

CHAPTER THREE

SEASONAL ASPECTS OF MACROPHYTE PRODUCTIVITY

Mark M. Littler

Steven N. Murray

INTRODUCTION

This study was part of a larger research program undertaken to determine the impact of the Wilson Cove sewage outfall on the bioenergetics of the rocky intertidal communities. Clearly, field studies on the role of sewage on the functionally important intertidal algae are desirable if our knowledge of human impact on marine resources is to advance beyond a level that, at present, is often subjective and emotionally charged. A prerequisite to understanding the effects of discharged sewage on community energetics is knowledge concerning seasonal and inherent variability in the rates of production of the dominant primary producer organisms. Those that show high or temporal variability in productivity or are preferable components of the diets of herbivores and omnivores (see Fig. 5-1, Chapter Five) may be of paramount importance in determining the structure and function of the entire community. Because primary producers provide the foundation for all subsequent trophic levels, any attempts at assessing the impact of sewage on community dynamics must include the relative energetic importances of the various constituents of this energy base.

Relatively few studies concerning pollutant effects on macrophyte producers have been performed (see Andrews, 1976); hence, broad generalizations cannot be made. Additionally, only limited information is available on individual macrophyte species populations from intertidal coastal waters (Littler and Murray, 1974; King and Schramm, 1976; Littler, 1977). Reviews of published data have led to statements (Ryther, 1963; Mann, 1973) that coastal benthic marine habitats contain, per unit of area, some of the most productive ecosystems on earth. However, the importance of benthic macrophytes to aquatic productivity is much more poorly understood than is the case for the phytoplankton.

As pointed out by Andrews (1976), sewage pollutants may have either stimulatory or deleterious effects on marine algae. The stimulatory effects, which are largely a result of the increased availability of nutrients, are well known on such macrophytes as *Ulva lactuca*. This species has been suggested (Burrows, 1971) as a potential indicator of sewage pollution in English waters. Specific chemical components of sewage, such as pine oil (see Chapter Two), will vary in their deleterious effects as a function of concentration and duration of exposure. The potential ability of certain stands of seaweeds to make use of and recycle organic materials back through the food web has also been stressed (see Prince, 1974).

If a probable effect of sewage is to change the levels of primary productivity or the availability of preferred food sources, then long-term changes in herbivore and carnivore populations might occur, resulting in structurally as well as energetically altered ecosystems. Our intent, therefore, was to concentrate on the temporal and inherent variability in the production and respiration of the dominant Wilson Cove macrophytes, in an effort to generate a baseline of the energy available to the sewage-polluted and control intertidal systems sampled for standing crop (see Chapter Two). Specifically, these studies were undertaken to determine quantitatively:

- The effect of sewage on primary production and respiration of macrophytes from the sewage outfall area vs. those of the unpolluted area.
- The relative energetic contribution of each species to polluted and unpolluted intertidal systems at different times of the year.

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METHODS AND MATERIALS

Studies were conducted at the control site (see Fig. 1-2, Chapter One) on five separate occasions (i.e., 19-20 May 1973; 25-27 January 1975; 17-18 May 1975; 15-18 December 1975; 22-24 October 1976) representing a total of over 400 experimental incubations of 13 different species. Light intensity and photosynthetically active radiation (PAR) were measured by a Lambda Instruments, Model LI-185 Quantum/Photometer; all production experiments were carried out over the range of 23 klux (510 $\mu\text{E}/\text{m}^2/\text{sec}$) to 85 klux (1700 $\mu\text{E}/\text{m}^2/\text{sec}$). The methods employed on 19-20 May 1973 have been presented earlier (Littler and Murray, 1974) and the modifications to these employed during subsequent work are detailed below.

Net primary production and respiration were determined using Beckman Fieldlab O_2 Analyzers with 1220 milliliter wide-mouth clamp-lid canning jars as light, dark, and blank incubation bottles. The bottles were cleaned in aqua-regia and aged in distilled water prior to being used. Dark bottles, created by wrapping bottles with two layers of taped extra-heavy-duty aluminum foil, were incubated separately so that light reflecting from the foil would not impinge upon the light or blank bottles.

