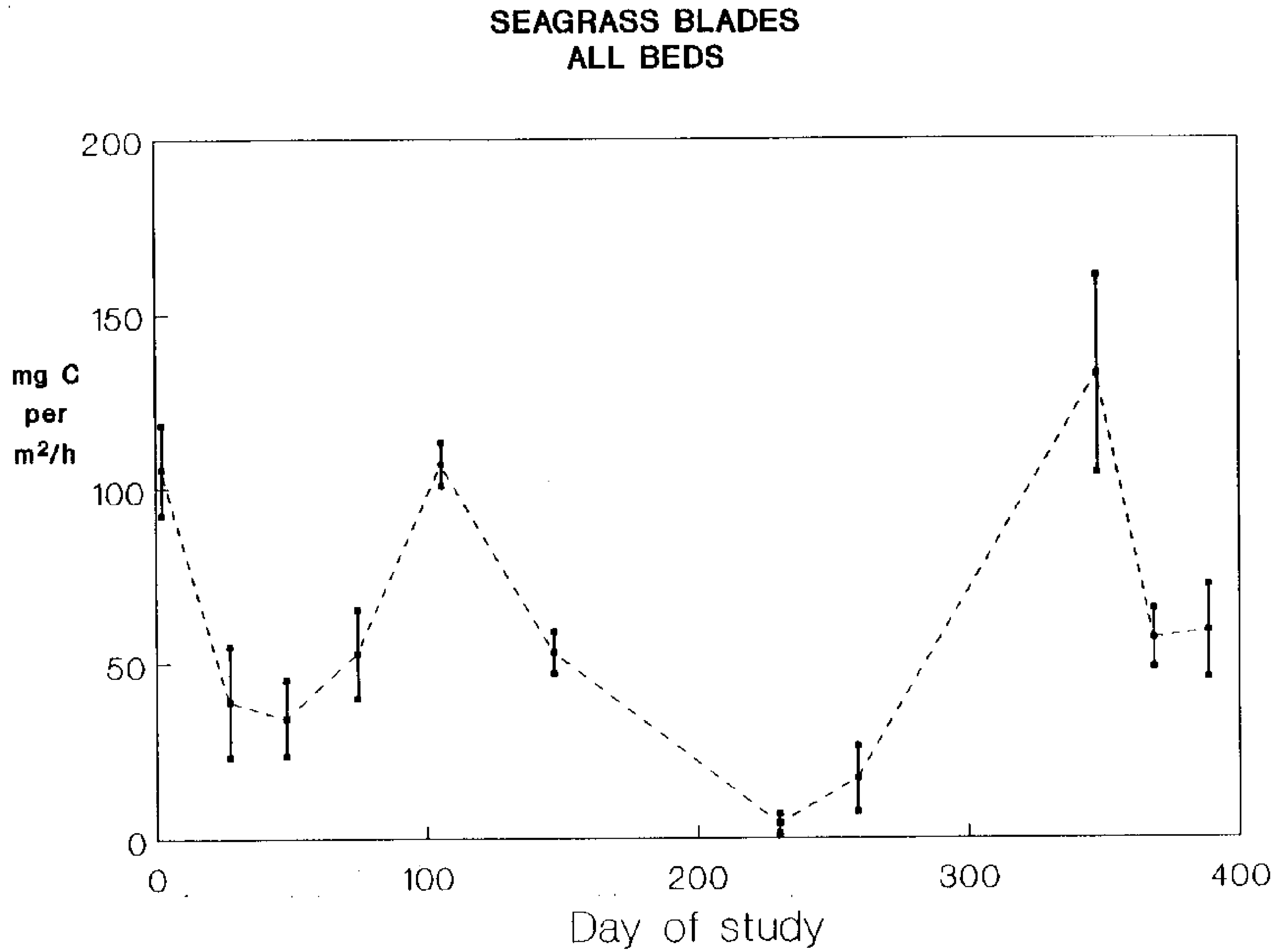

SEAGRASS BLADES
ALL BEDS
200
150
100
50
0
mg C
per
m²/h
0
100
200
300
400
Day of study

Figure 5

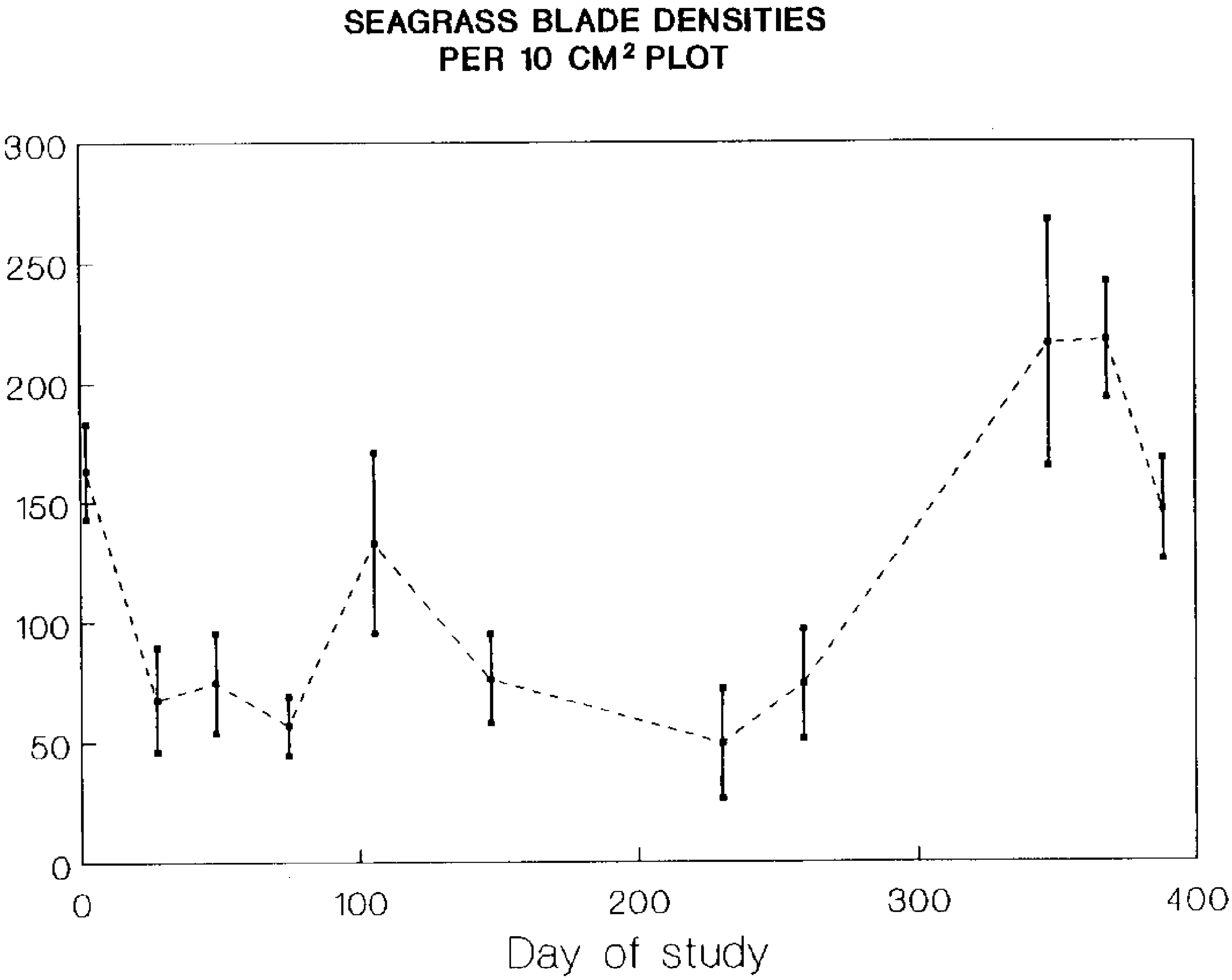

SEAGRASS BLADE DENSITIES
PER 10 CM^2 PLOT
300
250
200
150
100
50
0
0
100
200
300
400
Day of study

