SECTION 5

PRIMARY PRODUCTIVITY OF MACROPHYTES

by

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INTRODUCTION

Research has been undertaken to determine the impact of the Wilson Cove outfall on the bioenergetics of intertidal seaweed communities. A prerequisite to understanding the relative contributions of benthic macrophytes to production is the measurement of photosynthesis of the dominant (in terms of cover) populations. Only a few studies of this nature are available; hence broad generalizations are very limited. More information, however, is available concerning the production of entire ecosystems (e.g., reef and turtle grass communities) or single-species populations. Reviews of the data accumulated have led to statements (Refs. 55, 56) that some coastal marine regions are, per unit area, among the most productive on earth.

Considerable work has been completed with upstream/downstream flow respirometry techniques on biotic reefs. Such habitats have been shown (Refs. 57–62) to be highly productive (3 to 9 gross g C fixed/m^2 per day). The gross productivities of single reef populations have been examined in detail (Refs. 58, 63–67) and range from 0.6 to 10.0 g C fixed/m^2 per day. Estimates of the production of kelp and other seaweeds of potential economic importance have been reported by Tkihovskaya (Ref. 68), Alleem (Ref. 69), Sargent and Lantrip (Ref. 70), Walker and Richardson (Ref. 71), and Doty (Ref. 72) based on harvest methods. As discussed by Pomeroy (Ref. 73), however, few of these studies have been useful in estimating actual primary production because of unmeasured losses from export, excreted organic matter, and grazing.

Some benthic seaweeds appear to be extremely productive (Refs. 74, 75). Ryther (Ref. 55) suggested that the world-wide production of benthic seaweeds may approach 10% that of phytoplankton, even though these are confined to an area about 0.1% that available to plankton. The kelp beds of California are said to rank with the most productive areas of the world, with incredible net production rates estimated by Blinks (Ref. 74), according to Collier, *et al.* (Ref. 76), to be about 33 g C fixed/m^2 per day. Blinks (Ref. 74) 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 per day*. Kanwisher (Ref. 75) obtained a much higher net rate (20 g C/m^2 per day) for *Fucus* stands off Woods Hole, Massachusetts. Recent studies have yielded net annual rates of 1,750 g C/m^2 (Ref. 77) for the seaweed zone of St. Margaret's Bay, Nova Scotia and about 547 to 3,832 g C/m^2 (Ref. 78) for marine macrophytic communities in the Canary Islands.

Clearly, field studies on the effects of sewage effluents on the functionally important intertidal algae are desirable if our knowledge of man's impact on marine resources is to advance beyond a level that at present is often subjective and in some cases strongly emotional. Consequently, the present study was undertaken to determine quantitatively (1) the primary productivity of the sewage outfall area vs. that of unaffected neighboring control areas and (2) the relative energetic contribution of each species to these intertidal ecosystems.