Numerous whole thalli were collected *in situ* while submerged and were placed in clear trays of ambient sea water; representative blades or branches were then selected from a minimum of five different thalli and were carefully transferred to bottles of sea water which had been filtered (10 μm pore size) to remove planktonic organisms. The ambient sea water was typically supersaturated with O_2 ; consequently, 25 liter batches were poured from one contaminant-free bucket to another until a stock of incubation water approaching saturation was obtained. Bottles were slowly submerged and filled, excluding all air, from this common stock. Several bottles were used to determine the initial dissolved O_2 for each experimental period. Throughout the experiment, an average thallus dry weight of 0.33 g (0.05 to 0.97 g) was used for all species; preliminary linearity runs agreed well with the recommended combination of Johnston (1969) and showed that the largest weights of macrophytes chosen could be allowed to photosynthesize for as long as six hours without a rate decrease. Four light and two dark bottles were incubated in clear polycarbonate trays between starting times of 0930 and 1100 hrs and finishing times of 1230 to 1530 hrs (3.0 to 4.5 h of incubation) with the intent of minimizing effects due to endogenous metabolic periodicities. All bottles were thoroughly shaken at 15 minute intervals during the incubation periods to prevent large diffusion gradients from occurring. Cooling was applied by replenishing ambient sea water at 10-15 minute intervals while the trays were incubated in full sunlight near the water's edge. At the end of the incubation period, the O_2 content of each bottle was measured. Each bottle contained a perforated acrylic partition to separate the thalli from a magnetic stir bar; each tray contained four bottles placed upon specially constructed four-unit stir motors that were air driven and stirred thoroughly during all oxygen determinations. Air flow was provided by a foot pump from an inflatable boat kit. Oxygen produced or respired in the light and dark blanks was never significant, so blank corrections were unnecessary.

After the O_2 levels were recorded, thalli were placed in labelled polyethylene bags and were returned immediately to the laboratory. Measurable impressions of the macrophytes were made by carefully spreading and photocopying individual thalli. Area determinations (two-dimensional) were made from each photocopy by means of a point-intercept method. The inherent assumption in using only two-dimensional thallus area is that only a single side faces the light at any one time. Thalli were then dried at 60.0°C until constant weight was attained. In the case of coralline and blue-green algae, organic dry weight was used following five hours of combustion at 500°C.

All O_2 values were converted to mg C fixed/g dry weight/h and to g C fixed/ m^2 thallus/h by standard methods (Strickland, 1960), assuming a photosynthetic quotient of 1.00, which gives data that are easily converted for comparison with others where different PQ values are assumed. For each species, the replicate measurements of respiration were averaged and added to the values for light replicates, and the 95% confidence intervals were determined to obtain estimates of gross production.

The above methods also applied for an additional 250 experiments, involving 11 taxa, made under sewage stress with the following modifications:

- Sewage samples were taken directly from the outfall pipe in the early morning the day of the experiment, and large particulate matter was removed by filtration through a small mesh vegetable strainer.
- Incubation batches of sewage/sea water (10% by volume) were obtained by mixing raw filtered sewage with ambient sea water.
- Sewage light and dark blank bottles were incubated in addition to those blanks mentioned previously.

RESULTS

The seasonal respiration and net production rates of macrophytes incubated in unpolluted water are presented in Figures 3-1 and 3-2. As shown by the relatively large confidence intervals, the primary production rates obtained for most of these macrophytes were highly variable. For the most part, the high variability within populations, and between populations sampled at different seasons, prevented any definitive pattern of seasonality from emerging. Although the data must be considered to be tentative, it is still instructive to consider some of the general trends as based on the seasonal mean values.

The primary production per unit area (Fig. 3-1) of species characteristic of the outfall community showed varying seasonal production tendencies. *Ulva californica*, *Gelidium pusillum*, and blue-green algae demonstrated no significant seasonal differences. *Pterocladia capillacea* produced more in spring but declined through fall to a winter low, while *Corallina officinalis* var. *chilensis* exhibited somewhat higher production in the fall with decreasing values in winter and spring.

