

## SEASONAL VARIATIONS IN NET PHOTOSYNTHETIC PERFORMANCE AND COVER OF INTERTIDAL MACROPHYTES

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### ABSTRACT

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Standing stocks and net photosynthetic performances were determined concurrently for the 13 most abundant intertidal macrophytes from San Clemente Island, California over a four-season period. A summer cover maximum and winter minimum occurred for *Colpomenia sinuosa* (Roth) Derbes & Solier, *Egrecia menziesii* (Turner) Areschoug, *Gigartina canaliculata* Harvey, *Halidrys dioica* Gardner, and *Sargassum agardhianum* J. Agardh, whereas *Eisenia arborea* Areschoug and *Corallina officinalis* var. *chilensis* (Decaisne) Kützing had fall maxima and summer minima in cover. *Ulva californica* Wille and *Gelidium pusillum* (Stackhouse) Le Jolis had maximal cover during spring. *Pterocladia capillacea* (Gmelin) Bornet & Thuret was the only species with peak cover in winter while three macrophytes, *Lithothrix aspergillum* J.E. Gray, blue-green algae, and *Phyllospadix torreyi* Watson displayed little seasonality in standing stocks. Highest net production rates were measured during summer for nine of the 13 species and minimum rates were recorded in spring and to a lesser extent during winter. Correlations between seasonal fluctuations in standing stock and productivity were evident for only eight species. Total daily community production reached a peak in the fall ( $1.22 \text{ g C fixed m}^{-2} \text{ of substratum day}^{-1}$ ) and declined sharply through winter to a spring low ( $0.47 \text{ g C m}^{-2} \text{ day}^{-1}$ ), closely paralleling changes in ambient water temperature. Blue-green algae, *C. officinalis* var. *chilensis*, *P. capillacea*, and *E. menziesii* contributed 76% of the total community primary productivity for the year. Seasonal patterns of photosynthetic performances were highly variable with a tendency for most species to attain peak daily photosynthetic rates coincident with higher temperatures and longer daylength.

### INTRODUCTION

The role of benthic macrophytes in marine productivity is poorly known, even though coastal benthic communities have been described (Ryther, 1963; Mann, 1973) as some of the most productive systems on earth. Most information has been derived from short-term photosynthetic measurements (e.g., Johnston, 1969; Littler and Murray, 1974; Buesa, 1977) or long-term population dynamics and growth rate measurements (e.g., Mann, 1972a,b). There

have been few attempts to identify the potentially important contributors to community energetics by integrating seasonal variations in standing stocks (e.g., total biomass, cover, density) of benthic producers with their short-term photosynthetic rates. The forms with the highest photosynthetic rates are often not the most abundant members of the communities (Littler and Murray, 1974; Buesa, 1977) and standing stocks can show dramatic seasonal variability (Doty, 1971a,b). Therefore, to clearly understand overall community production dynamics, both standing stocks and photosynthetic rates must be assessed on a seasonal basis.

Most seasonal studies of macrophyte photosynthesis have been performed (King and Schramm, 1976; Brinkhuis, 1977a,b) on thalli that have been acclimated to artificial laboratory conditions for one to several days and no well-defined seasonal patterns have emerged. For example, Zavodnik (1973a) found laboratory rates of *Fucus virsoides* (Don) J. Ag. to be lowest during summer and highest in winter, while field measurements gave the opposite result. According to King and Schramm (1976), the highest rates of net photosynthesis tended to occur in the spring and summer corresponding with the seasonal growth patterns. The laboratory photosynthetic rates of salt marsh macro algae also have been shown to be closely related to seasonal irradiation levels and changes in standing stocks (Brinkhuis, 1977a,b), with maximum photosynthetic potential reported in the spring and fall for *Ascophyllum nodosum* (L.) Le Jolis ead *scorpioides* (Hornemann) Reinke and during the spring and summer months for *Fucus vesiculosus* L. and *Ulva lactuca* L. In contrast, the surface fronds of the giant kelp *Macrocystis* showed (Clendenning, 1971) a large summer decline in photosynthetic output in Southern California. *Chondrus crispus* Stackhouse was found (Mathieson and Norall, 1975) to vary greatly in its optimum photosynthetic response to light and temperature both seasonally and spatially. For all of the intertidal and subtidal algae examined by Yokohama (1973), the optimum temperature for photosynthesis was higher in summer than during winter; however, in some cases, photosynthetic rates at all temperatures were higher in winter-collected material than during summer.