Figure 6

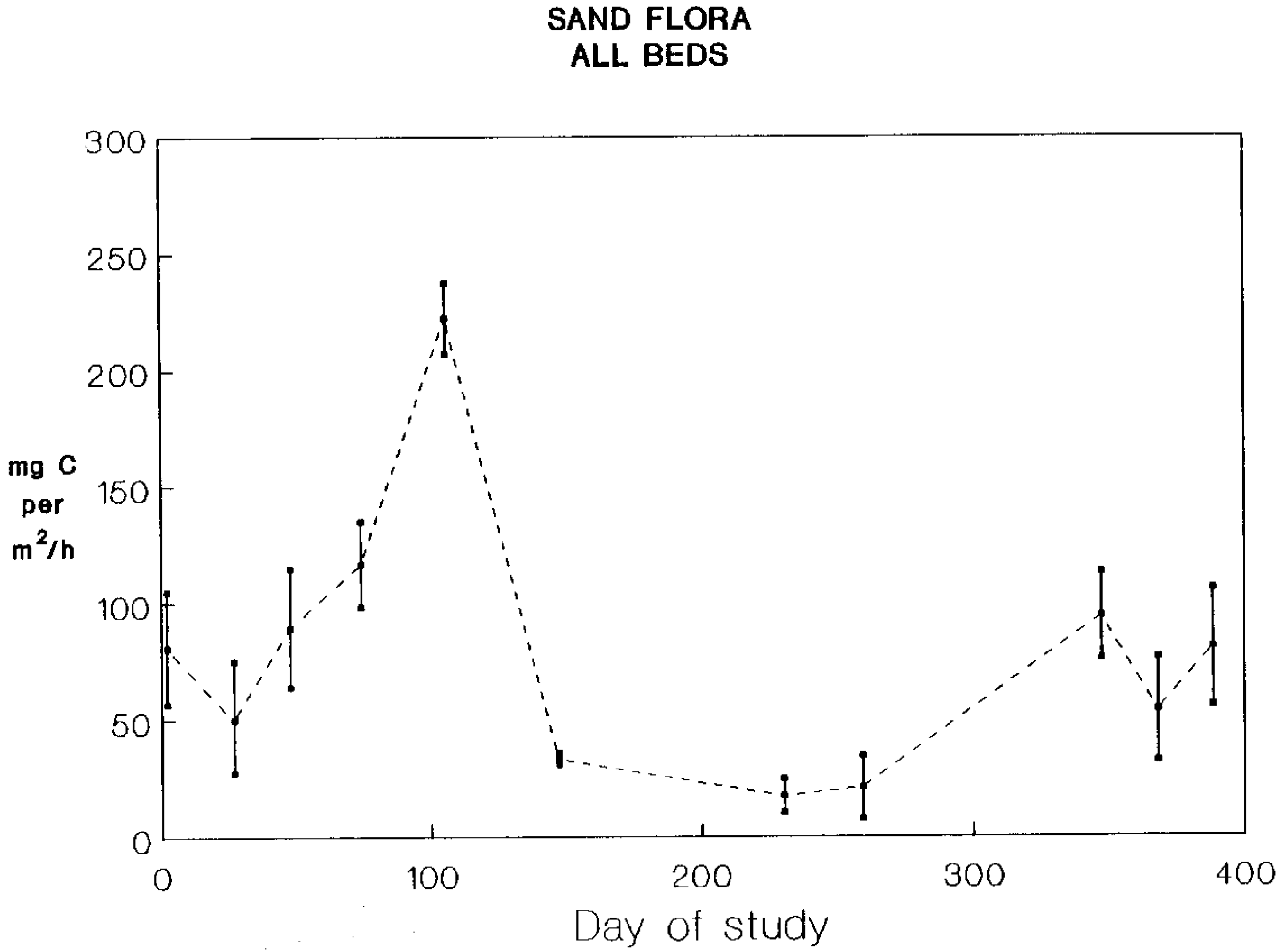
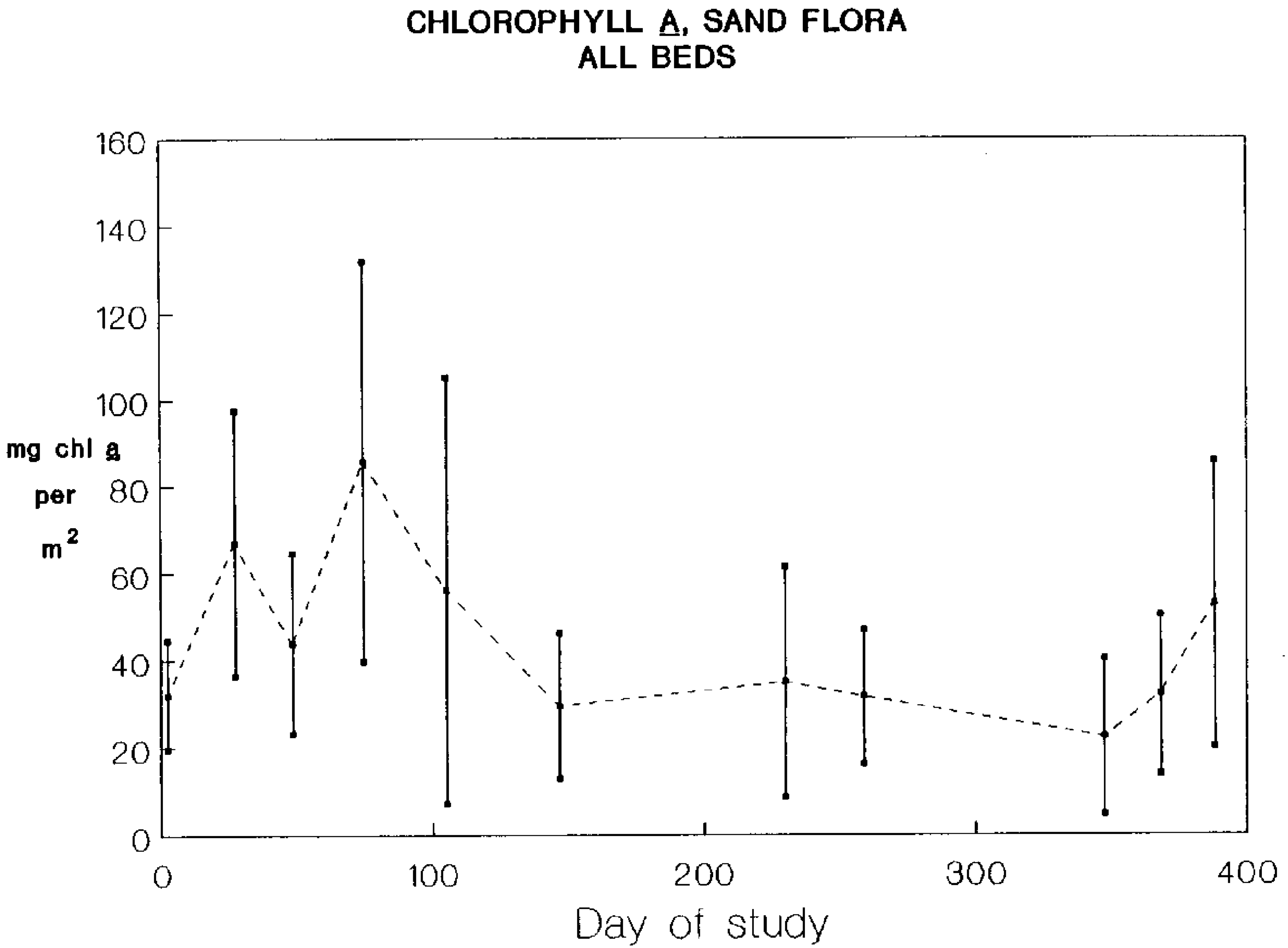

SAND FLORA
ALL BEDS
mg C per m^2/h
300
250
200
150
100
50
0
0
100
200
300
400
Day of study

