

## INFLUENCE OF DOMESTIC WASTES ON ENERGETIC PATHWAYS IN ROCKY INTERTIDAL COMMUNITIES

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### SUMMARY

(1) The calorific contents of eighteen macroinvertebrates and thirty-six macrophytes were determined in an unpolluted rocky intertidal habitat and in a nearby polluted habitat.

(2) Much of the variation in the calorific values of macrophytes was related to life span. The algae that characterized the unpolluted community usually contained comparatively fewer calories per unit weight. These forms had relatively more structural tissues and hence allocated relatively less energy to rapid growth and reproduction. In the polluted habitat, fugitive or opportunistic algal species were more prevalent; these had more rapid growth rates and higher productivities and tended to have relatively high calorific contents. Encrusting forms, that are easily accessible to many herbivores, had thallus constituents with lower calorific values, suggesting that these algae may have evolved reduced palatability.

(3) The major taxonomic groups of algae yielded the following sequence of mean calorific values: Chlorophyta, 4.78 kcal g<sup>-1</sup> ash-free dry weight; Rhodophyta, 4.39; Cyanophyta, 4.38; Phaeophyta, 4.22.

(4) In nearly every case, macroinvertebrate populations exposed to domestic sewage had higher energy contents than did corresponding populations from the unpolluted habitat.

(5) Macroinvertebrates in the polluted habitat grazed greater proportions of blue-green algae and bacteria. Omnivores and suspension feeders in the polluted habitat appeared to utilize energy-rich compounds in the sewage effluent; this may explain the greater standing stocks of omnivores and suspension feeders in the peripheral regions of the outfall plume.

### INTRODUCTION

Little is known about the utilization of energy-rich compounds in sewage by marine benthic communities. The Wilson Cove intertidal ecosystem on San Clemente Island (SCI), California (Fig. 1) was selected as an ideal site to study the effects of domestic waste waters on energetic pathways. This ecosystem is relatively simple and much is known about the primary productivity, distribution, abundance, and community structure of unpolluted and polluted areas (Littler & Murray 1974; Littler & Murray 1975). The intertidal communities are characterized by high standing stocks of primary producers but relatively low standing stocks of macroinvertebrates.

The environmental features of the Wilson Cove study site have been reported in detail by Kenis, Salazar & Tritschler (1972) and Littler & Murray (1975). The effluent discharged into the study area (95 000 litres d<sup>-1</sup>) consists primarily of untreated human excreta and food wastes with much smaller quantities of disinfectants, bleach, and detergents. The effluent is released onto the rocky shoreline 1.6 m above mean lower low water. The average concentration of dissolved O<sub>2</sub> is about 5.5 mg l<sup>-1</sup> at the point of

discharge, and about  $7.0\text{--}8.0\text{ mg l}^{-1}$  at shoreline locations 30 m beyond the outfall terminus (Kenis, Salazar & Tritschler 1972); the latter range is typical of unpolluted ocean surface waters. The biochemical oxygen demand of the effluent ranges from 90 to  $405\text{ mg O}_2\text{ l}^{-1}$  with a mean of  $223\text{ mg O}_2\text{ l}^{-1}$ ; this is typical of raw sewage, and is several hundred to a thousand times the concentration likely to affect sensitive marine organisms. The concentration of coliform bacteria is in excess of legal minimum standards for public water-contact areas (i.e. 1000/100 ml) within 30 m of the outfall. The sewage is in suspension, and no sedimentation was observed either intertidally or subtidally near the study region.