Seasonal differences were relatively minor in the cases of macrophytes characteristic of the unpolluted control area. Most showed slight maxima in the fall and tended to have their lowest rates during the winter, with the exception of *Phyllospadix torreyi*, which produced slightly less in the fall than at any other season. The fall peak was relatively more pronounced for *Sargassum agardhianum* than for any other alga (Fig. 3-1).

Production rates in terms of thallus dry weight (Fig. 3-2) showed similar trends wherein most species exhibited lowest rates during the winter. Perennial species characteristic of the control area (*Phyllospadix torreyi*, *Halidrys dioica*, and *Eisenia arborea*) showed very little change in productivity with season, with, at most, slight peaks observed in either the spring or the fall. *Ulva californica* and *Pterocladia capillacea*, species characteristic of the outfall community, were found to be significantly more productive in the spring, while the six remaining species showed significantly higher productivity during the fall.

Experiments conducted in 10% sewage and in ambient control sea water were also difficult to interpret owing to the high variability among the individual thalli incubated (Figs. 3-3 and 3-4). For the most part, similar trends were seen when production rates were expressed on either a unit weight or unit area basis. Species characteristic of the outfall (*Ulva californica*, *Pterocladia capillacea*, and blue-green algae) exhibited no significantly different production rates in sewage as compared to samples run in ambient sea water. *Corallina officinalis* var. *chilensis*, collected from both the outfall and the control areas, showed significantly lower rates of production in sewage. Similarly, *Egrecia menziesii*, a dominant macrophyte from the control area, exhibited decreased production in sewage, while other control species, e.g., *Halidrys dioica*, *Phyllospadix torreyi*, *Eisenia arborea*, and *Sargassum agardhianum*, showed no significant sewage effects on production.

Gelidium pusillum, a dominant macrophyte of the outfall area, displayed varying effects of sewage on production. Production rates taken during winter showed enhancement in sewage when production rates were based on either unit weight or unit area. In fall, however, production per unit weight was significantly reduced in sewage while production per unit area was the same in sewage and ambient control sea water. *Laurencia pacifica* also showed production differences in sewage, with production per unit weight being significantly lower in sewage, while production per unit area was the same in sewage as in ambient sea water.

DISCUSSION

One inescapable conclusion shown by the variability of the data is that production varies greatly between populations of the same species as well as between thalli within a given population (Figs. 3-1 to 3-4). Verduin (1964) made a strong case that photosynthetic processes under natural conditions are highly variable from time to time and place to place. Further, he cautioned that differences of up to 50% in production rates can be routinely expected in fresh-water phytoplankton samples collected a few moments or a few meters apart. The present data on marine macrophytes lend credence to a broader generalization concerning the variability of natural production rates. Unfortunately, this variability makes seasonal studies difficult because the broad variations encountered at any given season tend to obscure differences between seasons. The conclusion is that statistically reliable information can only be obtained by a relatively large sample size.