Figure 7



CHLOROPHYLL A, SAND FLORA
ALL BEDS

Figure 8

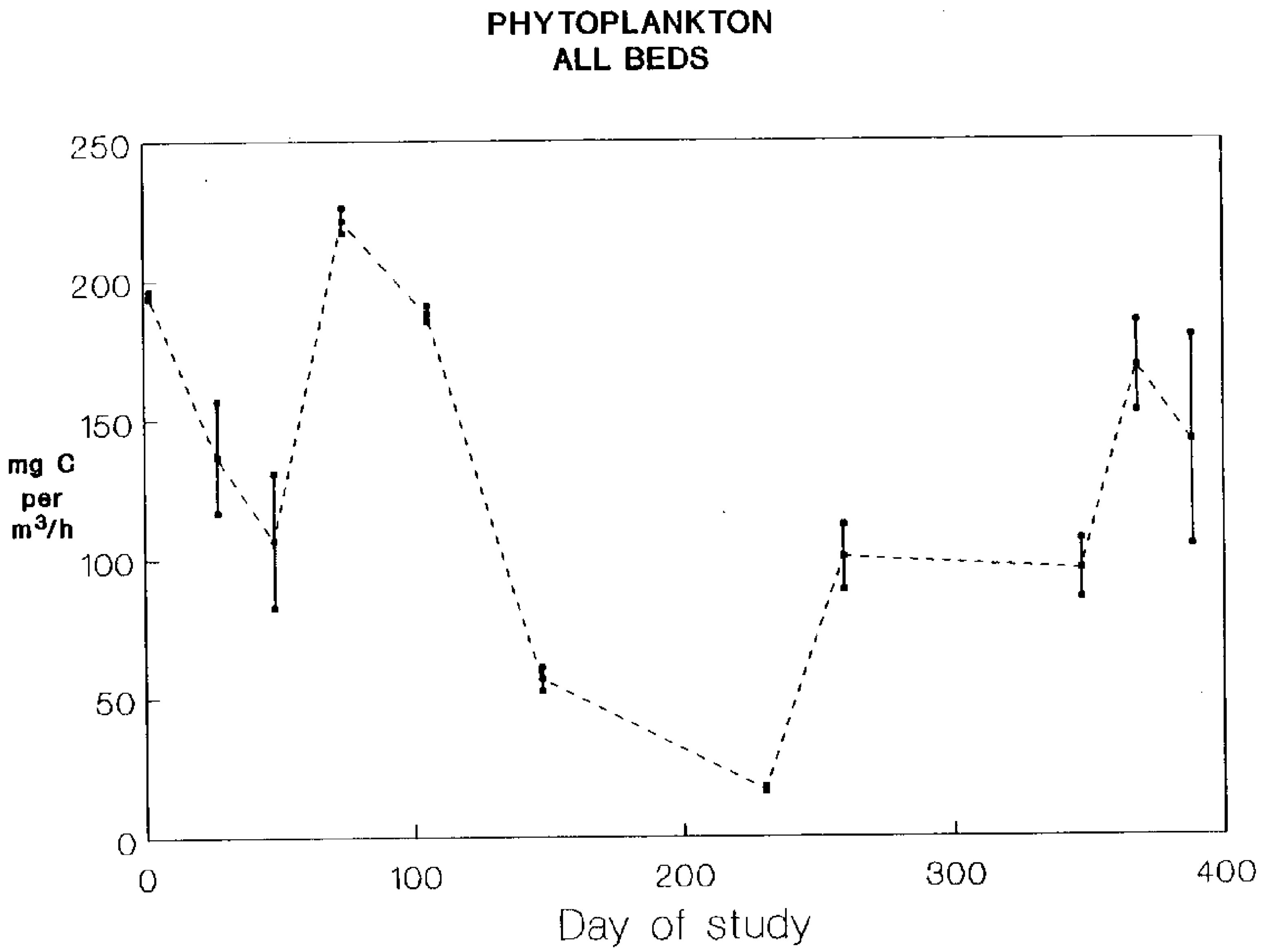

PHYTOPLANKTON
ALL BEDS
mg C
per
m^3/h
250
200
150
100
50
0
0
100
200
300
400
Day of study

Figure 9

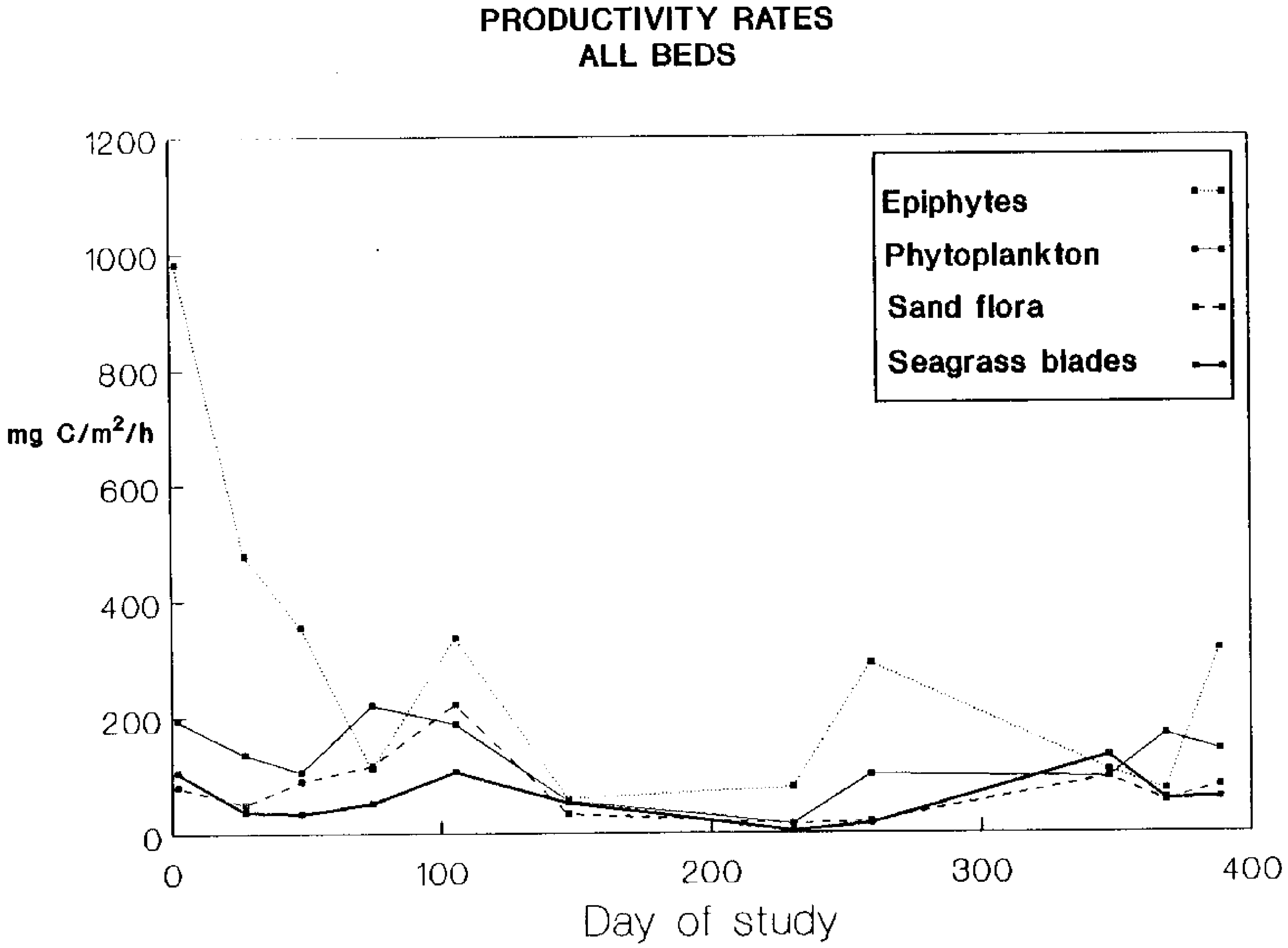
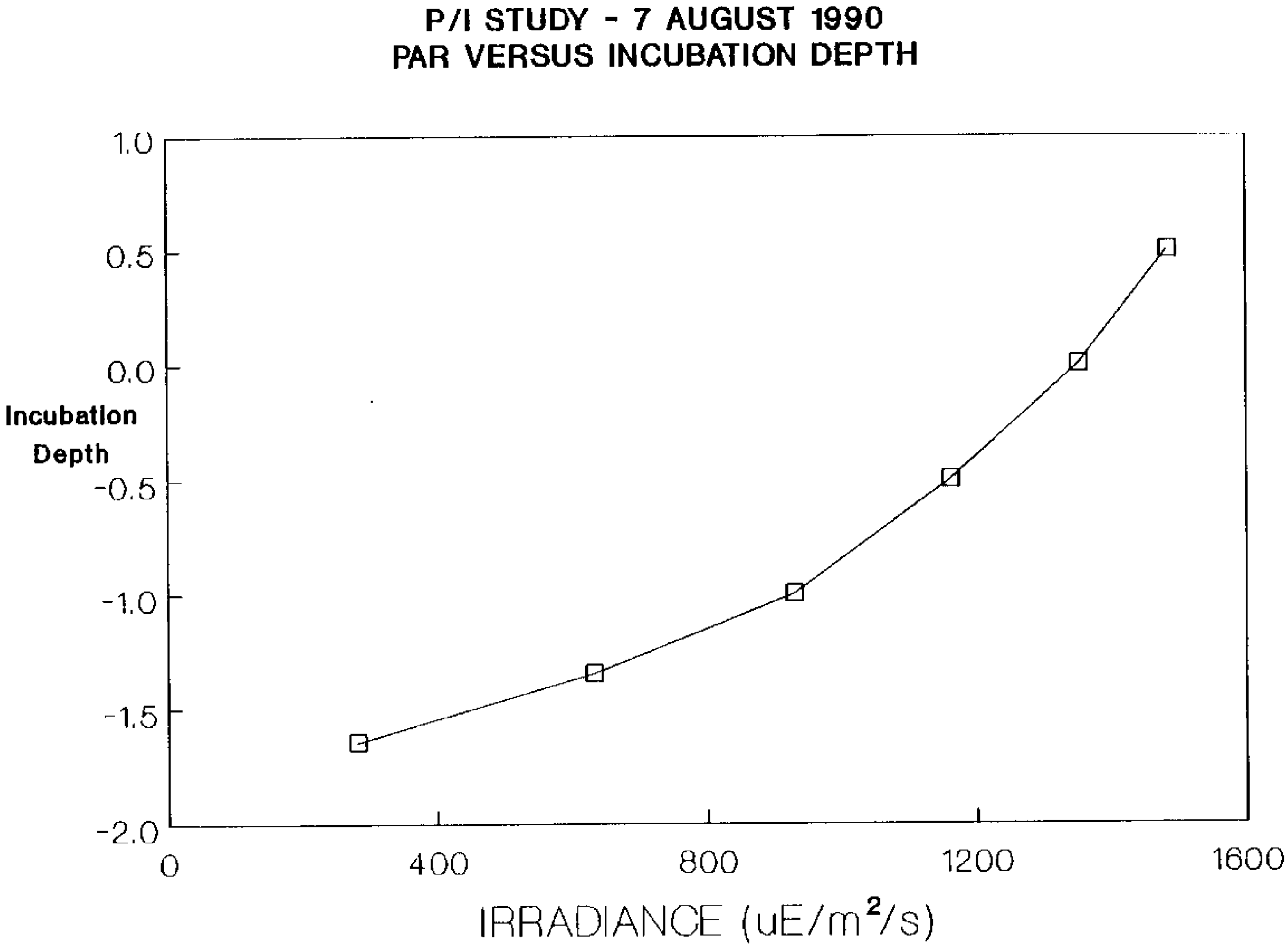