**Pomeroy (Ref. 73) converted these figures to 1 to 9 net g C/m^2 per day.*

METHODS AND MATERIALS

The work was done near the San Clemente Island outfall (Fig. 16) on 19 and 20 May 1973 under completely overcast skies. Light intensity was measured by a Weston photoelectric 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 five different thalli and carefully transferred into bottles filled from a single batch of ambient control-area seawater for which the initial dissolved O_2 was determined. During his study of production of marine macrophytes, Johnston (Ref. 78) found that if a ratio not exceeding 0.1–0.3 g dry wt alga per liter of seawater was employed, no nutrient or CO_2 deficiency effects were recorded in linearity experiments lasting as long as 24 hours. In the present study, 0.04 to 0.58 g dry wt of each alga per 300 ml of seawater were used but incubation times did not exceed 4 hours. A total of 160 bottles were incubated horizontally in clear acrylic trays between the starting times from 0920 to 1050 and finishing times from 1240 to 1450 (3 hours 20 min to 4 hours of incubation) over a 2-day period with the intent of minimizing any daily periodicity effects on production. Incubation was done near the high-water mark, and the trays were replenished with ambient seawater (15.0°C) at about 15-min intervals to maintain constant temperature and provide agitation. 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 four blank (phytoplankton only) controls 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 Whirl-pack 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 by means of a point-intercept method. The thalli were then weighed after being dried at 37.8°C until constant weight was attained. In the cases of *Corallina, Lithothrix, Lithophyllum, Phyllospadix* with *Melobesia*, 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 hours of combustion at 400° Celsius. All O_2 values were converted to g C fixed/g dry wt per hr and to g C/m^2 per hr by standard methods (Ref. 80), assuming a photosynthetic quotient of 1.20. For each species, the two replicates for each measurement of respiration were averaged, and this figure was added to each of the six light (net production) replicates. The mean of these six values and the 95% confidence interval were then computed to get gross production for the macrophytes. The production budgets for outfall and control regions were calculated using the percent cover and the net primary productivity per square meter for each of the dominant species. The cover data presented here (Table 14) are taken from standing stock assessments reported above (see Section 3). Daily net production rates were calculated from hourly rates by substracting 12 hours of respiration (night) from 12 hours of net production (daytime).