A prerequisite to understanding coastal, benthic community energetics is knowledge of the seasonal and intrinsic variability in the productivity of the dominant primary producers. The purpose of this study was to estimate the potential macrophytic production of an intertidal system, thus, we concurrently measured and integrated the light-saturated net photosynthetic performances and standing stocks of the dominant macrophytes over a four-season period.

## MATERIALS AND METHODS

Four seasonal assessments (i.e., 22–24 October 1976, 18–21 December 1976, 19–22 March 1977, and 16–19 June 1977) of productivity and standing stock (used herein to refer to the total % cover) were conducted at Wilson Cove, San Clemente Island, California using the same study site as Littler and Murray (1974). The methods employed to measure macrophyte standing stocks have

been evaluated and presented in detail elsewhere (Littler, 1971; Littler and Murray, 1975). A brief summary of these methods, including modifications used in the current study, is given below.

### *Standing stock assessments*

Because space and light have been documented (Connell, 1972) to be limiting resources in rocky-intertidal habitats and the fact that marine macrophytes compete for these using their cover, we felt that % cover would be the most appropriate estimate of the standing stock of macrophytes. During each seasonal assessment, photographs of 102 labelled, permanently-marked  $30 \times 50$  cm quadrats ( $0.15 \text{ m}^2$ ) were taken during low tide at right angles to the substratum with 35-mm cameras equipped with electronic flash units; also, detailed field notes were recorded of species composition and abundance. Sample plots were placed at 0.5-m intervals along three transect lines approximately 10 m apart located perpendicularly to the shoreline ( $\sim 30^\circ$  magnetic). A minimum of two transparencies were taken of each sample quadrat, one using color film (Kodachrome 64) and the other Ektachrome IR film. IR photographs increased the accuracy in measuring the abundances of certain macrophytes, particularly the blue-green algae, and revealed the presence of unhealthy or bleached thalli, which were not included in the analyses. In cases where sampling included multi-layered macrophyte canopies, additional photographs were taken after upper layers were carefully moved aside to measure stratification.

Species composition and cover were determined in the laboratory for each quadrat from analyses of photographs and the detailed field notes; cover estimates of the macrophytic standing stocks were made by the point-intercept method described by Littler and Murray (1975). Species observed in quadrats but not encountered by point-intercepts were assigned a value of 0.1% cover.

### *Primary production measurements*

More than 400 experimental incubations were performed on the 13 most abundant intertidal macrophytes. Net primary productivity (used synonymously with the rate of net photosynthesis in this paper) and respiration were determined using Beckman Field Lab oxygen analyzers with 1220-ml wide-mouth clamp-lid bottles as light, dark, and blank incubation containers. The bottles were cleaned in aqua-regia and aged for 30 days in distilled water prior to use. Dark bottles, produced by wrapping bottles with two layers of taped, heavy-duty aluminum foil, were incubated separately to prevent reflected light from impinging upon the light or blank bottles.

Care was taken to select healthy individuals that were representative of populations occurring within the intertidal quadrats assessed for cover. Several whole thalli were collected while submerged, from the same populations throughout the year, and placed in trays of ambient sea water. Thalli were

then gently cleaned of obvious epiphytes; those that were heavily overgrown were discarded. Whole organisms were incubated whenever possible and the use of multiple small blades or branches was minimized to prevent self-shading. Incubations of the larger kelps [*Egregia menziesii* (Turner) Areschoug, *Eisenia arborea* Areschoug, and *Halidrys dioica* Gardner] were conducted on representative blades or branches. After sorting and cleaning, thalli were carefully transferred to bottles completely filled with filtered ( $10\ \mu\text{m}$ ) sea water. To avoid bubble formation during incubation, we poured 25-l batches of ambient sea water (supersaturated with oxygen) from one contaminant-free bucket to another until a stock incubation medium at air saturation was obtained (Strickland, 1960). Several bottles were used to determine the initial dissolved oxygen content for each experimental period.