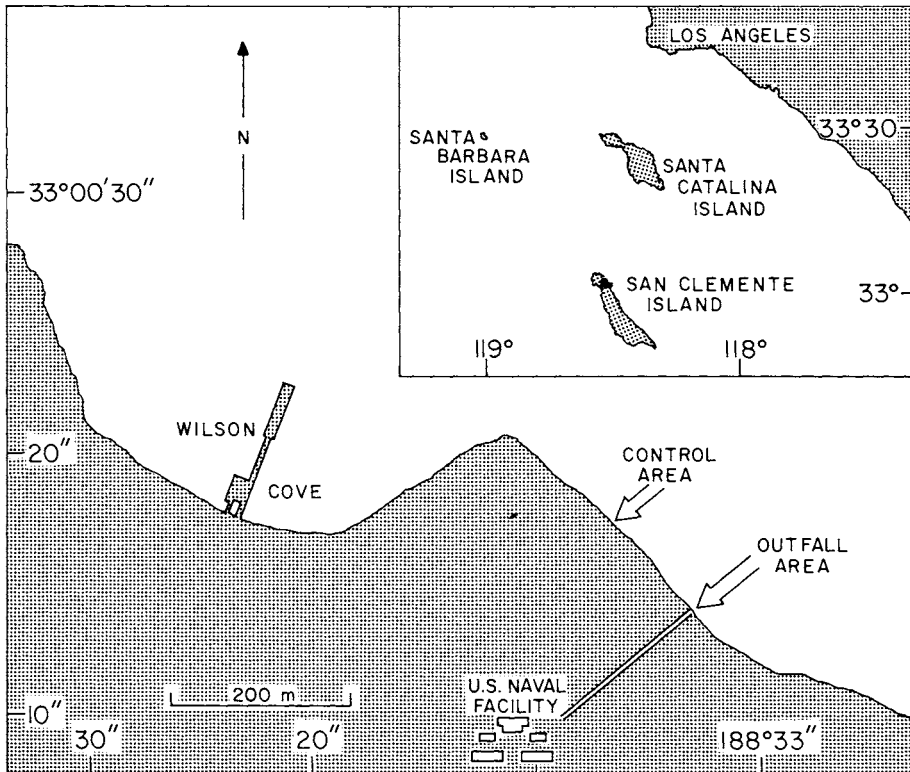


FIG. 1. Location of the outfall site and control study site on San Clemente Island.

The pathways of energy flow through the intertidal communities in the sewage-affected area appear to differ from those of the control region as a direct consequence of the presence of particulate organic matter. The research presented here represents an initial step towards quantifying these energetic pathways, including analyses of the calorific contents of the dominant benthic macrophytes and macroinvertebrates and the gut contents of the principal consumers from both habitats.

There appear to be two distinct food subwebs characteristic of the rocky intertidal systems of leeward San Clemente Island. The first is a macrophyte-based grazing subweb (Fig. 2) in which the limpets *Acmaea (Collisella)* spp.,\* and *Lottia gigantea*, the peri-

\*The nomenclature for the macrophyte and macroinvertebrate taxa mentioned is that of Abbott & Hollenberg (1976) and Smith & Carlton (1975), respectively.

winkle *Littorina planaxis*, and the omnivorous shore crab *Pachygrapsus crassipes* are important consumers of algae in the polluted and unpolluted areas, with the exception of much lower numbers of *L. gigantea* in the latter. Hypothetically, the abundance of grazers near the outfall is increased by the greater standing stocks (Littler & Murray 1975) of tolerant primary producers, such as blue-green algae, *Ulva californica*, *Gelidium pusillum* and the epiphytic filamentous brown algae, diatoms, and bacteria growing on them. The second food subweb is based on suspended and settled particulate materials as a primary energy source (Fig. 2). In both the outfall and control habitats, plankton and seston are