PRODUCTIVITY RATES
ALL BEDS
Epiphytes
Phytoplankton
Sand flora
Seagrass blades
mg C/m²/h
1200
1000
800
600
400
200
0
0
100
200
300
400
Day of study

Figure 10



P/I STUDY - 7 AUGUST 1990
PAR VERSUS INCUBATION DEPTH

Figure 11

P/I STUDY - 7 AUGUST 1990
PRIMARY PRODUCTIVITY VS. LIGHT
SEAGRASS EPIPHYTES

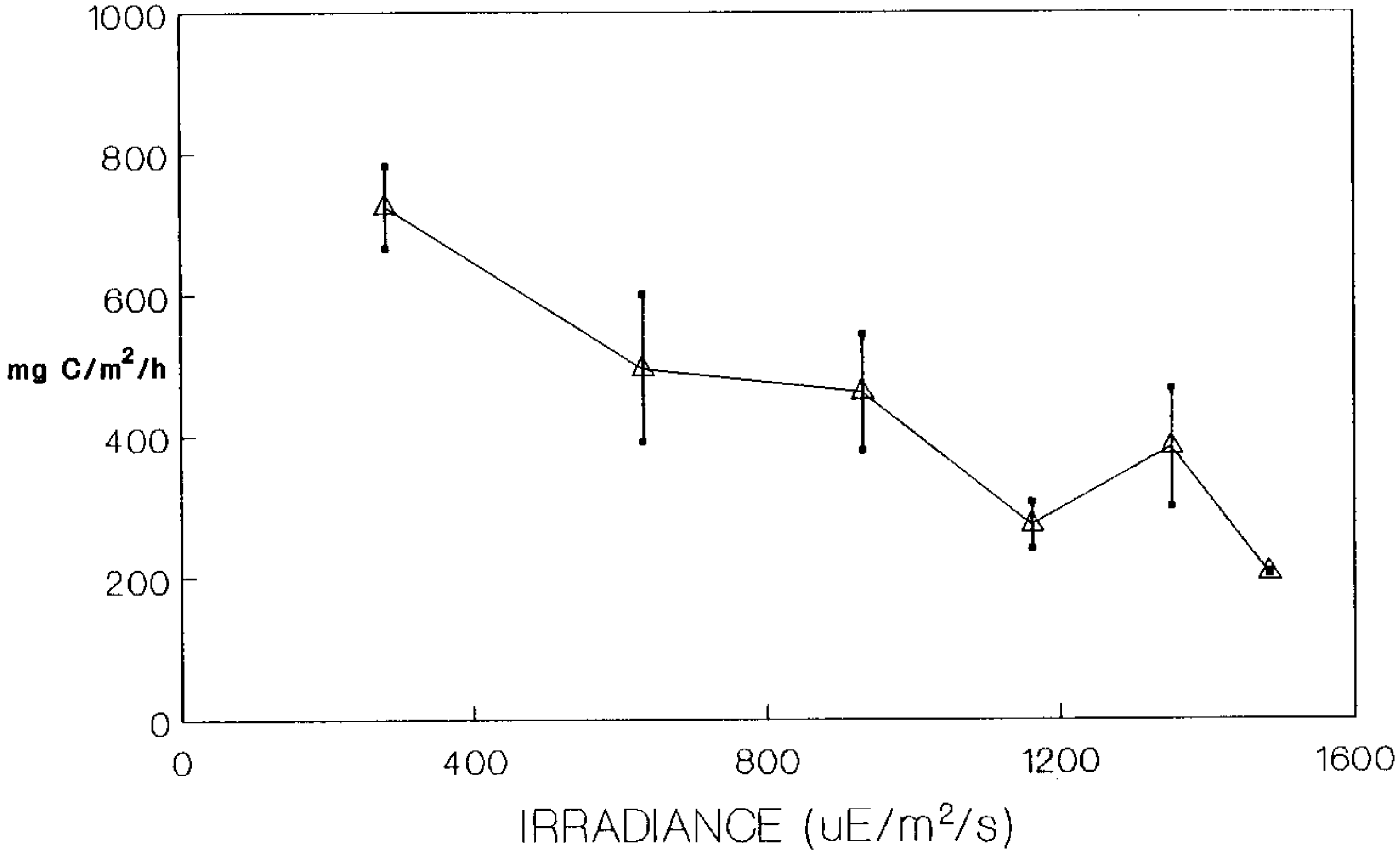


Figure 12

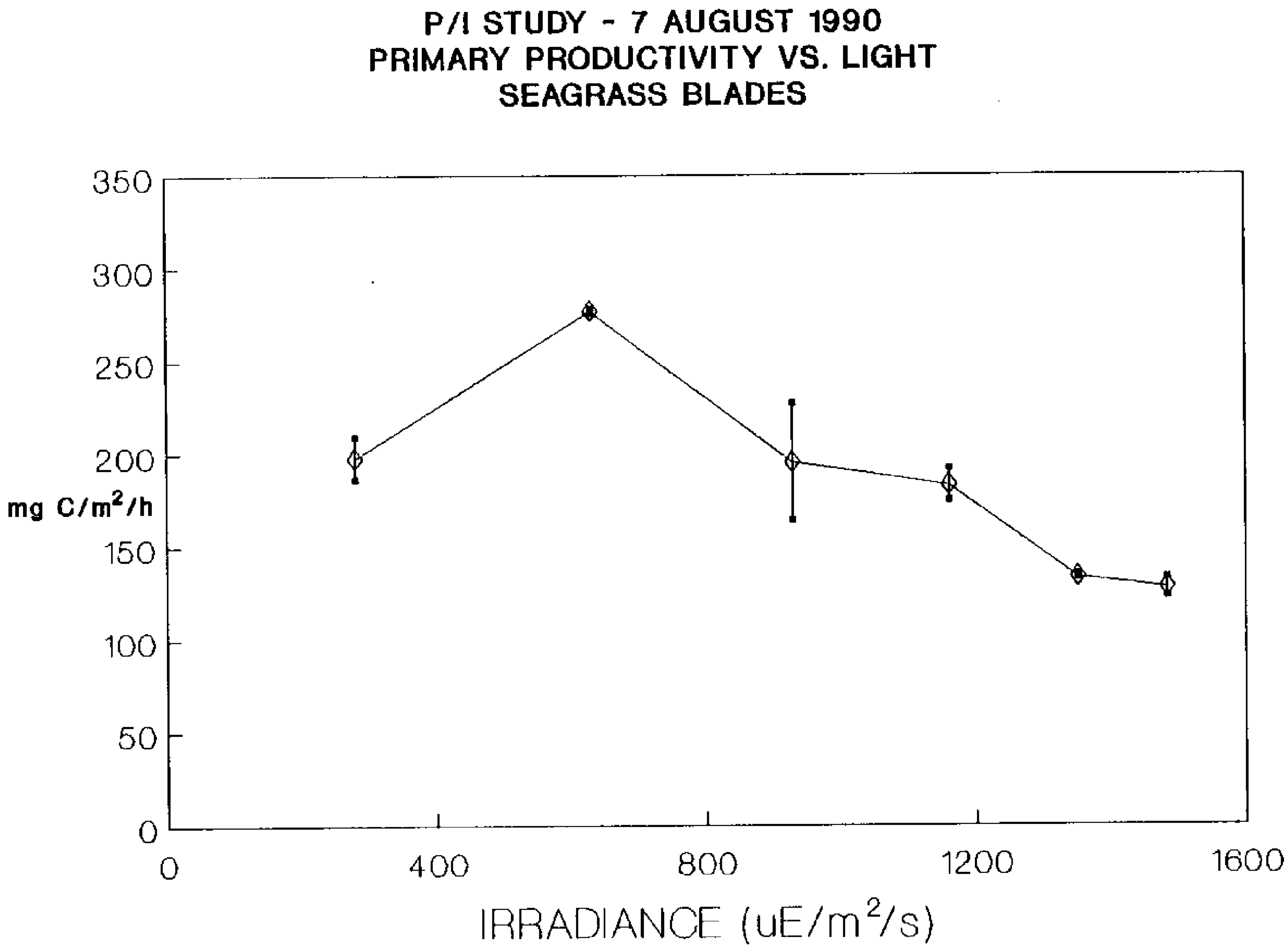
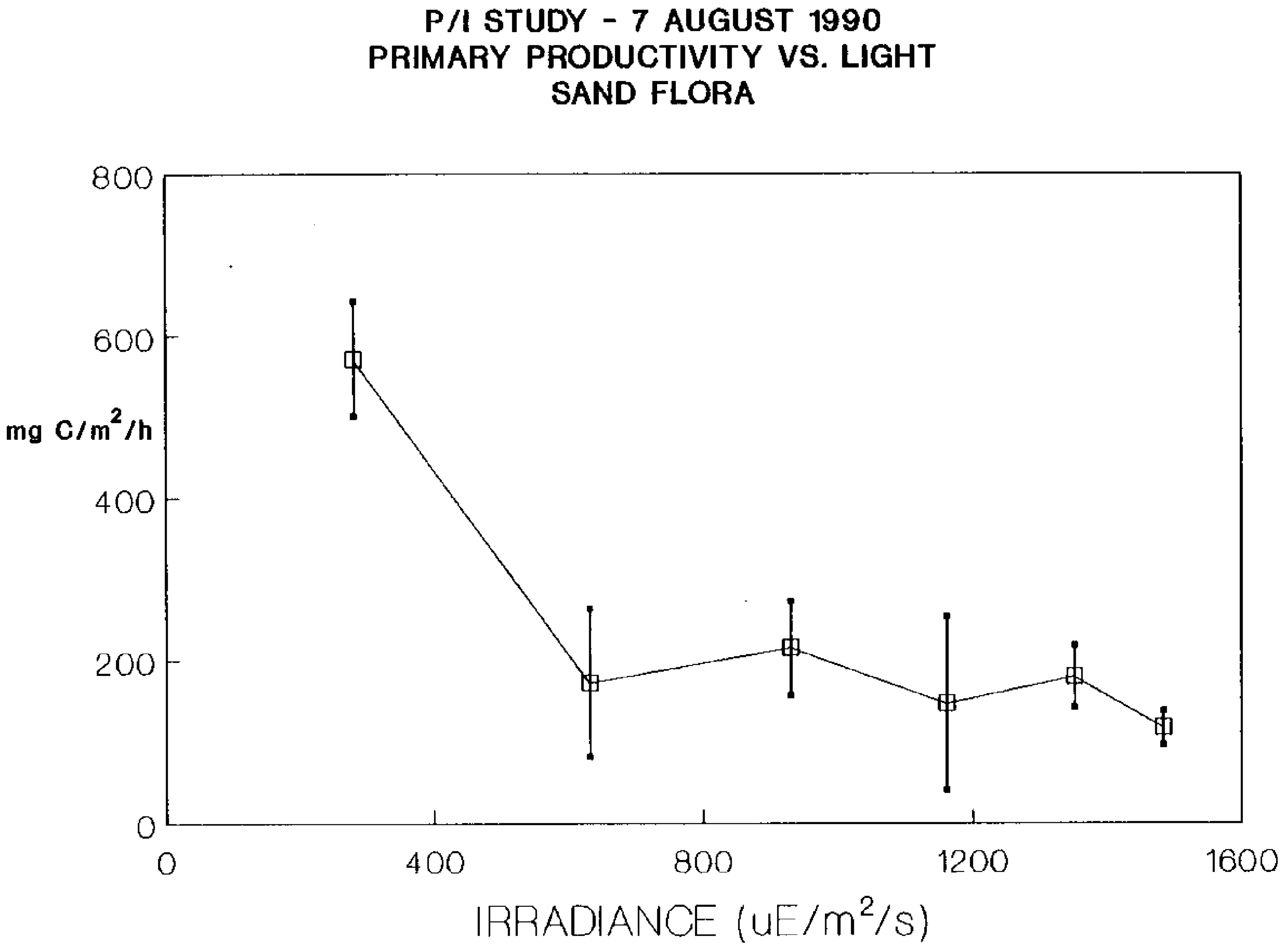

P/I STUDY - 7 AUGUST 1990
PRIMARY PRODUCTIVITY VS. LIGHT
SEAGRASS BLADES
350
300
250
200
mg C/m²/h
150
100
50
0
0
400
800
1200
1600
IRRADIANCE (uE/m²/s)