Throughout the experiments, an average thallus concentration of  $0.26\ \text{g dry wt. l}^{-1}$  ( $0.04\text{--}0.80\ \text{g l}^{-1}$ ) was used for all macrophytes. Dark bottles usually contained twice this amount of algal material with the final oxygen content seldom dropping below 70% saturation. Preliminary linearity runs showed that the largest weights of macrophytes chosen could be allowed to photosynthesize for as long as 6 h without a decrease in the photosynthetic rate and only a 12% depletion in total carbon dioxide. A minimum of four light and two dark bottles were incubated in clear polycarbonate trays between the starting times of 09.30 and 11.00 h and finishing times of 12.30 to 15.00 h (3.0–4.0 h of incubation) with the intent of minimizing differences due to endogenous metabolic periodicities. All bottles were thoroughly mixed at 10–15-min intervals during the incubation period to disrupt metabolically induced diffusion gradients. Cooling was maintained by replenishing ambient sea water at 10–15-min intervals while the trays were incubated in full sunlight near the water's edge. Illuminance (klux) and quantum flux [ $\mu\text{E m}^{-2}\ \text{s}^{-1}$ , photosynthetically active radiation (PhAR)] were measured next to the incubation trays with a Lambda Instruments L.I. 185 Quantum/Photometer at 15–30-min intervals throughout the experiments. Temperature in the trays was also monitored during the same intervals.

At the end of each incubation period, the oxygen contents of the bottles were determined. Each bottle contained a perforated acrylic partition to separate the thalli from a magnetic stirring bar; each tray contained four bottles placed upon specially-constructed four-unit stirring motors that were air-driven by a foot pump from an inflatable boat kit.

After oxygen levels were recorded, thalli were blotted, placed in labelled polyethylene bags, and returned to the laboratory. Measurable impressions of the macrophytes were made by carefully spreading and photocopying individual thalli. Area determinations (two-dimensional of one surface) were made from each photocopy by means of a point-intercept method. The inherent assumption in basing calculations on two-dimensional thallus area is that at any one time only a single thallus side faces the light. The specimens were then dried at  $80^\circ\text{C}$  until they reached constant weight. In the case of the corallines and blue-green algae, organic dry weight following 5.0 h of combustion at  $500^\circ\text{C}$  was used.

All oxygen values were converted to g C fixed  $m^{-2}$  of thallus  $h^{-1}$  (as well as mg C fixed g dry wt.  $^{-1} h^{-1}$ ), so that production rates could be related to the standing stock (cover) values, by standard methods (Strickland, 1960), assuming a photosynthetic quotient of 1.00 which gives data that are representative of carbohydrate metabolism and easily converted for comparison with others where different PQ values were assumed. Oxygen produced or respired in the light and dark blanks was never detectable, so blank corrections were unnecessary.

All hourly net production rates were converted to daily (24 h) rates by multiplying the net hourly rates by the number of hours of available daylight (sunrise to sunset) minus a correction for night respiration (i.e., subtracting the product of the hourly dark respiration rate and the total hours of darkness). This procedure enhanced seasonal differences in short-term net productivity by including a consideration of differences in daylight (10.05–14.45 h) throughout the year.

## RESULTS

The seasonal patterns of water temperature and light are shown in Table I. Water temperature typically lagged behind air temperature, ranging from a high of 21.5°C during October 1976 to a low of 15.5°C in March 1977. The mean illuminance and mean quantum flux averaged above saturation (see King and Schramm, 1976 for typical light curves of intertidal macroalgae) during

TABLE I

Physical data for San Clemente Island photosynthetic experiments made between 09.30 and 15.00 h

Date	Quantum flux $\mu E m^{-2} s^{-1}$ (PhAR)		Flux		Temp. (°C)
	Mean	Range	Mean	Range	
Oct. 1976	1130	370–1700	58	20–85	21.5
Dec. 1976	787	265–1150	38	7–65	16.5
March 1977	1494	800–1900	76	42–91	15.5
June 1977	1522	700–2400	82	40–130	18.0

all of the production experiments and were lowest in December 1976 (38.5 klux and 787  $\mu E m^{-2} s^{-1}$ ). The wide ranges (Table I) indicate that skies at San Clemente Island are intermittently overcast throughout the year. Salinity, as measured with an A.O. Spencer refractometer, remained constant at 33‰.