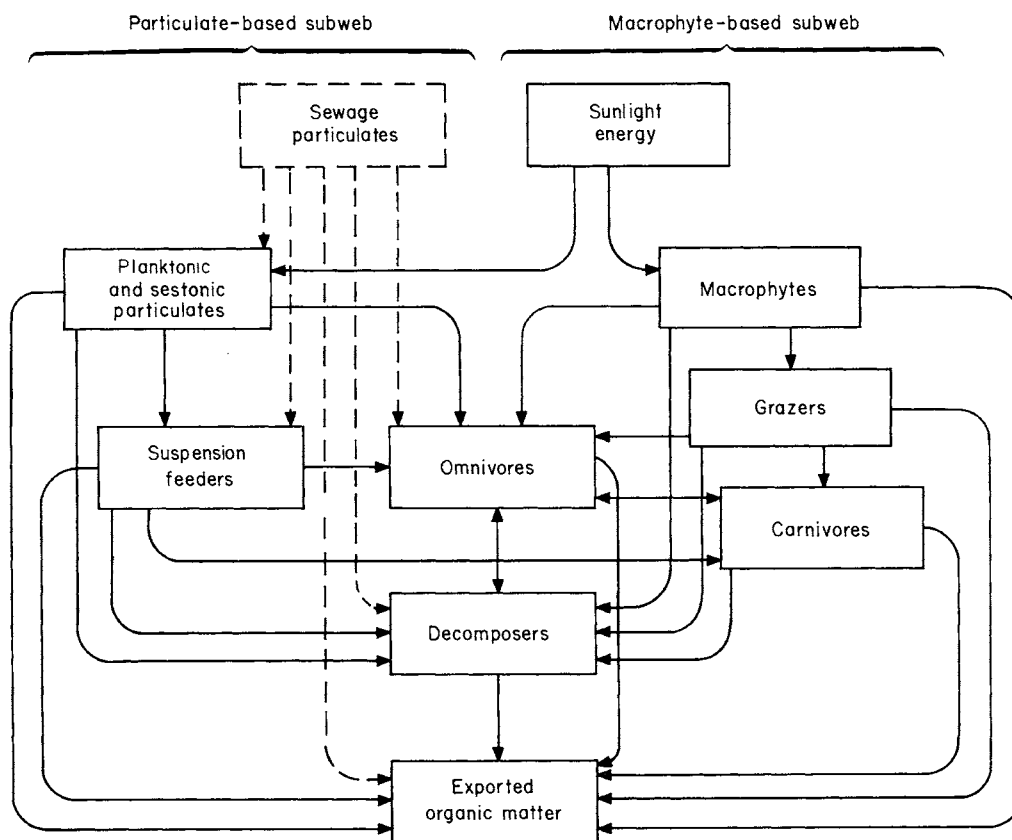


FIG. 2. Hypothetical pathways of organic matter through the intertidal food web. Pathways unique to the outfall system are shown by broken lines.

readily available to suspension feeders. Populations of barnacles, i.e. *Chthamalus fissus/dalli* and *Tetraclita squamosa rubescens*, occurred commonly in the control area and were the dominant suspension feeders there. However, for the outfall system, effluent apparently serves as a primary food source for the suspension feeder subweb (Fig. 2). The barnacle populations are much reduced in the outfall area (Littler & Murray 1975) but other suspension feeding organisms, which hypothetically utilize sewage, predominate. These populations include the omnivore *Pachygrapsus crassipes*, which consistently feed on sewage particles, as well as on algae during periods of low tide, and the anemone *Anthopleura elegantissima*. The latter was abundant in the zone bordering on the point of discharge and has been encountered only rarely in the unpolluted habitat. Additionally, an extremely dense population of very large *Serpulorbis squamigerus*, a vermetid gastro-

pod, occurred in the outfall zone. This mollusc feeds upon particles trapped from suspension and has formed an extensive bed at the lower intertidal margin of the outfall area. It apparently has been abundant for many years, as evidenced by the reef-like mass (50 cm thick in places) of calcareous tubes.

It is hypothesized, from our extensive data on standing stock (Littler & Murray 1975), that the energetic pathways in the polluted system have been altered in two ways. First, there is an increase in populations of suspension feeders and omnivores that utilize sewage and, secondly, the periodic emission of deleterious materials (Littler & Murray 1975) provides a stress that maintains a successional subclimax community, particularly in the upper mid-intertidal region. This subclimax community consists largely of 'opportunistic' or early successional species of algae (Littler & Murray 1975) whose high productivity (Littler & Murray 1974), rapid growth, and high energy content augment the subweb dominated by grazing gastropods (Fig. 2). To test these hypotheses, we compared the gut contents of the principal consumers and the calorific contents of the abundant macrophytes and macroinvertebrates between polluted and unpolluted populations.

The intent of this research was not to investigate every population in the system; Glynn (1965) has shown the impracticality of this approach for even a relatively confined and unstructured system. Instead, we focused on the energetic pathways originating from (i) the effluent particulate organic matter and, (ii) the 'opportunistic' algal-dominated producer base, concentrating on the calorific content of seventy-four samples which characterize the dominant macro-producers and consumers in both the polluted and unpolluted ecosystems.

## METHODS AND MATERIALS

The calorific contents of a total of forty-nine macroinvertebrates and macrophytes were assessed for the unpolluted area and fourteen for the polluted area. There were fifty samples of macrophytes, including analyses of different tissue types from five of the larger brown algae, and twenty-four samples of macroinvertebrates. All samples were collected on 14 December 1974 and taken alive to the laboratory where they were quickly cleaned in distilled water to remove salts, detritus and epibiota; all hard parts of calcareous animals were removed by dissection. The soft parts of algae and animals were dried at 80 °C, ground to a fine powder in a ball mill, pelletized, and ignited in a Parr Model 1411 semi-micro oxygen bomb calorimeter. An endothermy correction (Paine 1966) was applied to the samples of coralline algae, because of their high CaCO<sub>3</sub> content. The calorific content was expressed as kcal ash-free g dry weight<sup>-1</sup>, after correcting for the percentage of ash, determined on single aliquots of the homogeneous milled samples (dried at 80 °C) by igniting the material at 400 °C for 24 h in a muffle furnace. The total percentage of ash was determined in the same way for all animals including their hard parts. Three replicates were run for each calorific determination but between three and forty-one (mean, seven) replicates were used to determine the total ash content of the organisms under study. We also measured the water content of organisms and could therefore calculate kcal g wet weight<sup>-1</sup>, which may be ecologically more meaningful. We did not investigate seasonal differences. Paine & Vadas (1969) found no significant seasonal variation in the calorific content of seventy species of algae, though Himmelman & Carefoot (1975) found significantly higher values during late summer to autumn for the brown alga *Lessoniopsis*.