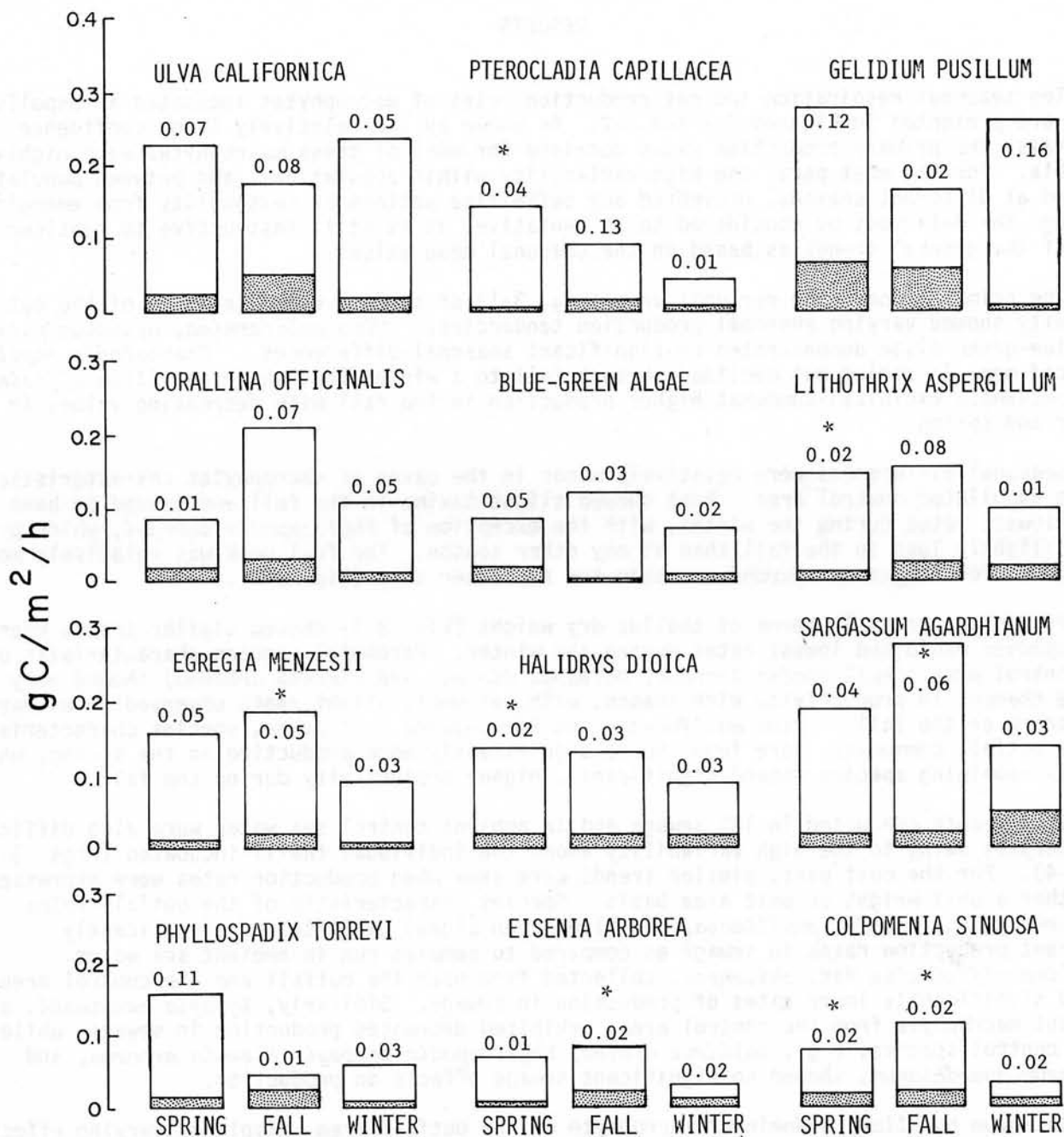


FIGURE 3-1 Seasonal net productivity and respiration (shaded portion) of dominant macrophytes near Wilson Cove on the basis of two-dimensional thallus surface area. Spring values were determined May 1973 and May 1975. Fall = October 1976, and winter = January 1975 and December 1975. $\pm 95\%$ confidence limits are given at the top of each histogram, and asterisks denote non-overlapping confidence intervals when compared to winter.

However, the general trend shown by most of the intertidal macrophytes examined was for a winter minimum and a spring to fall maximum in light-saturated net productivity (Figs. 3-1 and 3-2) correlated with the seasonal decline and increase in standing crop (Chapter Two). This agrees with the findings of King and Schramm (1976), who examined the photosynthetic light curves of 22 intertidal and subtidal marine algae over a 12-month period. In most instances, the highest rates of production were also encountered in the spring and summer corresponding with the seasonal growth patterns. Our interpretation is that lower winter temperatures affecting the light-saturated photosynthetic curve is probably an important contributor. Also, during the winter, daytime low tides typically result in desiccation and other physiological stresses (Chapter Two) throughout intertidal algal populations. This could have lowered photosynthetic performances even though all of the thalli incubated