Figure 13



P/I STUDY - 7 AUGUST 1990
PRIMARY PRODUCTIVITY VS. LIGHT
SAND FLORA

Figure 14

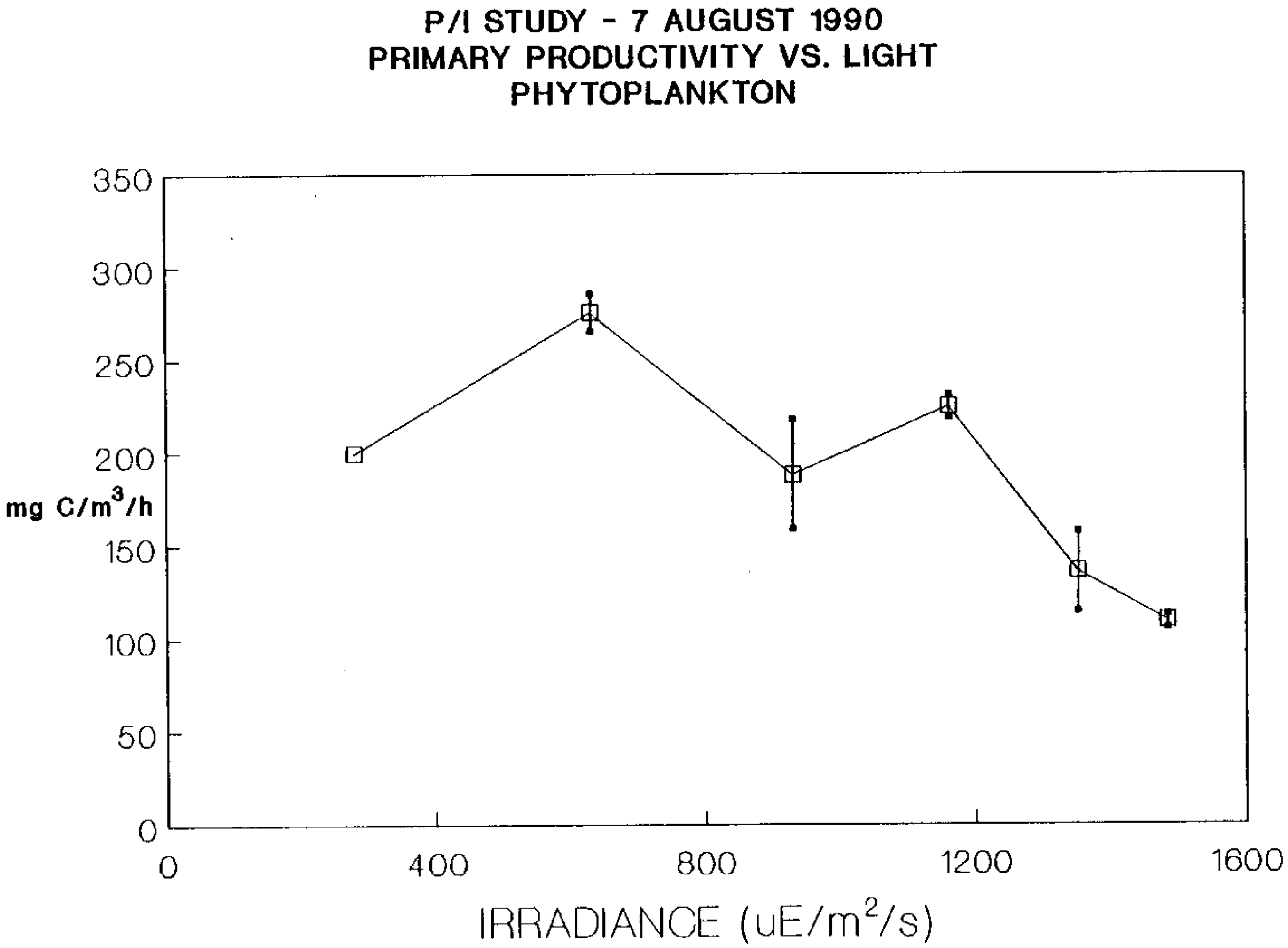

P/I STUDY - 7 AUGUST 1990
PRIMARY PRODUCTIVITY VS. LIGHT
PHYTOPLANKTON

Figure 15

P/I STUDY - 7 AUGUST 1990
PRIMARY PRODUCTIVITY VS. LIGHT

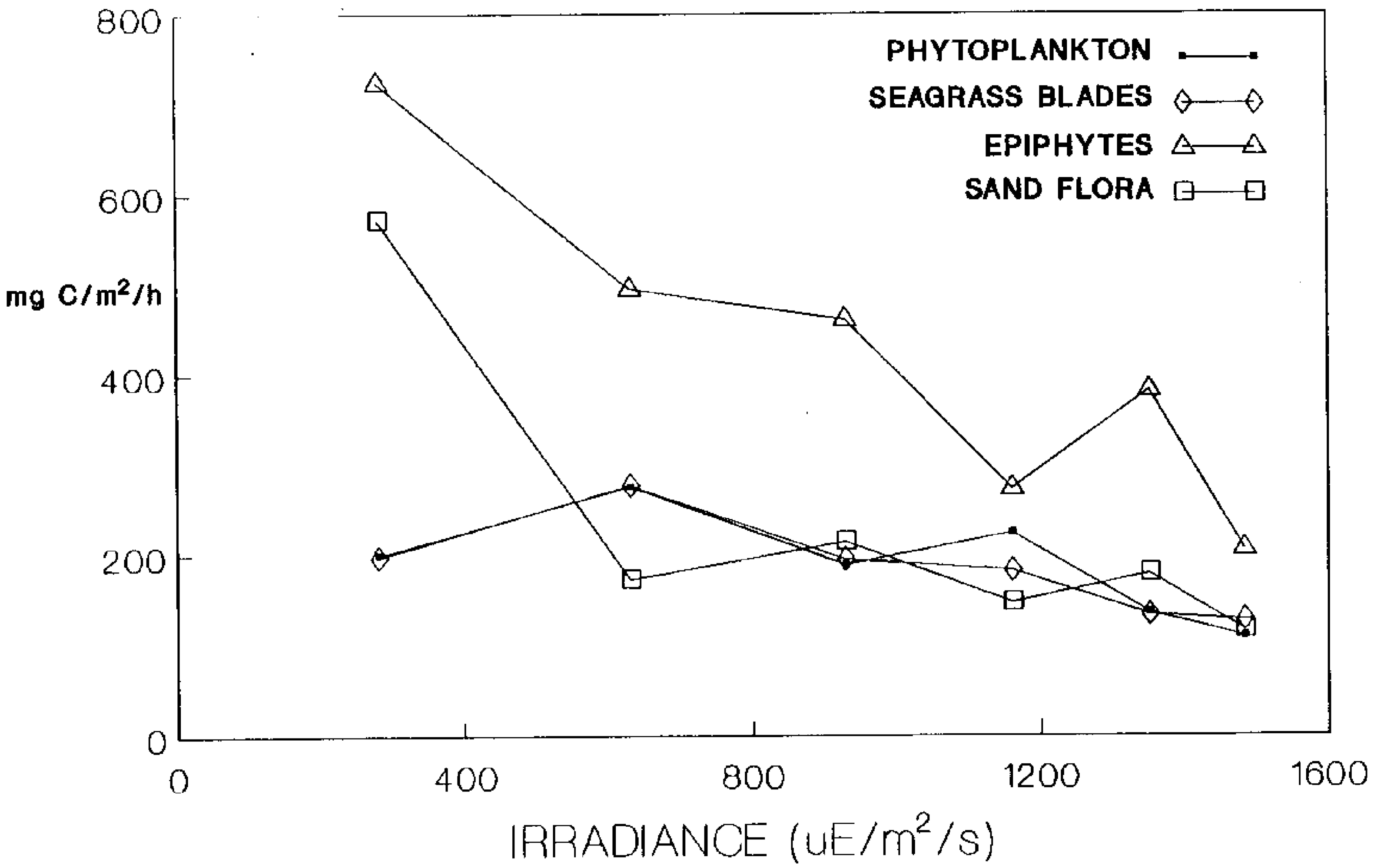


Figure 16

