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The Primary Productivity of Marine Macrophytes from a Rocky Intertidal Community

M.M. Littler[1] and S.N. Murray[2]

[1]Department of Population and Environmental Biology, University of California; Irvine, California, USA and [2]Department of Biological Science, California State University; Fullerton, California, USA

Abstract

This study represents the first report of primary production rates for Southern California intertidal producers. The production rates of 18 marine macrophytes near Wilson Cove, San Clemente Island, are close to those for other marine algal communities. No apparent relationship was revealed between the productivity of an alga and the division to which it belongs; however, productivity was associated with growth form. Encrusting prostrate forms were the lowest producers in terms of g $C/m^2/h$ and g C/g dry weight/h; sheet-like and finely-branched forms showed a greater productivity than coarsely-branched forms. *Gelidium pusillum* and *Ulva californica* had considerably greater production rates than the other algae measured.

Introduction

A prerequisite to understanding the contribution of macrophytic communities to production is the measurement of photosynthesis of the dominant (i.e., in terms of cover) populations. Only a few studies of this nature have been done; hence, the generalizations advanced are very limited. Still, some benthic seaweeds appear to be extremely productive (Blinks, 1955; Kanwisher, 1966; Mann, 1973). Ryther (1963) suggested that the world-wide production of benthic seaweeds may approach 10% that of phytoplankton, even though the former are confined to an area about 0.1% that available to plankton. Kelp beds are said (e.g., Towle and Pearse, 1973) to rank among the most productive systems on earth, with published rates for *Macrocystis pyrifera* ranging from 0.1 to 7.0 net g C/m^2/day. Measurements of *M. pyrifera* constitute the only published records of macrophyte production for the Southern California region. The net yearly rates for kelp reported by Aleem (1956) and Clendenning (1971) translate, respectively, to 0.1 and 1.5 to 3.0 g C/m^2/day. Gross production of *M. pyrifera* and associated macrophytes was estimated (McFarland and Prescott, 1959) at between 5 and 6 g C/m^2/day for Paradise Cove in Southern California (USA).

Blinks (1955) combined the standing stock of intertidal seaweeds with estimated turnover times to generate productivity data that ranged from 3 to 66 net g dry matter/m^2/day; Pomeroy (1961) converted these figures to 1 to 9 net g C/m^2/day. Kanwisher (1966) obtained a much higher net rate (20 g C/m^2/day) for *Fucus vesiculosus* stands off Woods Hole, Massachusetts. Recent studies yielded net daily rates of 4.8 g C/m^2 (Mann, 1972) for the seaweed zone of St. Margaret's Bay, Nova Scotia (Canada) and about 1.5 to 3.0 g C/m^2 (Johnston, 1969) for marine macrophytic communities in the Canary Islands.

The Channel Islands contain the most pristine intertidal communities that remain in Southern California but, presumably because of their inaccessibility, they have received remarkably little scientific attention. The intertidal ecology of the Channel Islands is known only for San Nicolas Island (Caplan and Boolootian, 1967) and Santa Cruz Island (Hewatt, 1946), of which the latter belongs to the Northern Channel Islands group. Collections of macrophytes have been made for most of the Southern California Islands, although of the information available (e.g. Dawson, 1949; Dawson and Neushul, 1966; Nicholson and Cimberg, 1971), little can be used to depict intertidal communities. As a consequence of its distant location from the mainland (about 80 km) and its controlled ownership by the U.S. Navy, San Clemente Island's marine resources are relatively little influenced by man's activities, particularly by

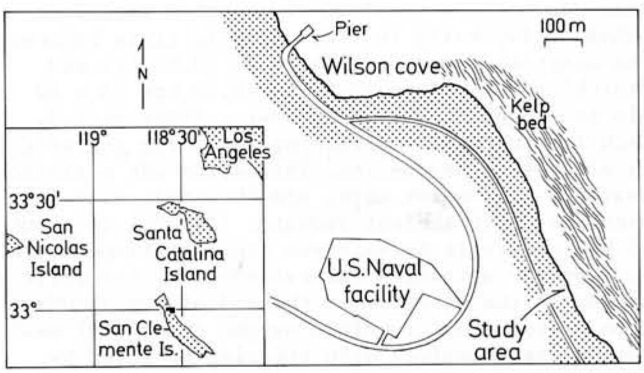

Fig. 1. Map showing location of Wilson Cove study site on leeward side of San Clemente Island, California, USA

his domestic and industrial sewage. Therefore, San Clemente Island (Fig. 1) provides an excellent site for studying natural communities of intertidal macrophytes.