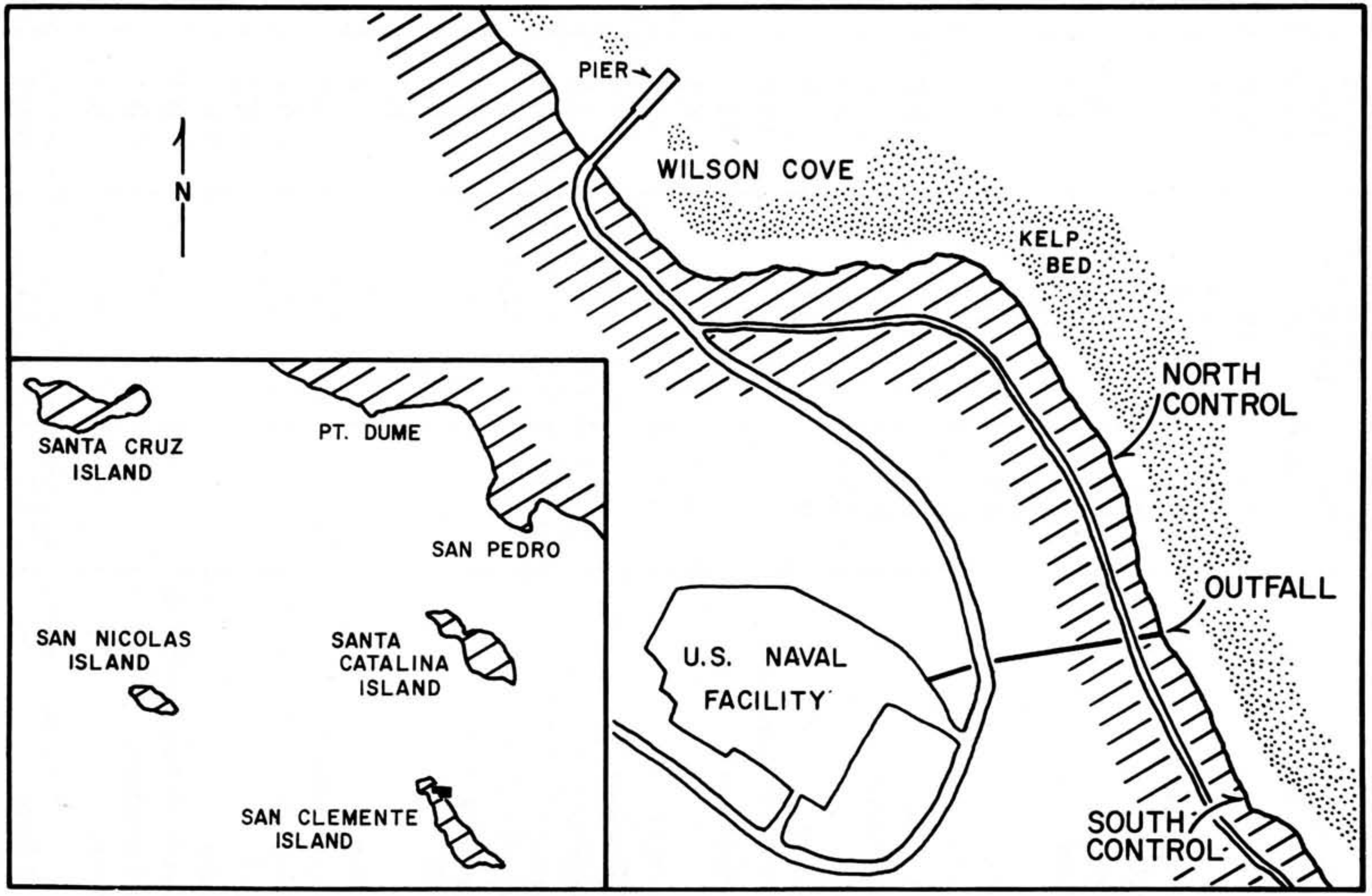

Figure 16. Map showing the location of the Wilson Cove outfall and the two control study sites on the leeward side of San Clemente Island, California.

TABLE 14. The mean cover and net production rates of the dominant macrophytes per square meter of primary substrate.

Plants	Outfall		Controls	
	Cover (%)	Productivity (mg C/hr)	Cover (%)	Productivity (mg C/hr)
Blue-green algae	43.1	46.1	18.4	19.7
Ulva californica	11.5	35.3	<0.1	0.3
Pseudolithoderma nigra	9.1	3.9	6.7	2.9
Pterocladia capillacea	8.8	12.3	3.1	4.3
Corallina chilensis	8.4	5.6	14.1	9.4
Gelidium pusillum	5.7	19.2	0.3	1.0
Eisenia arborea	3.2	2.5	3.1	2.4
Gelidium robustum	0.7	1.4	7.7	15.6
Petalonia fascia	0.5	–	–	–
Gigartina canaliculata	0.3	0.7	8.8	19.5
Scytosiphon lomentaria	0.2	–	–	–
Peyssonellia sp.	0.1	–	0.3	–
Colpomenia sinuosa	0.1	0.1	2.8	0.3
Egregia laevigata subsp. *borealis*	–	–	13.8	26.5
Lithophyllum decipiens	–	–	12.1	6.2
Halidrys dioica	–	–	5.3	8.0
Phyllospadix torreyi	–	–	1.8	2.5
Sargassum agardhianum	–	–	1.7	4.1
Rhodoglossum affine	–	–	1.1	1.0
Macrocystis pyrifera	–	–	0.8	1.1
Lithothrix aspergillum	–	–	0.4	0.6
Anisocladella pacifica	–	–	0.2	–
Gigartina spinosa	–	–	0.2	–
Codium fragile	–	–	0.2	–
Dictyota flabellata	–	–	0.1	–
Corallina vancouveriensis	–	–	0.1	–
Cladophora graminea	–	–	<0.1	–
Gelidium coulteri	–	–	<0.1	–
Laurencia pacifica	–	–	<0.1	–
Plocamium coccineum var. *pacificum*	–	–	<0.1	–
Unidentified red prostrate	–	–	<0.1	–
Lithothamnium sp.	–	–	<0.1	–
Totals	91.7	127.1	103.4	125.4