A total of 144 analyses were performed on the gut contents of macroinvertebrates from the two habitats. Replicate analyses were performed on six randomly selected animals for each of twelve consumer species from outfall area populations and for eleven of these, plus one additional species, obtained from the control site. All animals were collected between 10.30 and 14.00 hours on 10–11 March 1976 or 11–12 June 1976. In an attempt to measure the entire spectrum of potential food items, collections were made throughout all regions of both study sites, rather than from a specific zone or community. This included samples of the same species from many separate populations and undoubtedly increased the range of variability. Samples of a given species (with the exception of *Haliotis cracherodii*) were always collected separately from both the outfall and control areas during the same visit. The organisms were fixed in buffered formalin seawater immediately upon collection, identified and labelled in the field. Samples were returned to the laboratory, the gut contents dissected, then smeared evenly and mounted on a microscope slide. The percentage of dietary composition of each species was then measured by a point-intercept microscopic procedure, using a minimum of 100 points from ten random fields of view for each sample replicate.

## RESULTS

### *Calorific values of macro-epibiota*

Calorific values ranged from 5.44 kcal g<sup>-1</sup> ash-free dry weight in *Ulva californica* to 3.25 kcal ash-free g dry weight<sup>-1</sup> in *Lithothrix aspergillum*; the mean calorific content of macrophytes was 4.30 kcal (Table 1). Members of the Chlorophyta had the greatest mean calorific values (4.78), followed by Rhodophyta (4.39), Cyanophyta (4.38), and Phaeophyta (4.22). Generally, those forms with high surface to weight ratios (e.g. *Ulva californica*, *Pachydictyon coriaceum*, *Dictyota flabellata*) contained more energy than those with low ratios (e.g. *Ralfsia* sp., *Colpomenia sinuosa*, *Gigartina canaliculata*) or those with calcareous structure (e.g. all of the coralline algae).

The upper blade portions of *Eisenia arborea* and *Macrocystis pyrifera* thalli had higher calorific values than did the lower portions (i.e. stipe and holdfast) while the reverse trend was recorded for *Egregia menziesii* and *Pelvetia fastigiata* f. *gracilis*.

Calorific values for macroinvertebrate consumers were considerably greater than those for macrophyte producers, ranging from 7.01 kcal g<sup>-1</sup> ash-free dry weight for *Acmaea (Collisella) strigatella*, collected from the control area, to 4.46 kcal for *Chthamalus fissus/dalli* from the control area; the mean calorific value for macroinvertebrates was 5.43 kcal (Table 2). No ranking by phylum or trophic level was evident. In most cases populations of a given species from the outfall area had higher calorific contents than populations from the control area.

### *Dietary composition of grazers and suspension feeders*

More detrital material and remains of opportunistic producer organisms were present in the diets of *Pachygrapsus crassipes* from the outfall area than in specimens from the control habitat (Table 3). The diet of *P. crassipes* from the unpolluted region was more varied and included calcareous algae as an important constituent. The greater percentage of detritus material in specimens from the outfall area probably indicates increased consumption of sewage, a view also supported by direct observations of feeding. Other

TABLE 1. The calorific content, % ash and % water of the dominant primary producers collected from polluted (P) and control (C) areas near Wilson Cove, San Clemente Island, California on 14 December 1974. 95% confidence intervals are shown for kcal per g dry weight