The area studied (Fig. 1) lies at the base of a bluff approximately 6 m in height that forms the terminus of a long, steeply-pitched (30^o to 40^o) slope. This intertidal region is relatively uniform in character, consisting of a rocky substratum composed of large metamorphic boulders intermingled with numerous free rocks 25 to 50 cm in diameter. The intertidal extends over a horizontal distance of 10 to 15 m, with a vertical differential of 2.5 m. A continuous bed of *Macrocystis pyrifera* is located 25 m seaward of the study area.

Materials and Methods

The work was done south of Wilson Cove (Fig. 1) on 19 and 20 May, 1973, under completely overcast skies. Light intensity was measured by a Weston photo-electric cell; all productivity measurements were made between 21,500 and 64,500 lux. Net primary production and respiration were determined by means of two Beckman Fieldlab O_2 analyzers used with appropriate 300 ml light, dark and control bottles. Numerous whole thalli (submerged during collection) were hand-picked and placed in trays of seawater. Representative branches or blades were selected from a minimum of 5 different thalli and carefully transferred into bottles filled from a single batch of ambient seawater for which the initial dissolved O_2 was determined. During his study of production of marine macrophytes, Johnston (1969) found that if a ratio not exceeding 0.1 to 0.3 g dry weight alga/1 seawater was employed, no nutrient or CO_2 deficiency effects were recorded in linearity experiments lasting as long as 24 h. In the present study, 0.04 to 0.58 g dry weight of each alga per 300 ml seawater were used, but incubation times did not exceed 4 h. Preliminary linearity runs agreed well with the recommended combinations of Johnston, and showed that the largest weights of algae used could be allowed to photosynthesize for as long as 5 to 6 h without a rate decrease. A total of 160 bottles were incubated horizontally in clear acrylic trays between the starting times from 09.20 to 10.50 hrs and finishing times from 12.40 to 14.50 hrs (3 h 20 min to 4 h of incubation), over a 2-day period, with the intent of minimizing any daily periodicity effects on production. Incubation was performed near the high-water mark, and the trays were replenished with ambient seawater (15.0^oC) at about 15 min intervals to maintain constant temperature and provide agitation (as evidenced by the drifting motion of the thalli). At the end of the incubation period, the dissolved oxygen content of each bottle was measured, with stirring provided by air-driven magnetic stirrers to ensure uniform mixing of dissolved oxygen. Oxygen produced or respired in 4 light and 4 dark blanks (phytoplankton only) was averaged and subtracted from that produced or respired in the bottles containing the macrophytes.

After the O_2 levels were recorded, the thalli were placed in labelled polyethylene bags and returned to the laboratory. Measurable impressions of the macrophytes were made by carefully spreading and photocopying individual thalli. Two-dimensional area determinations (i.e., at right angles to the plane of light) were made from each photocopy employing a point-intercept method. The thalli were then weighed, after being dried at 37.8^oC until constant weight was attained. In the cases of *Corallina officinalis* var. *chilensis*, *Hydrolithon*

Table 1. Mean cover (%) and net production rates (mg C fixed/h) of dominant macrophytes/m^2 of primary substrate. Parts of study area have a multilayered canopy, and this yielded a mean cover of 103.4% (from Littler and Murray, unpublished)

Macrophytes	Cover	Productivity
Egregia laevigata	13.8	26.5
Blue-green algae	18.4	19.7
Gigartina canaliculata	8.8	19.5
Gelidium robustum	7.7	15.6
Corallina officinalis var. *chilensis*	14.1	9.4
Halidrys dioica	5.3	8.0
Hydrolithon decipiens	12.1	6.2
Pterocladia capillacea	3.1	4.3
Sargassum agardhianum	1.7	4.1
Pseudolithoderma nigra	6.7	2.9
Phyllospadix torreyi	1.8	2.5
Eisenia arborea	3.1	2.4
Macrocystis pyrifera	0.8	1.1
Gelidium pusillum	0.3	1.0
Rhodoglossum affine	1.1	1.0
Lithothrix aspergillum	0.4	0.6
Colpomenia sinuosa	2.8	0.3
Ulva californica	<0.1	0.3
Peyssonellia sp.	0.3	
Anisocladella pacifica	0.2	
Codium fragile	0.2	
Gigartina spinosa	0.2	
Cladophora graminea	<0.1	
Corallina vancouveriensis	0.1	
Dictyota flabellata	0.1	
Gelidium coulteri	<0.1	
Laurencia pacifica	<0.1	
Lithothamnium sp.	<0.1	
Plocamium coccineum var. *pacificum*	<0.1	
Red prostrate (?)	<0.1	
Totals	103.4	125.4