RESULTS AND DISCUSSION

The mean net contributions to overall production (in mg C/m^2 per hr) of the major species are given in Table 14. The total productivity of the outfall plume area (127.1) was not appreciably different from that of the controls (125.4) even though there was 11.7% less cover and 43% as many species as compared to the control areas. This interesting circumstance is mostly due to the relative increases in cover of *Pterocladia capillacea, Gelidium pusillum*, and *Ulva californica* (high producers) as opposed to decreases of nearly all other macrophytes in the mid-intertidal outfall area, and an increase in *Lithophyllum decipiens* (a low producer) in the mid-intertidal zone of control areas. The result of these changes in cover (Table 14) tend to minimize the reduction in productivity in the mid-intertidal zone of the outfall area relative to that of the control areas, and this reduction is balanced by the increase in blue-green algal cover in the upper intertidal zone (see Section 3) owing to the splashing of effluent on rocks that would otherwise remain dry and bare of macrophyte cover. One would conclude from these data and the small size of the area affected that the present outfall is having no profound effects on the overall production by macrophytes at Wilson Cove. However, if the outfall were slightly lower, the enhancement of upper intertidal blue-greens would not occur, and the productivity of outfall macrophytes would be about 15% less than control macrophytes on an equal-area basis.

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 observations (Section 3) indicated only slight seasonal changes in macrophyte community composition from June 1971 to May 1973. As mentioned, the effect of possible daily periodicity was controlled by making all of the measurements between 0920 and 1450 hours within a two-day period. Seasonal phenomena were not part of this study, but because most of the macrophytes are perennials and measurements were made during the early summer when growth rates appear to be high (also noted in Ref. 75), we feel that a cautious comparison of our control-area data with annual rates from similar studies is useful. With the foregoing precautions in mind, we generate a daily (24-hr) net rate of 1.33 g C/m^2, a rate intermediate (Ref. 56) between continental shelf waters and agricultural land. These rates are about 23 times lower than those (according to Collier, *et al.*, Ref. 76) for dense kelp beds. The highest net rate obtained during this study (3.13 g C/m^2 per day) translates into 1,142 g C/m^2 per year, a productivity comparable to that of beech forests and grasslands and about twice that of agricultural land (Ref. 56).

Published records of the annual production of marine communities and populations are given in Table 15. The lowest yearly value recorded (365 g/m^2) compares favorably with our data (485 g/m^2) and the highest (3,285 g/m^2) is nearly three times greater than the highest single rate (1,142 g/m^2) encountered in this study. The rates of this study, however, are remarkably close to those (Table 15) generated by Johnston (Ref. 78) and Mann (Ref. 77) for marine seaweed communities.

The macrophytes at Wilson Cove have been ranked (Fig. 17, Table 16) in order from highest to lowest producer on an equal-area basis. It is clear that the two encrusting prostrate forms (*Lithophyllum* and *Pseudolithoderma*) are the lowest producers. *Gelidium pusillum* and *Ulva californica* are associated with the disturbed outfall area and show greater

TABLE 15. The productivity of various aquatic populations and communities. All have been converted to yearly rates for comparability.

Populations and Communities	Net Production $g\ C/m^2/yr$	Source
Caulerpa beds, Eastern Canary Islands	365	Johnston (Ref. 78)
Nine seaweeds, California	365 to 3,285 (mean = 1,326)	Blinks (Ref. 74) as recalculated by Pomeroy (Ref. 73)
Marine macrophytic communities, Eastern Canary Islands	547 to 1,095 (highest = 3,832)	Johnston (Ref. 78)
Reef communities, Eniwetok Atoll	569 to 2,628	Smith (Ref. 62)
Turtle grass flat, Long Key, Florida	1,142	Odum (Ref. 79)
Seaweed zone, St. Margaret's Bay Nova Scotia	1,750	Mann (Ref. 77)
Crustose coralline algae, Waikiki reef, Hawaii	2,080	Littler (Ref. 67)
Thallassia and *Cymodocea* bed, Kavaratti Atoll, Laccadives	2,120	Qasim & Bhattathiri (Ref. 81)
Intertidal algal populations, San Clemente Island	135 to 1,142	This study