Major groups and taxa	Location	kcal g <sup>-1</sup> ash-free dry weight	% ash	kcal g <sup>-1</sup> dry weight	% H <sub>2</sub> O	kcal g <sup>-1</sup> wet weight
<b>Chlorophyta</b>						
<i>Ulva californica</i>	P	5.44	51.1	2.71 ± 0.13	90.6	0.25
<i>Codium fragile</i>	C	4.11	60.5	1.62 ± 0.10	92.9	0.12
<b>Cyanophyta</b>						
Blue-green algae	C	5.37	6.4	5.03 ± 0.22	85.2	0.74
Blue-green algae	P	3.40	5.3	3.22 ± 0.05	85.2	0.48
<b>Phaeophyta</b>						
<i>Pachydicyon coriaceum</i>	P	4.97	37.1	3.13 ± 0.14		
<i>Dictyota flabellata</i>	C	4.95	26.2	3.65 ± 0.02		
<i>Egria menziesii</i> (stipe)	C	4.45	29.7	3.13 ± 0.03	84.0	0.50
<i>Dictyopteris johnstonei</i>	C	4.37	32.5	2.95 ± 0.15		
<i>Eisenia arborea</i> (blade)	C	4.35	26.4	3.20 ± 0.14	84.2	0.51
<i>Sargassum agarthianum</i>	C	4.35	22.3	3.38 ± 0.11	85.5	0.49
<i>Eisenia arborea</i> (stipe and holdfast)	P	4.34	35.5	2.80 ± 0.07	84.2	0.44
<i>Pelvetia fastigiata f. gracilis</i> (stipe and holdfast)	C	4.28	20.1	3.42 ± 0.06	72.0	0.96
<i>Pseudolithoderma nigra</i> (stipe and holdfast)	C	4.27	19.6	3.43 ± 0.16		
<i>Halidrys dioica</i> (thick branch)	C	4.24	21.6	3.32 ± 0.12	82.7	0.58
<i>Macrocystis pyrifera</i> (blade)	C	4.22	36.2	2.69 ± 0.14	79.5	0.55
<i>M. pyrifera</i> (blade tips)	C	4.21	33.3	2.81 ± 0.15	79.5	0.58
<i>Eisenia arborea</i> (stipe)	C	4.19	36.1	2.68 ± 0.07	84.2	0.42
<i>Halidrys dioica</i> (branch tip)	C	4.18	24.1	3.17 ± 0.12	82.7	0.55
<i>Scytosiphon lomentaria</i>	C	4.18	20.1	3.34 ± 0.06		
<i>Pelvetia fastigiata f. gracilis</i> (stipe)	C	4.15	24.8	3.12 ± 0.04	72.0	0.87

<i>Eisenia arborea</i> (blade)	P	4-15	35-3	2-68 ± 0-16	84-2	0-42
<i>Zonaria farlowii</i>	C	4-09	25-7	3-04 ± 0-08		
<i>Cystoseira neglecta</i>	C	4-07	24-5	3-07 ± 0-06		0-88
<i>Pelvetia fastigiata</i> f. <i>gracilis</i> (blade)	C	4-07	22-8	3-14 ± 0-06	72-0	
<i>Egria menziesii</i> (holdfast)	C	4-04	23-4	3-10 ± 0-03	84-0	0-50
<i>Colpomenia sinuosa</i>	C	3-92	55-9	1-73 ± 0-08	83-0	0-29
<i>Macrocystis pyrifera</i> (holdfast)	C	3-86	28-4	2-76 ± 0-04	79-5	0-57
<i>Egria menziesii</i> (blade)	C	3-82	29-0	2-71 ± 0-12	84-0	0-43
<i>Macrocystis pyrifera</i> (stipe)	C	3-72	30-1	2-60 ± 0-08	79-5	0-53
<i>Eisenia arborea</i> (holdfast)	C	3-68	37-4	2-30 ± 0-14	84-2	0-36
<i>Ralfsia</i> sp.	C	3-54	44-7	2-80 ± 0-09	70-1	0-84
<b>Rhodophyta</b>						
<i>Gelidium purpurascens</i>	C	5-06	24-5	3-82 ± 0-06	70-4	1-13
<i>Rhodymenia pacifica</i>	C	4-76	23-1	3-66 ± 0-13		
<i>Laurencia pacifica</i>	C	4-73	26-5	3-48 ± 0-08	89-9	0-35
<i>Corallina officinalis</i> var. <i>chilensis</i>	P	4-73	84-7	0-72 ± 0-16	55-6	0-32
<i>Gelidium pusillum</i>	P	4-63	21-4	3-64 ± 0-08	83-9	0-58
<i>Pterocladia capillacea</i>	P	4-55	15-3	3-85 ± 0-15	74-0	1-00
<i>P. capillacea</i>	C	4-34	8-4	3-98 ± 0-03	74-0	1-04
<i>Plocamium cartilagineum</i>	C	4-33	22-5	3-35 ± 0-04	85-7	0-48
<i>Hydrolythion decipiens</i>	C	4-32	89-4	0-46 ± 0-07		
<i>Gelidium coulteri</i>	C	4-21	9-3	3-82 ± 0-22	77-0	0-87
<i>G. robustum</i>	C	4-19	14-3	3-59 ± 0-13	70-4	1-06
<i>Gigarina canaliculata</i>	C	4-18	22-2	3-25 ± 0-09	79-8	0-66
<i>Haliptylon gracile</i>	C	4-15	76-7	0-97 ± 0-13	61-9	0-37
<i>Rhodoglossum affine</i>	C	4-11	32-4	2-78 ± 0-25	80-4	0-55
<i>Rhodymenia californica</i> f. <i>californica</i>	C	4-07	18-9	3-30 ± 0-20	84-5	0-51
<i>Gigarina spinosa</i>	C	4-04	27-5	2-93 ± 0-08	83-0	0-50
<i>Corallina officinalis</i> var. <i>chilensis</i>	C	3-86	84-7	0-59 ± 0-04	55-6	0-26
<i>Lithothrix aspergillum</i>	C	3-25	79-1	0-68 ± 0-17	66-9	0-23
<b>Spermatophyta</b>						
<i>Phyllospadix torreyi</i>	C	4-27	19-5	3-44 ± 0-20	77-7	0-77