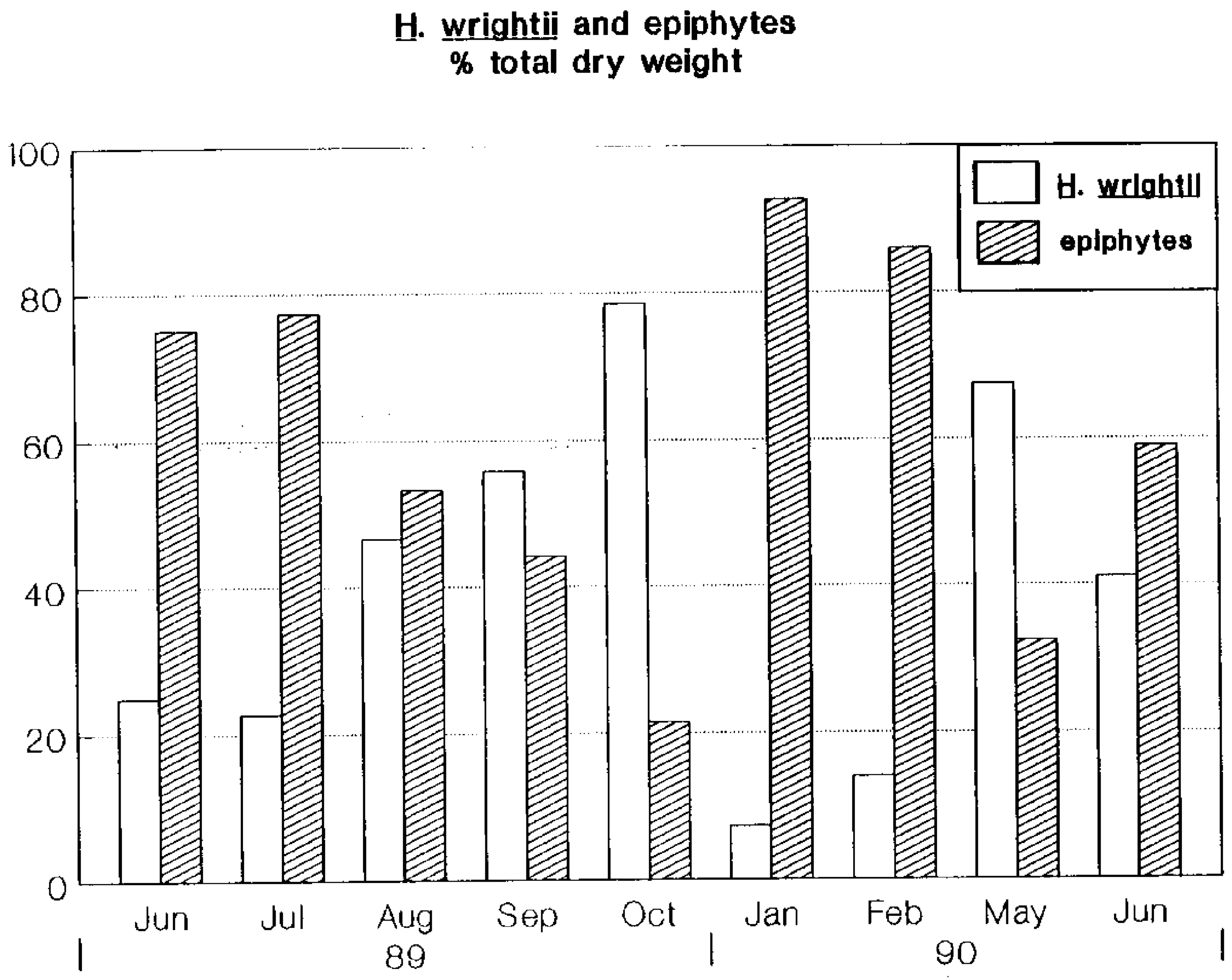

H. wrightii and epiphytes
% total dry weight
100
80
60
40
20
0
Jun
Jul
Aug
89
Sep
Oct
Jan
Feb
90
May
Jun
H. wrightii
epiphytes

Figure 17

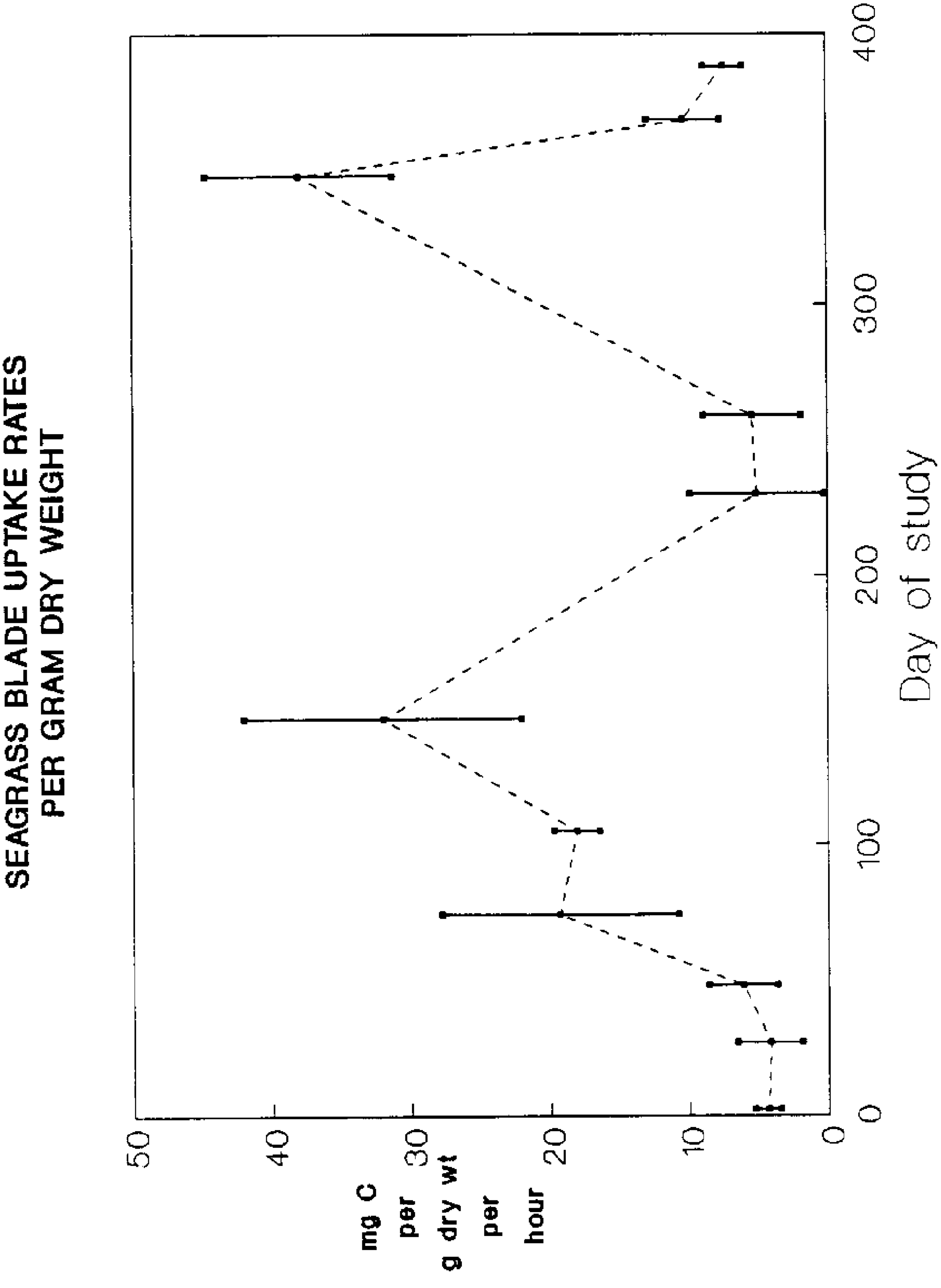

SEAGRASS BLADE UPTAKE RATES
PER GRAM DRY WEIGHT
mg C
per
g dry wt
per
hour
50
40
30
20
10
0
0
100
200
300
400
Day of study