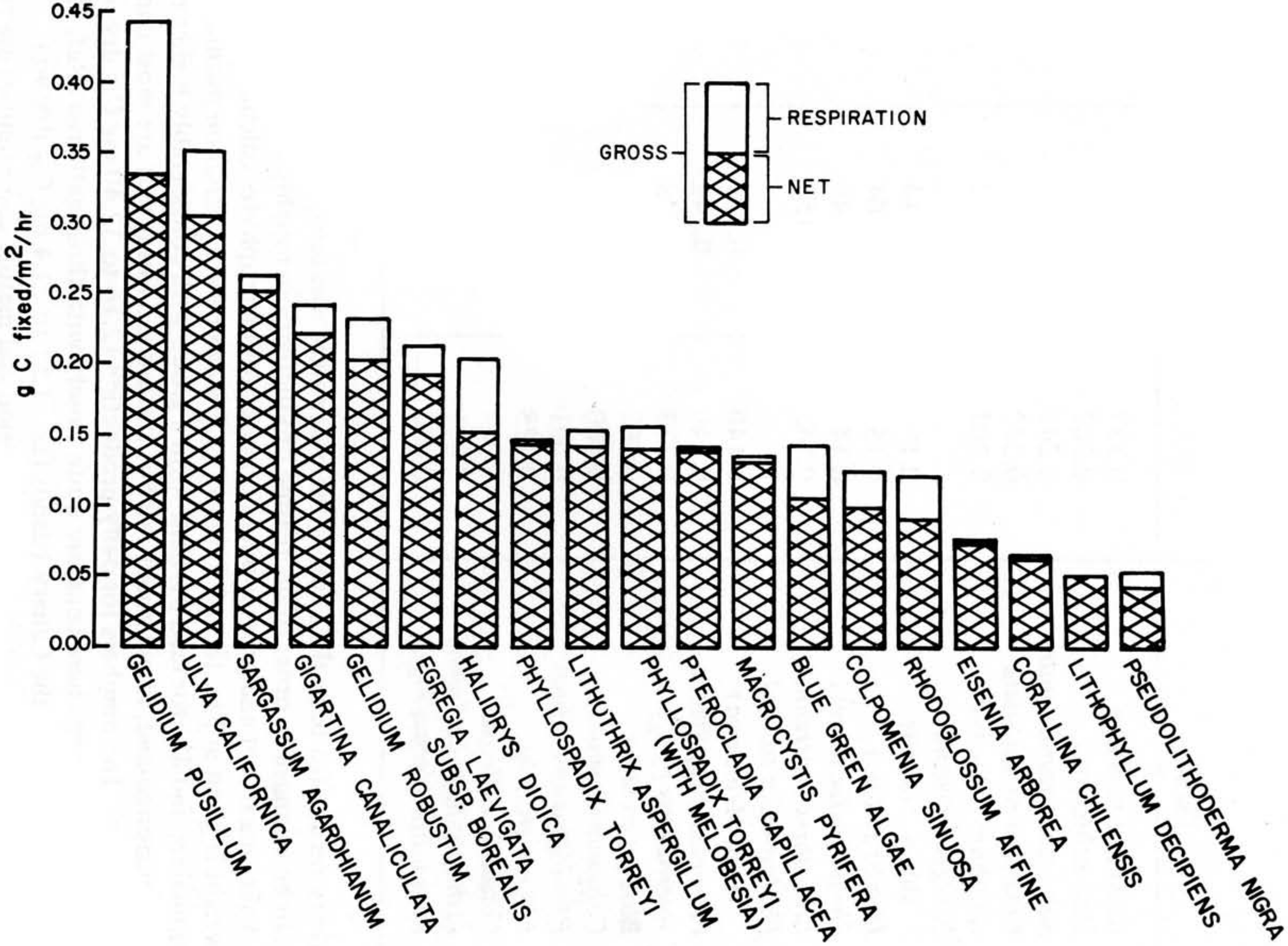

Figure 17. The respiration, net, and gross production rates of the dominant macrophytes near Wilson Cove on the basis of two-dimensional thallus surface area.

TABLE 16. The net and gross productivity of the dominant macrophytes of Wilson Cove, with confidence limits given at the P = 0.05 level.

