

ANALYSES OF PATHWAYS OF ENERGY FLOW

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INTRODUCTION

The metabolic role of high-energy, sewage-derived organic inputs in regard to the trophodynamics of marine benthic communities is largely unknown. Because of its relative simplicity and workability, and the fact that a detailed baseline concerning seasonal variability in distribution, abundance, and community structure has been established for both the sewage-affected and unpolluted control areas (see Chapter Two; Littler and Murray, 1975), the Wilson Cove ecosystem provides an ideal model for analyses of the effects of domestic waste waters on energetic pathways. The intertidal communities of this leeward island site are characterized by relatively low standing stocks of macro-invertebrates, including a notable paucity of large mobile carnivores. Based upon present data, the role of grazing fishes appears to be relatively minor; however, for temperate rocky intertidal systems in general, and Wilson Cove in particular, the functional role of fishes is in need of careful study.

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 organic sewage particulates. The research presented here represents the initial step toward the quantitative assessments of the differences in these energetic pathways. We report herein data on the calorific values of the dominant benthic macrophytes and macro-invertebrates, and preliminary analyses of the gut contents of the principal intertidal consumer organisms from both polluted and unpolluted systems.

There are two distinct food subwebs characteristic of the rocky intertidal systems of leeward San Clemente Island. The first is a macrophyte-based grazing subweb (Fig. 5-1) in which the limpets *Acmaea (Collisella)* spp. and *Lottia gigantea*, the periwinkle *Littorina planaxis*, and the omnivorous shore crab *Pachygrapsus crassipes* are the important herbivores in the outfall area. This subweb is also present in the unpolluted shoreline where a similar guild of grazers is apparent, with the exception of much lower numbers of *L. gigantea*. Hypothetically, these populations of grazers are enhanced energetically by the increased standing stocks of eurytolerant primary producers such as blue-green algae, *Ulva californica*, and *Gelidium pusillum*, including their epiphytic filamentous brown algae, diatoms, and bacteria. The second food subweb in the outfall and control areas utilizes suspended and settled particulate materials as the primary energy source (Fig. 5-1). In both the outfall and control areas, plankton and seston are available to suspension feeders. Populations of barnacles, i.e., *Chthamalus* spp. and *Tetraclita squamosa rubescens*, occur commonly in the control areas and comprise the dominant suspension feeders there. However, for the outfall system, the presence of discharged organic particles in the effluent serves as a primary food source to the suspension feeder subweb (Fig. 5-1), and organisms utilizing sewage particulates predominate. These populations include *Pachygrapsus crassipes*, which has been observed to consistently feed near the outfall on solid organic particles as well as algae during periods of low tide. Additionally, the anemone *Anthopleura elegantissima* is abundant in the area immediately fringing the point of discharge but was rarely encountered in the unpolluted habitat. Also occurring in the outfall fringing area is an extremely dense population of very large individuals of the vermetid gastropod *Serpulorbis squamigerus*. This mollusk, which characteristically feeds upon detrital particles trapped from suspension, has formed an extensive bed at the lower intertidal margin of the outfall area and has been abundant in the sewage impacted area for many years, as evidence by the reef-like build-up of dead calcareous tubes. Populations of suspension-feeding barnacles are notably reduced in numbers in the outfall area (see Chapter Two).