TABLE 2. The calorific content, % ash and % water of the dominant consumers collected from polluted (P) and control (C) areas near Wilson Cove, San Clemente Island, California on 14 December 1974. 95% confidence intervals are shown for kcal per g dry weight

Major groups and taxa	Location	kcal g <sup>-1</sup> ash-free dry weight	%ash	kcal g <sup>-1</sup> dry weight	% H <sub>2</sub> O	kcal g <sup>-1</sup> wet weight
Arthropoda						
Crustacea						
<i>Chthamalus fissus/dalli</i>	P	6.73	90.4	0.65 ± 0.26	44.5	0.36
<i>Tetraclita squamosa rubescens</i>	P	5.97	94.1	0.35 ± 0.24	33.7	0.23
<i>Pachygrapsus crassipes</i>	P	5.49	47.8	2.86 ± 0.13	82.1	0.51
<i>P. crassipes</i>	C	5.16	47.3	2.72 ± 0.27	82.1	0.49
<i>Pollicipes polymerus</i>	C	4.90	75.0	1.22 ± 0.26	49.0	0.62
<i>Tetraclita squamosa rubescens</i>	C	4.77	94.1	0.28 ± 0.02	33.7	0.19
<i>Pagurus samuelis</i>	C	4.77	50.7	2.35 ± 0.12	40.2	1.40
<i>Chthamalus fissus/dalli</i>	C	4.46	90.4	0.43 ± 0.10	44.5	0.24
Cnidaria						
Anthozoa						
<i>Anihipleura elegantissima</i>	P	6.48	31.5	4.44 ± 0.11	70.0	1.33
Mollusca						
Gastropoda						
<i>Acmaea (Collisella) strigatella</i>	C	7.01	77.4	1.58 ± 0.15	40.4	0.94
<i>A. (Collisella) limatula</i>	P	5.86	85.0	0.88 ± 0.21	61.1	0.34
<i>Lottia gigantea</i>	P	5.83	86.0	0.82 ± 0.15		
<i>L. gigantea</i>	C	5.69	86.0	0.80 ± 0.10		
<i>Acmaea (Collisella) limatula</i>	C	5.60	85.0	0.84 ± 0.21	61.1	0.33
<i>A. (Collisella) scabra</i>	C	5.58	86.6	0.75 ± 0.05	41.3	0.44
<i>A. (Collisella) digitalis</i>	P	5.44	86.0	0.76 ± 0.05	44.4	0.42
<i>Haliotis cracherodii</i>	C	5.39	68.0	1.72 ± 0.04	40.0	1.03
<i>Norrisia norrisi</i>	C	5.35	89.0	0.59 ± 0.11	11.1	0.52
<i>Acmaea (Collisella) digitalis</i>	C	5.34	86.0	0.75 ± 0.27	44.4	0.42
<i>Littorina planaxis</i>	C	5.32	82.2	0.95 ± 0.42	33.5	0.63
<i>Haliotis fulgens</i>	C	5.05	76.0	1.21 ± 0.18	45.6	0.66
<i>Tegula funebris</i>	C	4.87	88.0	0.58 ± 0.03		
<i>Littorina scutulata</i>	C	4.79	86.1	0.67 ± 0.39	27.7	0.48
<i>Serpulorbis squamigerus</i>	P	4.67	92.0	0.37 ± 0.12		

grazers from the polluted area, e.g. *Acmaea (Collisella) scabra*, *A. (Collisella) limatula*, and *Lottia gigantea*, were found to preferentially utilize high-energy, subclimax forms of algae. There was little qualitative difference in the gut contents of unpolluted versus polluted populations of *Serpulorbis squamigerus*, *Littorina planaxis*, and *L. scutulata*.