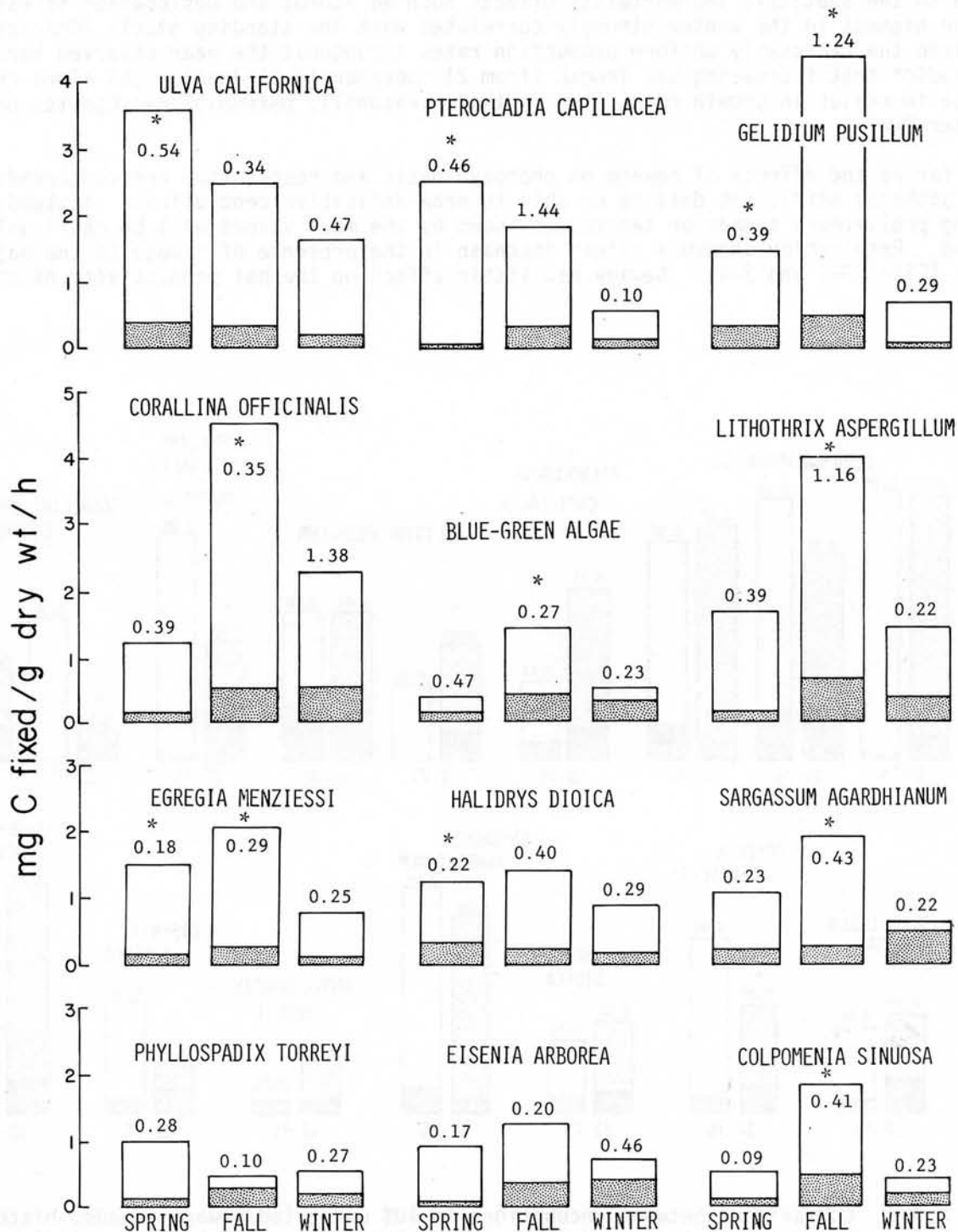


FIGURE 3-2 Seasonal net productivity and respiration (shaded portion) of dominant macrophytes near Wilson Cove on the basis of thallus dry weight. See Fig. 3-1 for details.

appeared to be healthy. Other existing literature on seasonal production rates of intertidal algae is extremely limited and has presented anomalous patterns. For example, *Fucus virsoides* showed a winter gross production minimum and a summer maximum in the field, while the reverse was observed during laboratory experiments under low light (Zavodnik, 1973a). On the other hand, *Wrangelia penicillata* reached its maximum gross production in the field during winter and its minimum in the summer months (Zavodnik, 1973b).