decipiens, *Lithothrix aspergillum*, *Phyllospadix torreyi* with *Melobesia mediocris*, and the blue-green algae, dry (organic carbon) weight was determined by the difference between the dry weight (including any rock substrate or $CaCO_3$) and that following 24 h of combustion at 400°C. All O_2 values were converted to g C fixed/g dry weight/h and to g C/m^2/h by standard methods (Strickland, 1960), assuming a photosynthetic quotient of 1.20 which is an average value for carbohydrate-protein-lipid metabolism. For each species, the 2 replicates for each measurement of respiration were averaged and this figure was added to each of the 6 light (net production) replicates. The mean of these 6 values and the 95% confidence interval were then computed to express gross production for the macrophytes. The production budget for the region was calculated using the per-cent cover and the net primary productivity per square meter for each of the dominant species. The cover data (Table 1) are taken from standing stock assessments (Littler and Murray, unpublished) of the biological features of the intertidal communities near Wilson Cove. Daily net production rates were calculated from hourly rates by subtracting 12 h of respiration (night) from 12 h of net production (daytime).

Results and Discussion

The macrophytes at Wilson Cove have been ranked (Fig. 2) in order from highest to lowest producer on an equal thallus-area basis. There appears to be no relationship between the productivity of a given alga and the major divisional group to which it belongs, since both brown and red algae have species among the highest and lowest producers. This is somewhat contrary to the trend noted by Johnston (1969), where brown algae produced considerably in excess of other algae. It is clear that the two encrusting forms (*Hydrolithon decipiens* and *Pseudolithoderma nigra*) are the lowest producers. This is probably due to their comparatively low surface-to-volume ratios, which might restrict their ability to obtain nutrients, and their saxicolous prostrate form (placing them at a disadvantage in obtaining light energy). *Gelidium pusillum* and *Ulva californica* show greater productivity on an area basis than any of the other algae measured. The rest of the macrophytes can be arranged in order of decreasing productivity in roughly a linear fashion.

A ranking of net and gross production rates for macrophytes calculated on the basis of dry weight is given in Fig. 3. The sheet-like forms are by far the greatest producers per unit of biomass, followed by branched forms, with saxicolous prostrate forms producing considerably less than other macrophytes. Finely-branched forms were found to produce more than coarsely-branched forms, in agreement with the finding of Kanwisher (1966). Again, a life-form more suited to obtaining light energy and nutrients would seem, as a working hypothesis, to explain the differences measured. *Ulva californica*, *Macrocystis pyrifera*, *Gelidium robustum*, *Pterocladia capillacea* and *G. pusillum* form a group with considerably higher rates on a weight basis than other algae measured. The numbers for daily production (2.16 to 32.40 mg C/g dry weight)

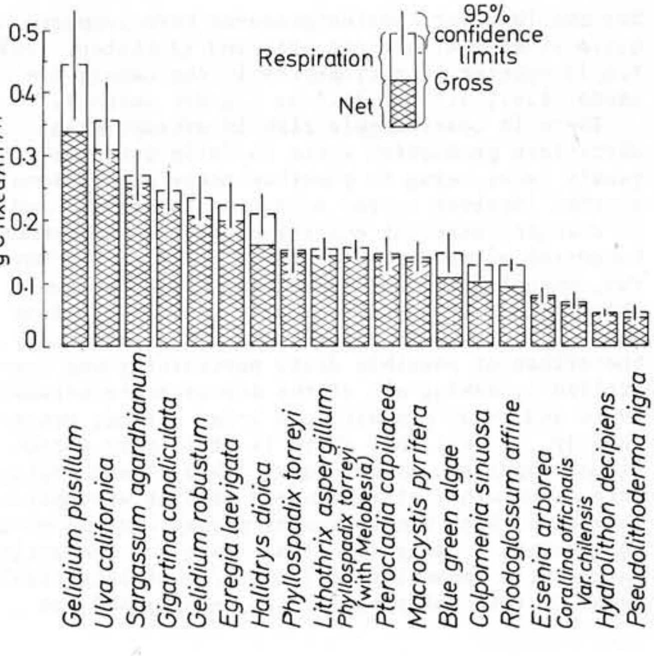

Fig. 2. Respiration, net and gross production rates of dominant macrophytes near Wilson Cove on basis of two-dimensional thallus-surface area