Figure 18

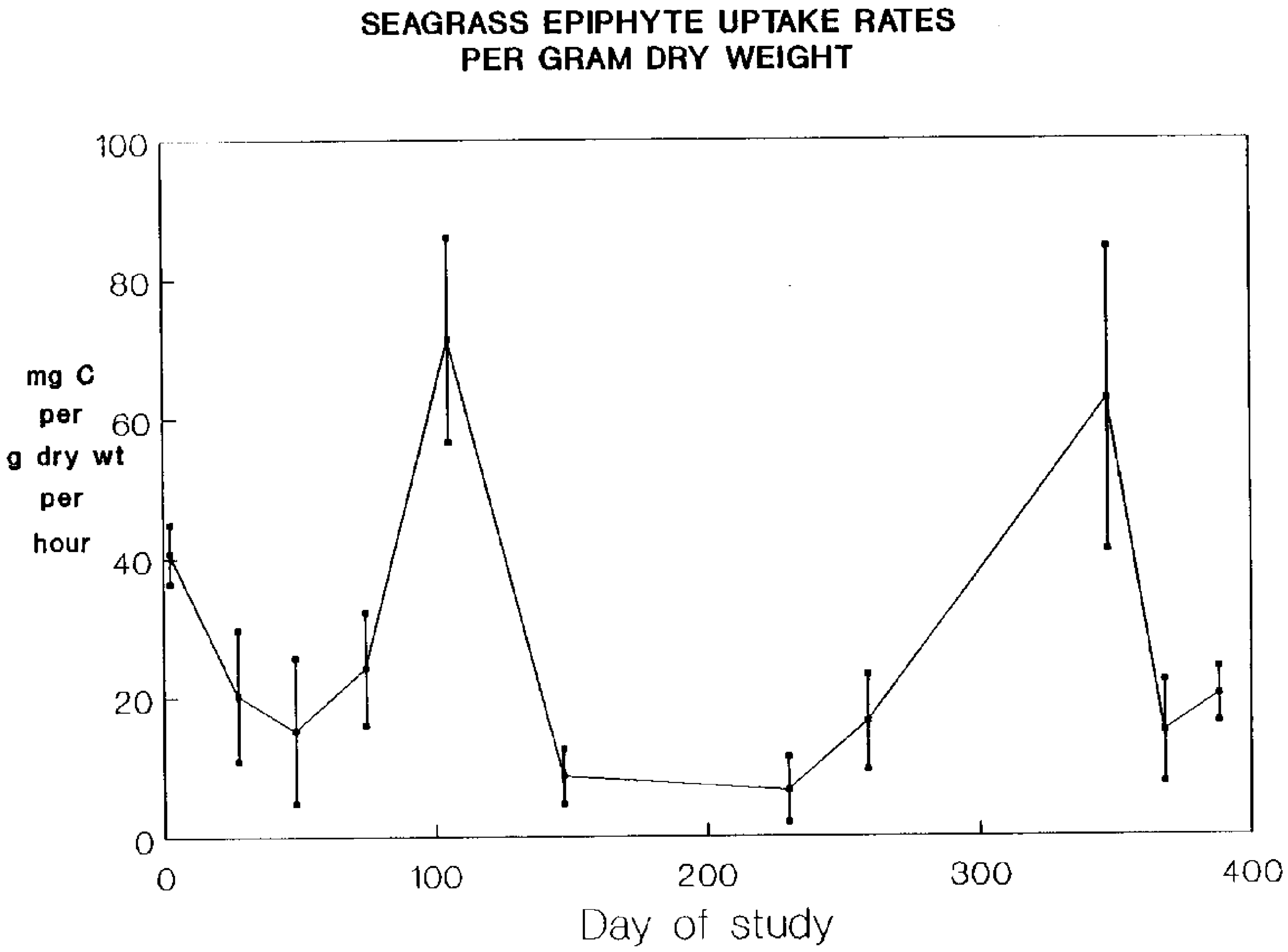
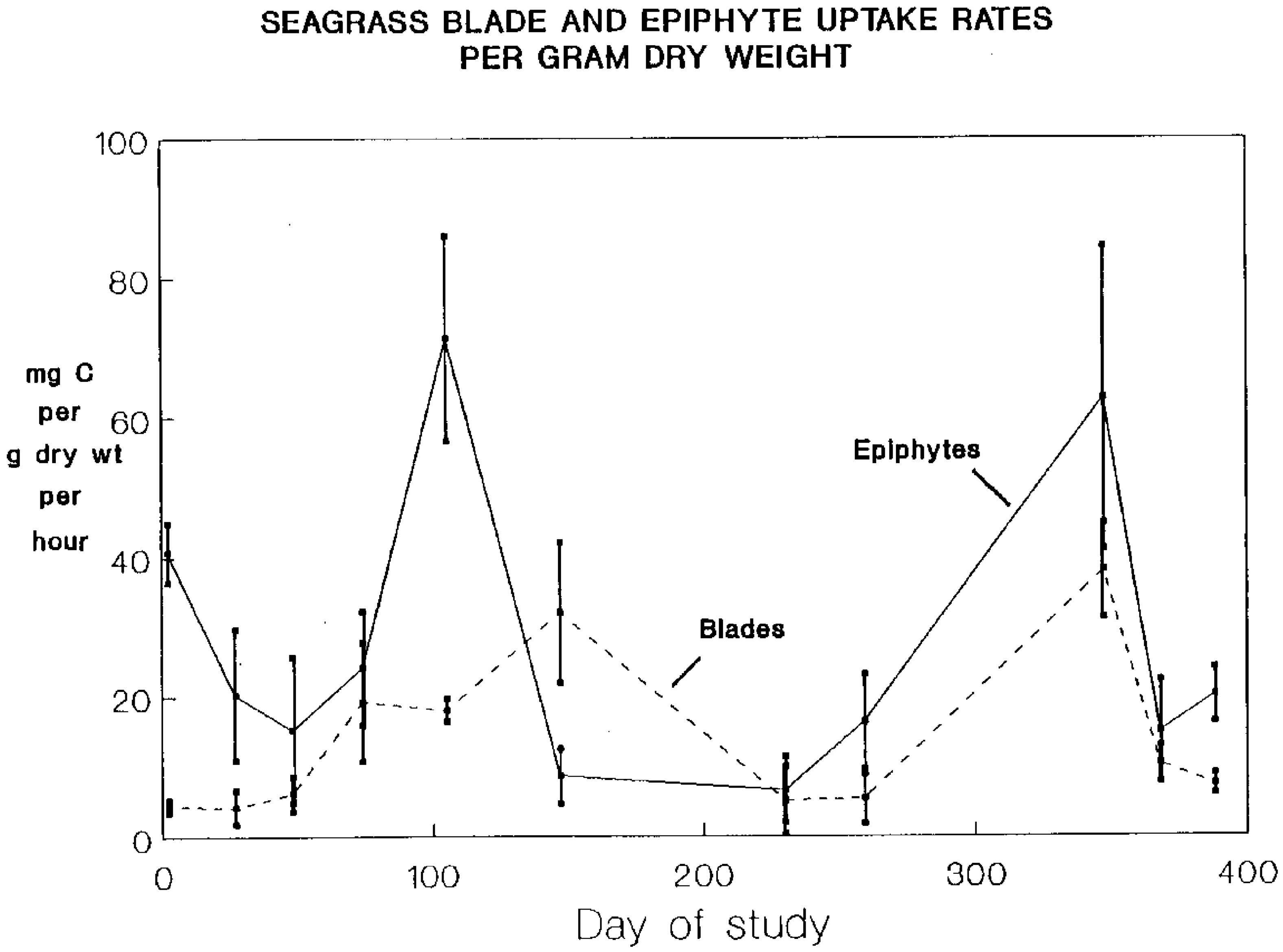

SEAGRASS EPIPHYTE UPTAKE RATES
PER GRAM DRY WEIGHT
mg C
per
g dry wt
per
hour
100
80
60
40
20
0
0
100
200
300
400
Day of study

Figure 19



SEAGRASS BLADE AND EPIPHYTE UPTAKE RATES
PER GRAM DRY WEIGHT

Figure 20