We suspect that seasonal metabolic variations, such as temperature dependence of light saturation, although present, may be relatively minor in determining the seasonal changes observed in standing stocks of primary producers on San Clemente Island. This is based on the observation that most of the macrophytic standing stock appears ultimately to be exported to the subtidal, and mortality effects such as storms and desiccation stress tend to be the highest in the winter strongly correlated with low standing stocks (Chapter Two). Also, given the reasonably uniform production rates throughout the year observed here, one would predict that increasing day length (from 21 December to 21 June) might alone result in the large increases in growth rate shown by those seasonally perennial macrophytes documented in Chapter Two.

As far as the effects of sewage on photosynthesis and respiration are concerned, we have not yet gathered sufficient data to be able to draw definitive conclusions. Instead, the following preliminary trends or tendencies shown by the mean values will be cautiously indicated. Respiration showed a slight increase in the presence of sewage in the majority of cases (Figs. 3-3 and 3-4). Sewage had little effect on the net productivity of *Ulva*

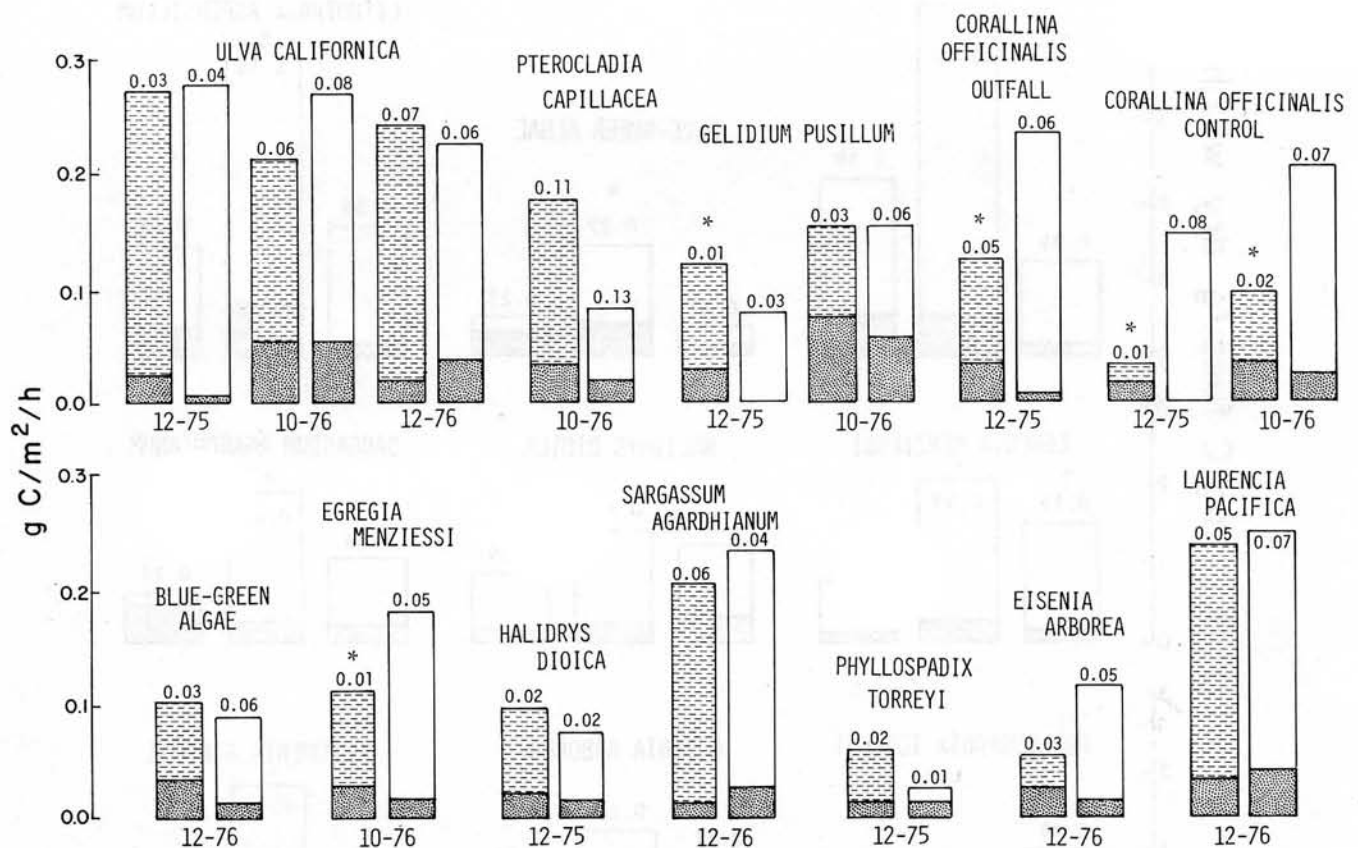


FIGURE 3-3 Comparisons between incubations in 10% untreated sewage (shaded histograms) and non-polluted water (unshaded histograms). Each histogram indicates net productivity by thallus surface area, respiration is represented by the dotted portion within, and the month and year are given beneath. $\pm 95\%$ confidence limits are given at the top of each histogram, and asterisks indicate non-overlapping confidence intervals when compared to non-polluted water.