### Seasonal standing stock patterns

The cover data, standardized to relative (% of seasonal maximum) cover to facilitate comparisons with patterns of productivity (see Fig. 1), revealed seasonal variations for 10 of the 13 macrophytes examined. A summer maximum

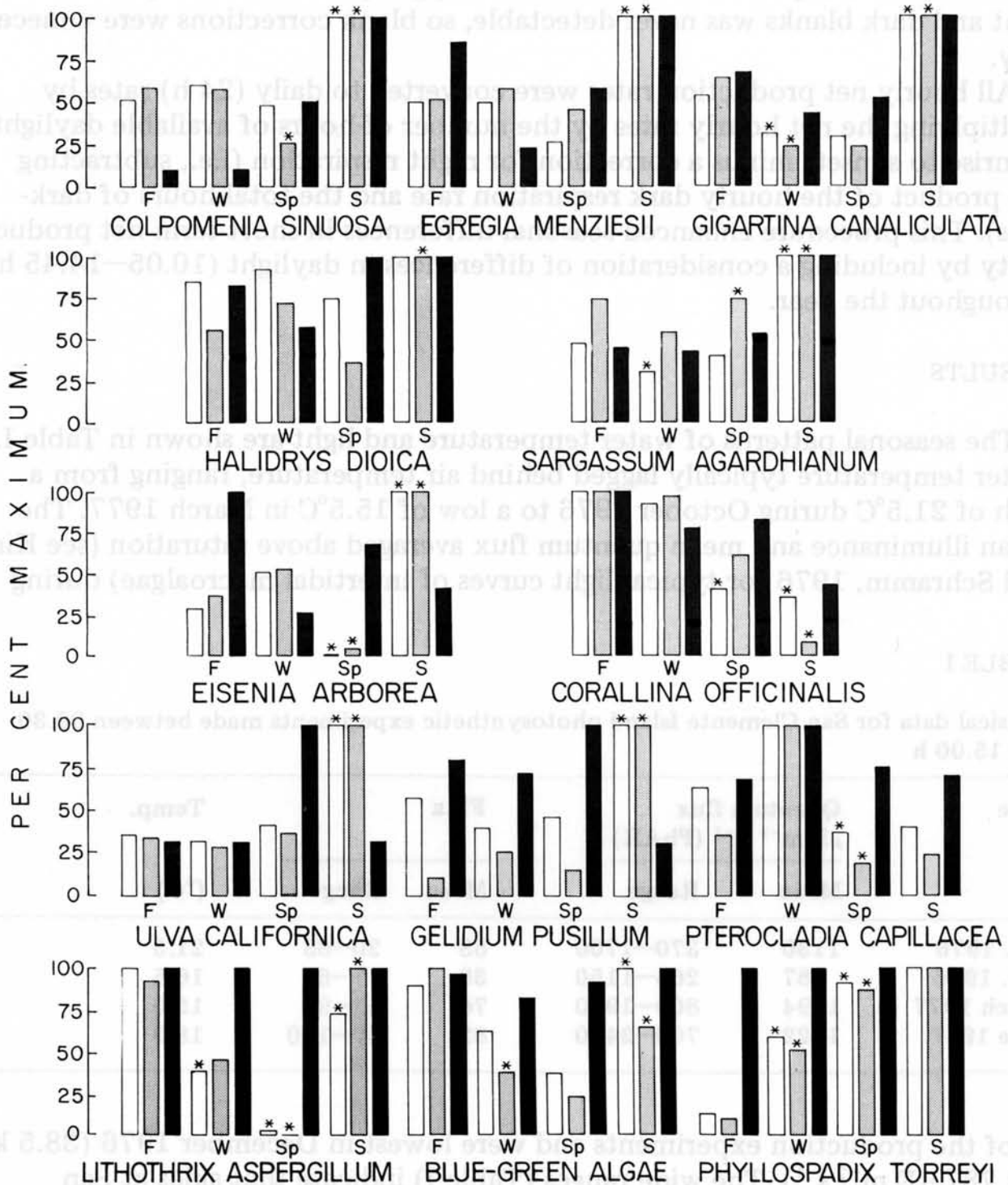


Fig. 1. Per cent of maximum potential  $\text{mg C g dry wt.}^{-1} \text{ day}^{-1}$  (unshaded histograms),  $\text{g C m}^{-2}$  of thallus  $\text{day}^{-1}$  (grey histograms), and cover of standing stock (black histograms) for fall (F), winter (W), spring (Sp), and summer (S) seasons. \* indicate absolute differences significant from the preceding season's value at  $P < 0.05$  level according to the Eberhardt (1968) method.

and winter minimum occurred for five of these [*Colpomenia sinuosa* (Roth) Derbes & Solier, *Egredia menziesii*, *Gigartina canaliculata* Harvey, *Halidrys dioica*, and *Sargassum agardhianum* J. Agardh] while two [*Eisenia arborea* and *Corallina officinalis* var. *chilensis* (Decaisne) Kützing] had fall maxima and summer minima. *Ulva californica* Wille and *Gelidium pusillum* (Stackhouse) Le Jolis, which had maximal cover during spring, also exhibited reduced standing stocks in the summer. *Pterocladia capillacea* (Gmelin) Bornet & Thuret was the only macrophyte that demonstrated a winter maximum in cover. Three macrophytes, *Lithothrix aspergillum* J.E. Gray, blue-green algae, and the tracheophyte *Phyllospadix torreyi* Watson, displayed little or no seasonality in standing stocks.

### *Seasonal patterns of productivity*

There was relatively good overall agreement between both area and weight based, seasonal, daily productivity data (Fig. 1). Highest production rates (per unit area and weight) were noted in summer for nine of the 13 species; minimum production rates were recorded in spring and to a lesser extent during winter. Blue-green algae showed maximum weight-based rates in summer whereas area-based rates peaked during fall. The coralline algae *Lithothrix aspergillum* and *Corallina officinalis* var. *chilensis* exhibited highest productivity in fall, with minimal rates being demonstrated during spring based on both area and weight values.