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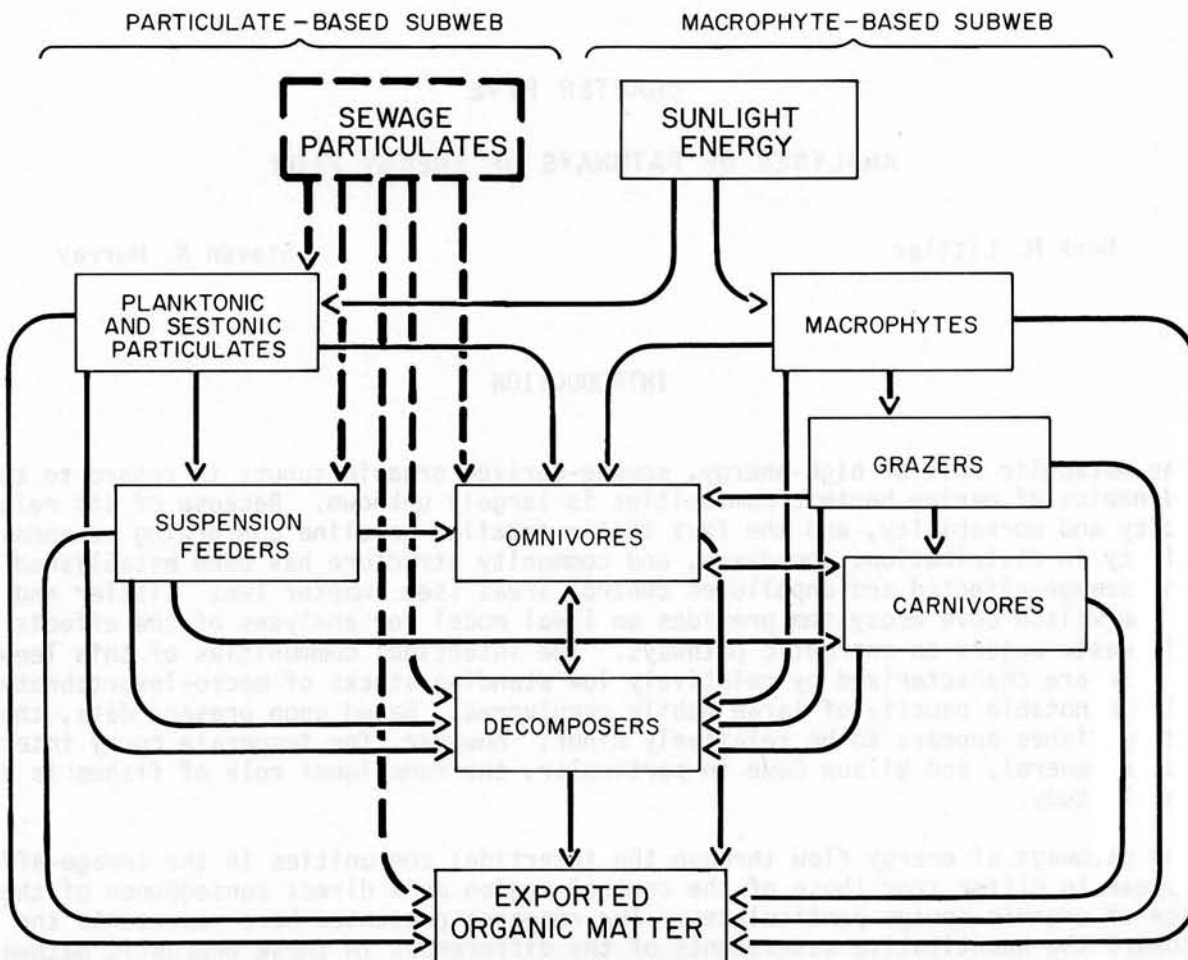


FIGURE 5-1 Diagram depicting the hypothetical energetic pathways through that portion of the food web utilizing particulate organic matter as an energy source. Pathways unique to the outfall system are shown by broken lines.

It is hypothesized, from analyses of the extensive standing stock data, that the energetic pathways in the outfall system differ from those for the controls in two ways. First, there is an enhancement of the suspension feeders and omnivores that utilize discharged sewage particulates and, second, the periodic emission of deleterious agents (such as disinfectants) provides a stress source that maintains a disclimax community, particularly in the upper and mid-intertidal portions of the outfall plume region. This disclimax community consists largely of "opportunistic" or r-selected algae (see Chapter Two) whose rapid growth and high energy content augment the gastropod-dominated grazing subweb (Fig. 5-1). To begin to test these hypotheses, we examined the gut contents of the principal consumer organisms and the calorific contents of the dominant macrophytes and macro-invertebrates for both outfall and control area populations.

The intent of this research was not to investigate every population in the system [Glynn's work (1965) shows the impracticality of this approach for even a relatively confined and unstructured system], but to focus on the energetic pathways originating from (1) the input of sewage particulates contained in the effluent and (2) the "opportunistic" alga-dominated producer base. A primary contribution of this work lies in the calorific determinations and their interpretations for the 74 samples which comprise the dominant macro-producers and consumers in both the sewage-affected and unpolluted intertidal ecosystems.