## DISCUSSION

For reasons explained by Paine & Vadas (1969), Paine (1971) and Cummins & Wuycheck (1971), the most relevant basis for comparisons of calorific values between taxa and habitats are those for kcal ash-free g dry weight<sup>-1</sup>. Our data for macrophytes (Table 1) agree closely with those published by Paine & Vadas (1969) for species from colder north temperate habitats. These workers noted that each major group was characterized by a different mean calorific value (i.e. Chlorophyta, 4.92 kcal ash-free g dry weight<sup>-1</sup>; Rhodophyta, 4.65; Phaeophyta, 4.50). Although the means are slightly lower in our study, the same sequence is shown (i.e. Chlorophyta, 4.78 kcal ash-free g dry weight<sup>-1</sup>; Rhodophyta, 4.39; Cyanophyta, 4.38; Phaeophyta, 4.22).

Much of the variation between taxa in our data (Table 1) is likely to be due to differences in growth form and life span. Paine & Vadas (1969) emphasized that, within a





given algal division, ranking for calorific values followed ranking for thallus longevity (ephemeral > annual > perennial). While not disagreeing with this interpretation, we prefer to assess the direct relationship for this trend in terms of growth form. For example, those macrophytes which have a high ratio of structural tissues to photosynthetic tissues (presumably of selective advantage in competition for space and light or protection from predation and physical stress) allocate relatively less energy to rapid growth and reproduction and produce thalli with lower total calories per unit weight. In contrast, structurally simple, opportunistic macrophytes that have high growth and production rates and associated large surface to weight ratios (see Odum, Kuenzler & Blunt 1958; Littler & Murray 1974) tend to have higher calorific values. The former typically are perennials while the latter are usually annuals or ephemerals, and hence, convey less temporal and spatial predictability to herbivores (Paine & Vadas 1969).

The rapidly growing regions of some of the more structurally complex macrophytes were richer in calories. For example, the blades of *Eisenia arborea* contained higher values than did the stipe or the holdfast (4.35, 4.19 and 3.68 kcal, respectively); similarly, for *Macrocystis pyrifera* the values were: blade, 4.22; holdfast, 3.86; stipe, 3.72 kcal. However, the reverse trend was recorded for *Egregia menziesii* (stipe, 4.45; holdfast, 4.04; blade, 3.82) and possibly *Pelvetia fastigiata* f. *gracilis* (stipe including holdfast, 4.28; stipe, 4.15; blade, 4.07). In addition, the thalli of *Eisenia arborea* from the polluted area (stipe plus holdfast, 4.34; stipe, 4.15 kcal) did not show the same trend as those from the control area. Therefore, our data agree with those of Paine & Vadas (1969) who concluded that the rapidly growing portions of thalli of brown algae are not consistently richer in energy than the slower growing portions. The crustose saxicolous and saccate cushion-like forms of algae had quite low calorific values (e.g. *Hydrolithon decipiens*, 4.32; *Pseudolithoderma nigra*, 4.27; *Colpomenia sinuosa*, 3.92; *Ralfsia* sp., 3.54 kcal g<sup>-1</sup> ash-free dry weight). These data support the suggestion (Paine & Vadas 1969) that encrusting forms, which are easily accessible to herbivores, may have evolved reduced predator appeal through selection for thallus constituents with lower calorific values. The low calorific values for coralline algae, even when corrected for endothermy, (e.g. *Hydrolithon decipiens*, 4.32; *Haliptylon gracile*, 4.15; *Corallina officinalis* var. *chilensis*, 3.86; *Lithothrix aspergillum*, 3.25) support the interpretation of Larkum, Drew & Crossett (1967) and Paine & Vadas (1969) that calcification and low calorific content may be important for survival under conditions of high grazing pressure by reducing the energetic return per unit effort to the consumer.

In contrast to our observations on macrophytes, and others by Paine & Vadas (1969) on marine algae, and Bliss (1962) on alpine tundra plants, the animal phyla near Wilson Cove (Table 2) did not have characteristically high or low calorific values. This last observation has also been reported for other animal phyla by Slobodkin & Richman (1961), and by Cummins & Wuycheck (1971) who reviewed the published data and found no relationship between trophic level and calorific content.