Correlations between seasonal fluctuations in % cover and productivity were evident for only eight of the 13 species examined (Fig. 1). With the exception of *Pterocladia capillacea*, these species showed highest standing stocks and productivity in the summer and lower values during the fall, winter, and spring. *Pterocladia capillacea*, however, displayed its maximal standing stock and productivity during the winter with reductions in the spring and summer. Little agreement between changes in standing stock and productivity was demonstrated for *Eisenia arborea*, *Gelidium pusillum*, and *Ulva californica* — which showed highest productivities but lowest cover values in the summer — and *Lithothrix aspergillum* and *Phyllospadix torreyi* — which displayed very large seasonal differences in productivity but relatively little changes in standing stock.

The potential contribution to total daily productivity for the intertidal system on San Clemente Island was determined for each species by combining production rates  $\text{m}^{-2}$  of thallus with the seasonal cover data (Table II). The 13 macrophytes studied contributed 82% of the total intertidal (−0.3 to +2.1 m, 0 datum mean lower low water) macrophyte cover; therefore, the sum of individual productivity values represents a reasonable, but somewhat low, estimate of the total daily community productivity. Other major macrophyte species not examined in the present study [i.e., *Pseudolithoderma nigra* Hollenberg, *Lithophyllum proboscideum* (Foslie) Foslie, and *Hydrolithon decipiens* (Foslie) Adey], which comprised most of the remaining cover (~10–13%),

TABLE II

Seasonal potential net productivity of the thirteen most abundant macrophytes from San Clemente Island  $\text{m}^{-2}$  of intertidal surface from  $-0.3$  to  $+2.1$  m relative to mean lower low water