Plants	Productivity Net (g C fixed/m^2 per hr)	Productivity Gross (g C fixed/m^2 per hr)	±
Gelidium pusillum	0.337	0.445	0.090
Ulva californica	0.307	0.353	0.063
Sargassum agardhianum	0.242	0.262	0.038
Gigartina canaliculata	0.222	0.243	0.034
Gelidium robustum	0.203	0.232	0.026
Egregia laevigata subsp. *borealis*	0.192	0.214	0.033
Halidrys dioica	0.151	0.204	0.029
Phyllospadix torreyi	0.144	0.149	0.037
Lithothrix aspergillum	0.143	0.152	0.018
Phyllospadix torreyi (with *Melobesia*)	0.140	0.159	0.014
Pterocladia capillacea	0.140	0.142	0.030
Macrocystis pyrifera	0.133	0.138	0.022
Blue-green algae	0.107	0.144	0.032
Colpomenia sinuosa	0.100	0.126	0.023
Rhodoglossum affine	0.091	0.121	0.010
Eisenia arborea	0.078	0.079	0.012
Corallina chilensis	0.067	0.068	0.012
Lithophyllum decipiens	0.051	0.051	0.007
Pseudolithoderma nigra	0.043	0.055	0.013

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. 18 and Table 17. *Ulva californica, Gelidium pusillum, Pterocladia capillacea,* and *Macrocystis pyrifera* form a group with considerably higher rates than other algae measured and, interestingly, all but the last are forms that are most conspicuous in the outfall area. The numbers for daily production (2.16 to 32.40 mg C/g dry wt) for the 19 major species measured here compare quite closely with those gathered (Ref. 78) for 11 species of macrophytes in the Canary Islands (i.e., 1.51 to 21.4 mg C/g dry wt).

Contrasts between seral stages of succession and mature communities are relevant when one compares the productivities of dominant mid-intertidal macrophytes in the control areas with those of the outfall plume region. One of the most important characteristics of communities in early seral stages of succession is a high net community productivity (Ref. 47). Krebs (Ref. 82) points out that such early seral stages are characterized by