californica and blue-green algae, taxa that dominate in the effluent plume and which otherwise seem to be quite eurytopic (Littler and Murray, 1975). The picture is still far from clear because *Corallina officinalis* var. *chilensis*, a species equally abundant in the sewage-polluted and unpolluted habitats (Littler and Murray, 1975), was clearly inhibited by sewage. However, another species, *Gelidium pusillum*, found abundantly in the outfall plume was significantly enhanced by sewage in the winter but not during fall (Figs. 3-3 and 3-4). Different responses to sewage effluents measured at different times of the year may be due to the variability of sewage components, which are stimulatory at certain times and inhibitory at other times. Thomas, Seibert, and Dodson (1974), working with municipal sewage enrichment effects on phytoplankton, also observed a lack of consistency in either stimulation or inhibition, which they attributed to extreme variability with time in the materials discharged in the effluent. However, during the present study considerable care was taken in the collection of the sewage used at the various seasons to ensure that toxic substances such as pine oil disinfectant, bleach, etc. were not being discharged.

In cases such as those presented by *Gelidium pusillum* and *Laurencia pacifica* (Figs. 3-3 and 3-4), where results were at odds when performance in sewage was considered on an area basis as opposed to a weight basis, we believe the differences to be attributable to the relative imprecision in determining thallus area for these highly-branched forms.