Taxa	g C fixed $\text{m}^{-2}$ intertidal surface $\text{day}^{-1}$			
	Fall	Winter	Spring	Summer
Blue-green algae	0.665	0.221	0.160	0.457
<i>Corallina officinalis</i> var. <i>chilensis</i>	0.198	0.151	0.102	0.007
<i>Pterocladia capillacea</i>	0.061	0.246	0.036	0.042
<i>Egregia menziesii</i>	0.132	0.037	0.036	0.153
<i>Gigartina canaliculata</i>	0.075	0.017	0.020	0.169
<i>Sargassum agardhianum</i>	0.042	0.029	0.048	0.125
<i>Halidrys dioica</i>	0.027	0.061	0.034	0.069
<i>Gelidium pusillum</i>	0.012	0.024	0.020	0.042
<i>Ulva californica</i>	0.002	0.002	0.007	0.013
<i>Colpomenia sinuosa</i>	0.001	0.001	0.002	0.016
<i>Eisenia arborea</i>	0.001	0.003	0.000	0.004
<i>Lithothrix aspergillum</i>	0.003	0.001	0.000	0.003
<i>Phyllospadix torreyi</i>	0.000	0.001	0.001	0.001
Total productivity	1.219	0.794	0.466	1.101

are known (Littler and Murray, 1974) to exhibit extremely low productivity.

All of the species except blue-green algae, *Corallina officinalis* var. *chilensis*, and *Pterocladia capillacea* contributed their maximum daily productivity per square meter of intertidal substratum in the summer (Table II). However, bimodal productivity patterns were evident for *Egregia menziesii*, *Gigartina canaliculata*, and *Lithothrix aspergillum*; these species showed high values in fall and spring. *Gelidium pusillum*, *Ulva californica*, and *Colpomenia sinuosa* displayed minimum values in fall and winter that increased to substantial summer maxima. Blue-green algae and *C. officinalis* var. *chilensis* were the only species that reached peak net daily productivity during fall with lowest values in spring. Conversely, *P. capillacea* was found to have winter maximum and spring minimum in daily net productivity  $\text{m}^{-2}$  of substratum. *Phyllospadix torreyi* showed no measurable net photosynthesis in the fall and only minimal net daily productivity from winter through summer.

Total daily net productivity of the macrophyte community (Table II) reached a peak in the fall ( $1.22 \text{ g C m}^{-2}$  of substratum  $\text{day}^{-1}$ ) and rapidly declined through winter to a spring low ( $0.47 \text{ g C m}^{-2} \text{ day}^{-1}$ ); this pattern closely followed seasonal changes in ambient water temperatures (Table I). Most of the seasonal difference in overall, daily net productivity was due to higher blue-green algal productivity rates throughout the summer and fall. Blue-green algae, *Corallina officinalis* var. *chilensis*, *Pterocladia capillacea*, and *Egregia menziesii*



comprised 76% of the total, yearly community primary productivity (which averaged  $0.90 \text{ g C m}^{-2}$  of substratum  $\text{day}^{-1}$ ).

## DISCUSSION

Species exhibiting seasonality in standing stocks were divided equally between those with fall through spring maxima and those that showed strong summer maxima (Fig. 1). The absence of clear-cut uniform patterns for all of the species is not surprising since individual macrophyte populations are potentially regulated by different abiotic and biotic factors. For instance, Doty (1971a,b) provided evidence that the abundance of large frondose algae on tropical reef flats is controlled as much by unpredictable storm turbulence as by regular seasonal factors. Smaller and less branched frondose algal forms were less affected by storms (Doty, 1971a,b) and showed greater seasonal predictability than larger species.