The most striking feature of the data on invertebrates was that, in nearly every case, populations from the outfall area had higher energy contents than those from the control area (Table 2). This was especially pronounced for *Chthamalus fissus/dalli* (outfall, 6.73; control, 4.46 kcal), *Tetraclita squamosa rubescens* (outfall, 5.97; control, 4.77 kcal) and *Pachygrapsus crassipes* (outfall, 5.49; control, 5.16 kcal). Paine & Vadas (1969) also reported that the energy content of algae from polluted waters was 7–14% higher than the same species from clean waters. They suspected that the higher energy content in algal

species from the enriched environment might be due to: (i) the presence of a bacterial epifauna, (ii) the shallower depths of collection, or (iii) the accumulation of energy-rich compounds such as oils. We can eliminate the first and second of these possibilities, in the case of our macroinvertebrate data, because the collection depths were the same and microscopic examination showed no important differences in bacterial floras associated with animal soft parts. This leads to the conclusion that energy-rich compounds are indeed entering the food web through the populations of omnivores and suspension feeders in the outfall community, and partially supports our first hypothesis, that the difference may be due to the utilization of sewage matter as an energy source.

The second hypothesis, that the high energy algal subclimax community is maintained by stress and augments a gastropod-dominated grazing subweb, is also supported by our data, though not as strongly. For example, outfall populations of the grazers *Acmaea (Collisella) limatula*, *Lottia gigantea*, and *Acmaea (Collisella) digitalis* all had slightly higher energetic contents than corresponding control populations (Table 2) and the same tendency was observed for the algal species in the two habitats, i.e. *Eisenia arborea* (both blade and stipe portions separately), *Corallina officinalis* var. *chilensis*, and *Pterocladia capillacea*. The blue-green algae from the control area were from a different taxon and cannot be compared directly with those from the outfall. The algae from the outfall area often contained epiphytic bacteria and fungal hyphae which probably contributed, in a minor way, to the calorific differences.

We could not microscopically distinguish between sewage and other detritus in the gut contents, so it was assumed that, if organisms in the outfall area were using sewage as an energy source, they would have greater amounts of detritus relative to other prey items. This seems to be the case for the outfall population of *Pachygrapsus crassipes*, whose diet included  $\approx 18\%$  more detritus than did control populations. This rock crab, in accordance with our second hypothesis, apparently used the opportunistic, high-energy algal forms, *Ulva californica* and blue-greens, which are probably maintained as components of subclimax communities by the sporadic discharge of toxins such as disinfectants (Littler & Murray 1975). The diet of *Pachygrapsus crassipes* was more diverse in the control area, where articulated coralline algae were important constituents. The omnivorous suspension feeder *Anthopleura elegantissima* occurred only rarely outside of the outfall fringe zone, so comparisons with an unpolluted population could not be made, but the gut contents of this anemone regularly contained sewage as a major component.

The outfall grazer populations in several instances utilized high-energy subclimax algae, which our second hypothesis had predicted. For example, the diets of *Acmaea (Collisella) limatula*, *A. (Collisella) scabra*, and *Lottia gigantea* consisted of relatively large quantities of blue-green algae near the outfall, while *Acmaea (Collisella) digitalis* (one specimen) was feeding on considerable quantities of *Enteromorpha* sp. However, these data are preliminary since only six individuals of each species were examined from each habitat.

Two of the six specimens of the high-intertidal limpet *Acmaea (Collisella) digitalis* (Table 3), which occurred nearer the outfall terminus than most other grazers, had considerably more bacteria in their guts. Littorine snails were sampled above the sewage-affected zone ( $> 1.6$  m); hence, there was little difference in dietary composition between control and outfall populations.

The diet of *Serpulorbis squamigerus*, a suspension feeder with exceptionally high densities in the fringe of the sewage plume, contained a relatively high detritus content

(Table 3). This gastropod, however, is primarily a detritivore and, consequently, its gut contents should consist predominantly of detritus regardless of the presence of sewage.

We regularly made qualitative assessments of the gut volumes for all specimens and found that populations of five species (*Acmaea (Collisella) digitalis*, *Chthamalus fissus/dalli*, *Littorina planaxis*, *L. scutulata*, and *Pachygrapsus crassipes*) from the control area consistently had much larger gut volumes, though the other consumers had about the same gut volumes in both habitats. This difference suggests that organisms with a high diet selectivity, such as *P. crassipes*, may need to consume less food volume to meet their energetic requirements in the enriched environment. Gut contents were included in the combustion procedure and undoubtedly influenced the calorific values obtained. Thus, it would seem that the reduction in gut contents, along with the presumably higher lipid content contained in the diet, would contribute in a small part to the increased calorific values observed in consumer populations in the outfall area.

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