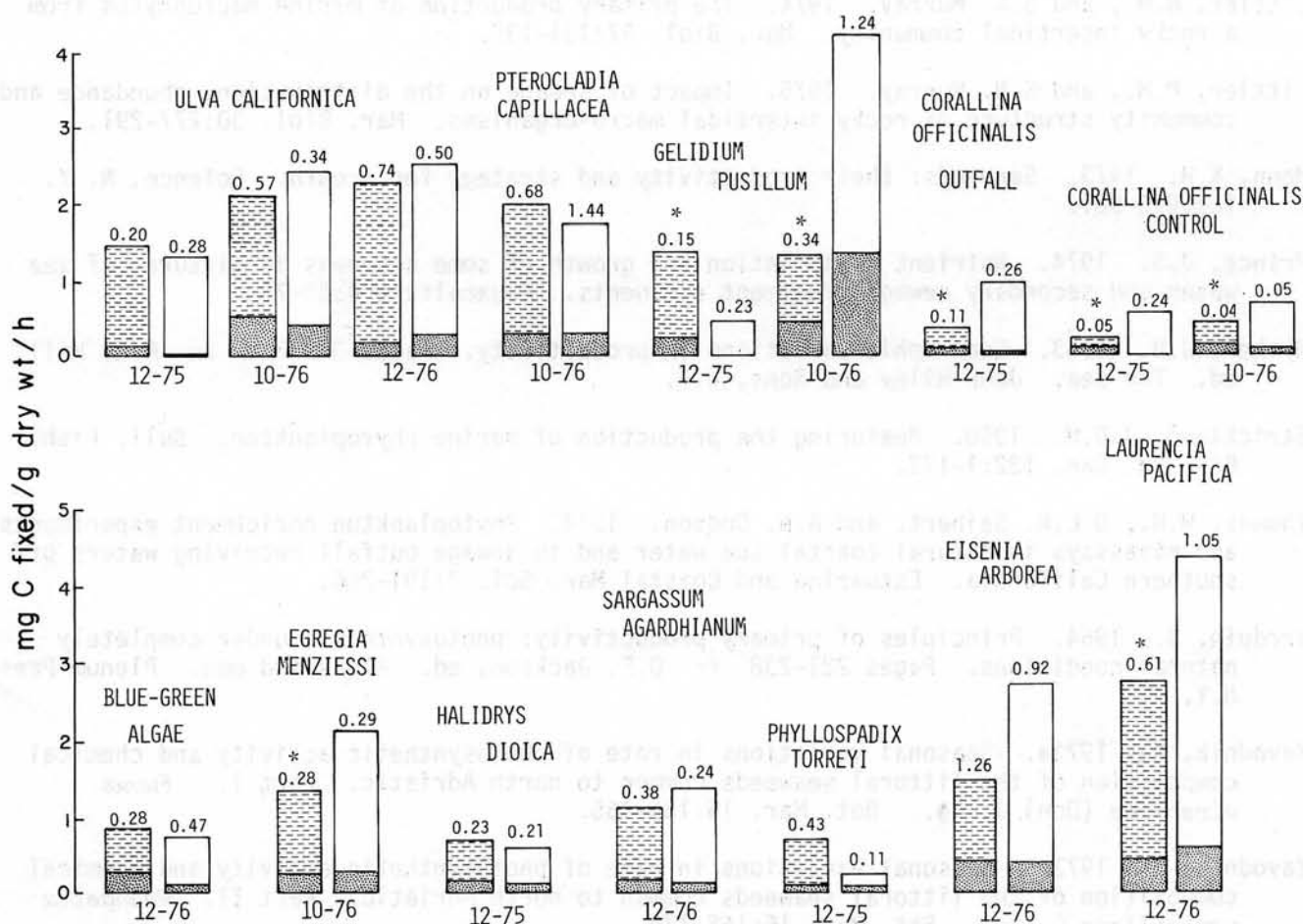


FIGURE 3-4 Comparisons between incubations performed in 10% untreated sewage (shaded histograms) and nonpolluted water (unshaded histograms). Each histogram indicates net productivity on the basis of thallus dry weight, respiration is represented by the dotted portion within, and the month and year are given beneath. See Fig. 3-3 for details.

As is the case in general for much of the published data base concerning the biological effects of pollutants, there is a considerable further need to determine the specific toxic components of the sewage under examination, their specific effects on metabolic processes, and the levels at which such effects take place. This will entail focusing on just several "key" species representative of polluted and unpolluted environments, while greatly increasing the number of replicates drawn from any given population.

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INFLUENCE OF DOMESTIC WASTES ON THE STRUCTURE AND
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WILSON COVE, SAN CLEMENTE ISLAND

by

MARK M. LITTLER

Department of Ecology and Evolutionary Biology
University of California, Irvine

and

STEVEN N. MURRAY

Department of Biological Science
California State University, Fullerton

CALIFORNIA WATER RESOURCES CENTER

University of California

Davis, California

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by

Mark M. Littler

Department of Ecology and Evolutionary Biology
University of California, Irvine

and

Steven N. Murray

Department of Biological Science
California State University, Fullerton



CALIFORNIA WATER RESOURCES CENTER

University of California, Davis
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