Consequently, effects of seasonal metabolic variations, such as temperature dependence of photosynthetic light saturation (Yokohama, 1973) may be relatively minor in determining the seasonal changes observed in standing stocks of primary producers. This is based on the observation that most of the macrophytic cover on San Clemente Island appears to be ultimately exported to the subtidal and mortality effects, such as storms and desiccation stress, tend to be highest in the winter. For example, the strong correlation between maxima in wave height, wind velocity, and abundance of seaweeds on Southern California beaches during November through February noted by ZoBell (1971) provides evidence of the importance of storms in reducing seaweed stocks. Intertidal macrophytes in Southern California also experience extreme desiccation, heat, and insolation stress throughout the late fall and winter (Littler, in press) from a combination of daytime low tides and hot, dry seasonal winds ("Santa Anas") that blow seaward from inland desert regions. These physical factors probably account for the minimal winter standing stocks found for the large lower-intertidal brown algae *Egregia menziesii*, *Eisenia arborea*, *Halidrys dioica*, and *Sargassum agardhianum*. Other parameters, such as preferential grazing (Vadas, 1977), environmentally-induced alterations in life-history patterns (Wynne and Loiseaux, 1976), or seasonal growth strategies (Hatcher et al., 1977) could also be important. All of these factors are largely independent of those that regulate photosynthesis, hence, as expected, strong positive correlations between standing stocks and net photosynthetic rates were not consistently found (Fig. 1). This finding is somewhat counter to that of Brinkhuis (1977a,b) who observed a close relationship between seasonal productivity and standing stock patterns of salt-marsh algae. For similar reasons, uniform correlations between seasons of minimum and maximum photosynthesis and growth rate, such as those noted by King and Schramm (1976), would not be predicted to occur universally under natural conditions.

The calculation of daily rates provided the most meaningful data on seasonal net productivity patterns because differences in daylight length were taken

into account. Winter increases in intermittent cloud cover and steepness of sun angle did not reduce the mean experimental light intensities between 09.30 and 15.00 h on San Clemente Island (Table I) below that considered to be saturating for most intertidal algae (King and Schramm, 1976). The transformation of hourly to daily numbers, to obtain our estimates of overall contributions to yearly primary productivity, only affected the magnitude of the seasonal patterns; however, extrapolations of short-term rates to daily rates could be problematical because of the possible existence of endogenous metabolic periodicities. Daily photosynthetic rhythms have been observed in some macroalgae (Oohusa et al., 1977a,b) but are not present in others (Blinks and Givan, 1961). In this study, the effect of possible daily periodicity was controlled by conducting experiments at the same time of day. Although not within the scope of this study, the effects of exposure to air during low tides may have influenced photosynthetic rates (Johnson et al., 1974), probably resulting in a lowering of productivity values for most of the species. With these precautions in mind, it is worth noting that the mean, overall community productivity ( $0.9 \text{ g C m}^{-2}$  of substratum  $\text{day}^{-1}$ ; Table II) falls within the range of values previously reported for rocky-intertidal systems (see Littler and Murray, 1974; Seapy and Littler, 1978) where similar assumptions were made.

Seasonal patterns of photosynthesis showed a strong summer and fall maximum for the majority of species; this agrees with the findings of King and Schramm (1976) who assessed the effects of light intensity on the laboratory photosynthetic rates of 22 species of marine macroalgae. In most instances, the highest rates of light-saturated photosynthesis were recorded (King and Schramm, 1976) in the spring and summer corresponding to the seasonal growth patterns. Similar seasonal patterns of  $^{14}\text{C}$ -fixation in *Ulva lactuca* and *Fucus vesiculosus* were shown (Brinkhuis, 1977b) to occur under optimal laboratory light conditions. In *Chondrus crispus* (Mathieson and Norall, 1975), optimum light and temperature conditions for net photosynthesis were found to vary both seasonally and spatially. It is likely that the higher summer/fall temperatures (Table I) affecting light saturated photosynthesis are important in contributing to seasonal differences in photosynthetic rates.

Other existing literature on seasonal production rates of intertidal algae is extremely limited and has indicated in some instances anomalous patterns. For example, *Fucus virsoides* was shown to have a winter gross production minimum and summer maximum in the field while the reverse was found (Zavodnik, 1973a) simultaneously in laboratory experiments under low light. Conversely, *Wrangelia penicillata* C. Ag. reached its maximum gross production in the field during winter (Zavodnik, 1973b) with a minimum in the summer months.

In summary, we conclude that seasonal patterns of marine macrophyte production are highly variable with a tendency for most species to show a maximum in daily photosynthesis coincident with higher temperatures and longer daylength. No uniform correlations between seasonal productivity

patterns and variations in macrophyte cover were apparent. The present paucity of seasonal productivity data taken in the field greatly limits our current understanding of benthic community energetics. Much more information, including reliable assessments of seasonal standing stocks, from both temperate and tropical systems is needed before we will be in a position to generalize further or make reliable predictions.

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