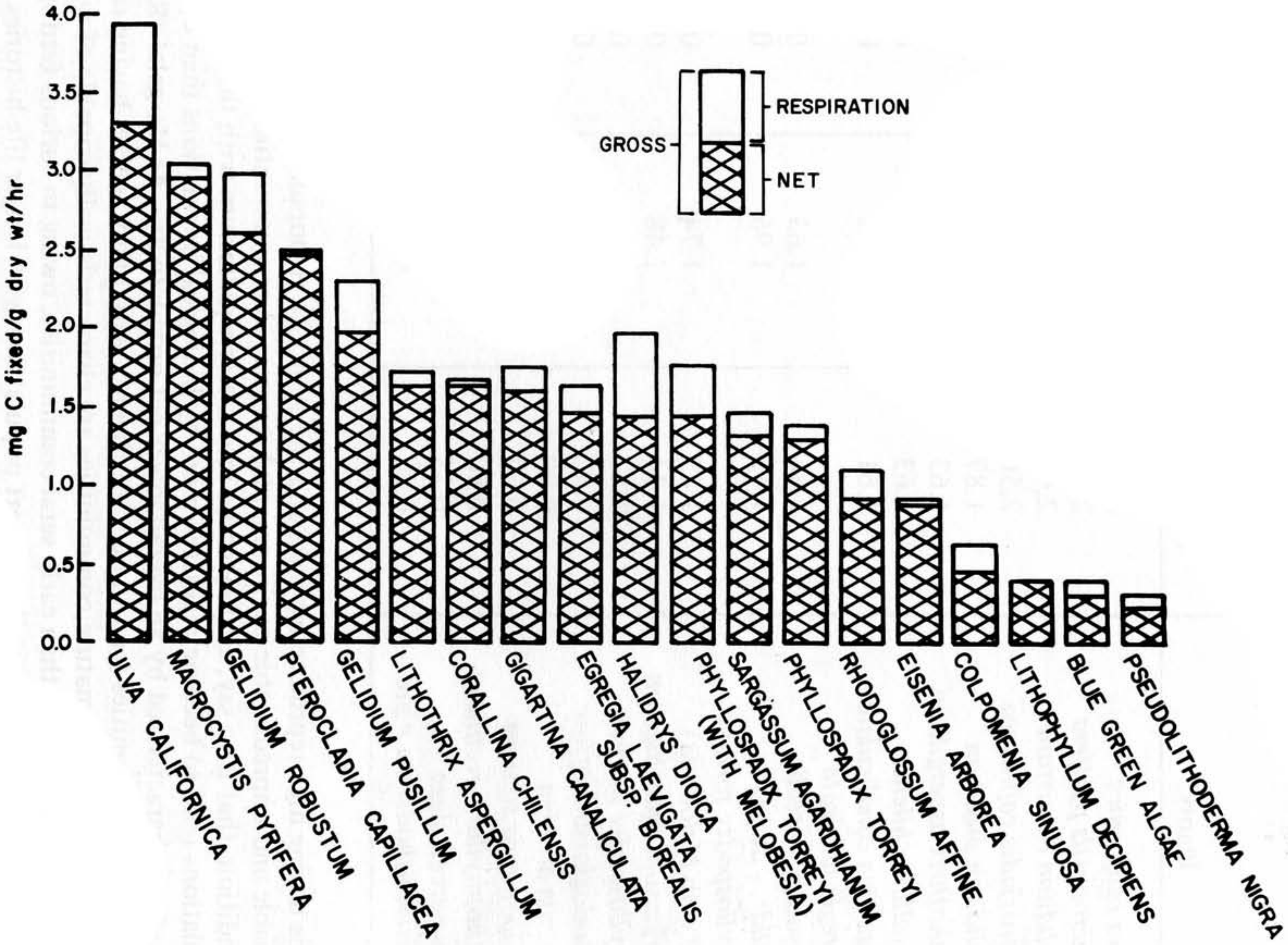

Figure 18. The respiration, net, and gross production rates of the dominant macrophytes near Wilson Cove on the basis of thallus dry weight.

TABLE 17. The net and gross productivity of the dominant macrophytes of Wilson Cove, with confidence limits given at the P = 0.05 level.

Plants	Productivity		±
	Net	Gross	
	(mg C fixed/g dry wt per hr)		
Ulva californica	3.31	3.92	0.59
Macrocystis pyrifera	2.94	3.04	0.70
Gelidium robustum	2.64	2.98	0.32
Pterocladia capillacea	2.50	2.51	0.37
Gelidium pusillum	1.87	2.33	0.78
Lithothrix aspergillum	1.63	1.72	0.32
Corallina chilensis	1.63	1.66	0.26
Gigartina canaliculata	1.61	1.74	0.14
Egregia laevigata subsp. *borealis*	1.46	1.63	0.17
Halidrys dioica	1.45	1.96	0.27
Phyllospadix torreyi (with *Melobesia*)	1.45	1.74	0.55
Sargassum agardhianum	1.34	1.48	0.04
Phyllospadix torreyi	1.31	1.40	0.19
Rhodoglossum affine	0.92	1.13	0.10
Eisenia arborea	0.90	0.92	0.14
Colpomenia sinuosa	0.54	0.63	0.08
Lithophyllum decipiens	0.50	0.50	0.11
Blue-green algae	0.33	0.50	0.27
Pseudolithoderma nigra	0.26	0.34	0.05

populations having high reproductive rates and the ability to re-populate quickly following highly variable and unpredictable environmental stresses. As communities approach the climax condition, that is to say, as they come into closer equilibrium with their environment, their populations tend to become regulated more by biological interactions than by physical controls and are characterized by an overall lower net productivity. As Margalef (Ref. 83) indicates, mature communities tend to be more diverse, with many species having relatively low production rates. Such mature communities are characteristically capable of withstanding more environmental stress than early seral communities, owing to various feedback and homeostatic mechanisms, and usually support populations with longer life histories. Also, mature systems often have, as pointed out by Odum (Ref. 47) and Connell (Ref. 44), relatively well-organized patterns of spatial heterogeneity.