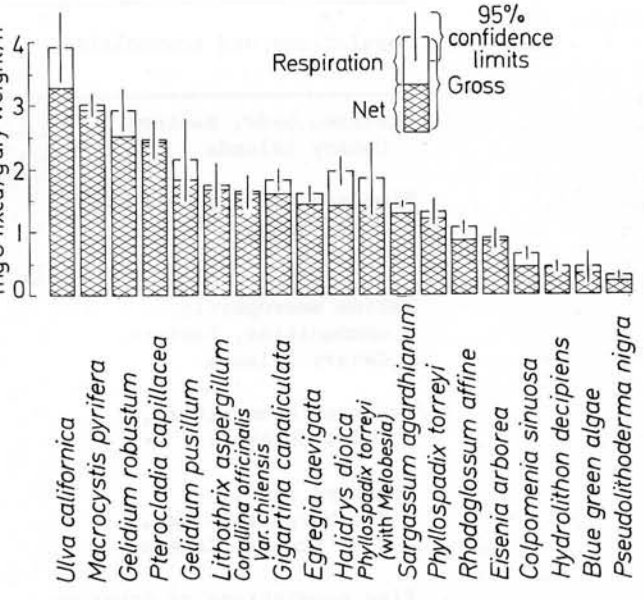

Fig. 3. Respiration, net and gross production rates of dominant macrophytes near Wilson Cove on basis of thallus dry weight

for the 18 major species measured here compare quite closely with those gathered (Johnston, 1969) for 11 species of macrophytes in the Canary Islands (i.e., 1.51 to 21.4 mg C/g dry weight).

There is considerable risk in extrapolating short-term production rates to daily rates or yearly rates owing to possible daily and seasonal rhythms inherent in the organisms themselves and to changing external conditions in the environment. Extensive observational records (Littler and Murray, unpublished) indicated only slight seasonal changes in macrophyte community composition from June, 1971 to May, 1973. As mentioned previously, the effect of possible daily periodicity was controlled by making all of the measurements between 09.20 and 14.50 hrs within a 2-day period; consequently, we feel that there is utility in a cautious comparison of our data (Table 1) with daily rates from other studies where similar assumptions were made. With the foregoing precautions in mind, we generate a daily (24 h) net rate for the entire macrophytic community of 1.3 g C/m^2 of intertidal area. Of this daily production, nearly 46% was contributed by Rhodophyta, 36% by Phaeophyta, 16% by Cyanophyta, 2% by Spermatophyta and only a slight amount by Chlorophyta. Four seaweeds (i.e., *Egregia laevigata*, blue-greens, *Gigartina canaliculata* and *Gelidium robustum*) contributed almost two-thirds of the total production.

Published records of the daily production of marine communities and populations are given in Table 2. The lowest daily value (0.5 g/m^2) compares favorably with our data (0.4 g/m^2), and the highest (9.0 g/m^2) is nearly three times greater than our highest single rate (3.1 g/m^2). Additionally, Bakus (1967) obtained net rates for tropical blue-green populations ranging from 0.6 to 2.2 g C/m^2/day; blue-green algae at Wilson Cove produced within this range (i.e., 0.8 g C/m^2/day). *Macrocystis pyrifera* from Wilson Cove fixed 1.5 net g C/m^2/day, a rate comparable to that obtained by Clendenning (1971) for the same alga. We found that, while generally tending toward the lower end, most of the Wilson Cove macrophytes produced within the range calculated by Pomeroy (1961) for other Californian seaweed populations. Our rates,

Table 2. Productivity contributions of populations and communities to various marine systems. All have been converted to daily rates for comparability

Populations and communities	Net production (g C/m^2/day)	Source
Caulerpa beds, Eastern Canary Islands	1.0	Johnston (1969)
Nine seaweed populations, California, USA	1.0-9.0	Blinks (1955), as recalculated in Pomeroy (1961)
Marine macrophytic communities, Eastern Canary Islands	1.5-3.0	Johnston (1969)
Two reef communities, Eniwetok Atoll	1.6 & 7.2	Smith (1973)
Sea-weed zone, St. Margaret's Bay, Nova Scotia, Canada	4.8	Mann (1972)
Five populations of crustose coralline algae, Waikiki reef, Hawaii	0.5-2.6	Littler (1973)
Thallassia and *Cymodocea* bed, Kavaratti Atoll, Laccadives	5.8	Qasim and Bhattathiri (1971)
Eighteen intertidal algal populations, San Clemente Island, USA	0.4-3.1	This study

however, are reasonably close to those (Table 2) generated by Johnston (1969), Mann (1972), and Littler (1973) for marine seaweed communities.

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Dr. M.M. Littler
Department of Population
and Environmental Biology
University of California
Irvine, California 92664
USA

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