The productivity data generated here are consistent with the concepts of r- and K-selection (as presented by Pianka, Ref. 45) from studies of succession in terrestrial systems. The high production rates of the outfall seaweeds (Figs. 17, 18; Tables 16, 17) indicate fast-growing populations; the most productive of these (the green alga, *Ulva*) has been characterized as "opportunistic" (Ref. 44) and has a short and simple life history as does the most abundant (blue-green algae). In close agreement, a successional study of the intertidal zone near Woods Hole, Massachusetts, (Ref. 84) revealed that the green alga *Enteromorpha* and the blue-green alga *Calothrix* were among the first macroscopic organisms to occur and that these appeared to be rapidly growing forms. Species diversity, spatial heterogeneity, and abundance (92% cover) are contrastingly low near the outfall (see Section 3), most likely because of environmental stress and instability (e.g., periodic sewage influx) that would appear to maintain a disclimax community composed of generalist (r-strategist, sensu Pianka, Ref. 45; or opportunistic, sensu Connell, Ref. 44) populations.

On the other hand, and in accordance with statements by Connell (Ref. 44), the relatively less productive dominant algae of the control zones indicate a long-established mature community structure. Species diversity and abundance (103% cover) is higher (see Section 3) and perennial forms predominate with relatively complex life histories and greater spatial heterogeneity (e.g., greater layering of canopies and more substrata levels). These algae appear to be slower-growing specialists (i.e., K-strategists), with their populations regulated by biological interactions such as intensive competition for space and light. To our knowledge this study represents the first assessment of marine macrophytic communities treated in view of the r- and K-selection concepts and shows, in this case, that such principles have general applicability and utility in the interpretation of the role of pollution on marine ecosystems.

SUMMARY

The U. S. Navy outfall on San Clemente Island would appear to be having no profound effect on the overall productivity contribution by macrophytes, although there is an 11.7% reduction in cover and a 57% reduction in species numbers.

The net primary productivity of intertidal macrophytes near Wilson Cove (485 g C/m^2 per yr) is comparable to rates reported for most marine communities, but lower than numbers given by two previous studies of seaweeds.

Of the 19 predominant species near Wilson Cove, *Ulva californica* and *Gelidium pusillum* are the highest producers on the basis of thallus surface area and are associated with the disturbed outfall region.

The concepts of r- and K-selection, which were derived from studies of terrestrial ecosystems, are illustrated by this study, and our data show the applicability and utility of these principles in studies of pollution effects on marine ecosystems.

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Studies on the effects of a low-volume discharge of raw sewage on rocky marine intertidal communities near Wilson Cove, San Clemente Island, California included taxonomic surveys and quantitative assessments of standing stock, community structure and primary production for the sewage-affected area and nearby unpolluted (control) areas. Additionally, a comparative populational study of the limpet *Acmaea limatula* revealed that only larger individuals were present in the outfall area. Near the outfall pipe, intertidal

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communities were characterized by lower species diversity, reduced standing stocks of large, canopy-forming intertidal macrophytes (which largely had been replaced by a low-growing algal turf) and an abundance of suspension-feeding animals. The most productive macrophytes were among those most abundant in the outfall area. Additional manipulative studies revealed that the outfall area consisted of disclimax communities.

DEPARTMENT OF THE NAVY
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BIOLOGICAL FEATURES OF INTERTIDAL COMMUNITIES NEAR THE U. S. NAVY SEWAGE OUTFALL, WILSON COVE, SAN CLEMENTE ISLAND, CALIFORNIA

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ADMINISTRATIVE STATEMENT

This report describes ecological studies of intertidal communities near the San Clemente Island sewage outfall conducted by scientists from California State University, Fullerton, and the University of California, Irvine, in cooperation with the Naval Undersea Center. These studies provide basic information on the environmental impact of typical domestic sewage from a small community.

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