METHODS AND MATERIALS

The calorific contents of 49 macro-invertebrates and macrophytes were assessed for the control areas, and 14 for the outfall. These represented determinations for a total of 50 macrophytes and 24 macro-invertebrates, including data from different tissue types for several of the larger brown algae (Tables 5-1 and 5-2). All samples were collected on 14 December 1974 and returned to the laboratory alive, 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 algae and animal soft-parts were dried to constant weight 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 CaCO₃ content. The kcal/g ash-free dry weights (kcal/g AFDW) were calculated by correcting for the percent ash determined on single aliquots of the homogeneous milled samples (dried at 80°C) by igniting the material at 400°C for 24 hours in a muffle furnace. Total percent ash was determined in the same way for all animals including their hard parts. Three replicates were run for each calorific determination, whereas 3-41 (mean = 7) replicates were used to determine the total ash content of the organisms under study. These data are tabulated (Tables 5-1 and 5-2) as kcal/g AFDW, and the total percent ash used to calculate kcal/g dry weight. We also determined the percent water for the organisms in conjunction with the ash determinations and used this information to generate the ecologically more meaningful value kcal/g wet weight. We did not investigate seasonal differences; however, Paine and Vadas (1969) found no significant variation or shifts in calorific values with season for 70 species of algae. On the other hand, significantly higher values (kcal/g AFDW) have been noted (Himmelman and Carefoot, 1975) for *Lessoniopsis* in late summer and fall.

Six replicate (randomly selected) gut analyses were performed for each of 12 consumer species taken from the outfall area, and for 11 of these, plus one additional species, taken from the control site between 1030 and 1400 hours on 10-11 March 1976, or 11-12 June 1976. In this preliminary attempt, sampling was performed throughout all portions of both study sites and not localized in any specific zone or community, in an attempt to obtain a wide spectrum of potential food items (this no doubt increased the range of variability for the data set presented in Table 5-3). Samples of a given species (with the exception of *Haliotis cracherodii*) were always collected from both the outfall and control areas during the same visitation. The organisms were fixed in buffered formalin seawater immediately upon collection, then identified, and labelled in the field. Samples were returned to the laboratory and the gut contents dissected, smeared evenly, and mounted on a microscope slide. The percent dietary composition of each sample was then quantified by means of an ocular point-intercept microscopic procedure (Table 5-3), where a minimum of 100 points subtending gut materials was scored.

RESULTS

CALORIMETRY

Fifty macrophyte specimens were combusted; their calorific and associated values are presented by division in Table 5-1 from highest to lowest, with emphasis on the kcal/g AFDW data. Calorific values ranged from 5.44 (*Ulva californica*) to a low of 3.25 kcal/g AFDW (*Lithothrix aspergillum*); the mean macrophytic calorific content was 4.30 kcal/g AFDW (Table 5-1). Chlorophyta had the greatest calorific value on the average (4.78 kcal/g AFDW), followed by Rhodophyta (4.39), Cyanophyta (4.38), and Phaeophyta (4.22). Generally, those forms with high surface to volume ratios (e.g., *Ulva*, *Pachydictyon*, *Dictyota*) contained more energy than those with low ratios (e.g., *Ralfsia*, *Colpomenia*, *Gigartina*) or those with calcareous structure (e.g., all of the coralline algae).

The upper portions of *Eisenia arborea* and *Macrocystis pyrifera* contained 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*.

Twenty-four macro-invertebrates were combusted to produce the ranking by phylum given in Table 5-2 based on the kcal/g AFDW data. Calorific numbers for consumers were considerably greater than those for the primary producers, ranging from a high of 7.01 [*Acmaea* (*Collisella*) *strigatella* from the control area] to 4.46 kcal/g AFDW (*Chthamalus fissus/dalli*

TABLE 5-1

CALORIC AND ASSOCIATED VALUES OF DOMINANT PRIMARY PRODUCERS NEAR WILSON COVE, SAN CLEMENTE ISLAND, CALIFORNIA, ON 14 DECEMBER 1974

Species collected from the sewage-affected area are indicated by O, those from the unpolluted control area by C, and C.I. = \pm the 95% confidence interval for the kcal/g dry weight measurements (N=3 combustions).

Major Groups and Taxa	Location	kcal/g ash-free dry weight	% ash (N)	kcal/g dry weight	C.I. (N=3)	% H ₂ O (N)	kcal/g wet weight
Chlorophyta							
<i>Ulva californica</i>	O	5.44	51.1 (4)	2.71	0.13	90.6 (16)	0.25
<i>Codium fragile</i>	C	4.11	60.5 (3)	1.62	0.10	92.9 (14)	0.12
Cyanophyta							
Blue-green algae	C	5.37	6.4 (3)	5.03	0.22	85.2 (12)	0.74
Blue-green algae	O	3.40	5.3 (3)	3.22	0.05	85.2 (12)	0.48
Phaeophyta							
<i>Pachydietyon coriaceum</i>	C	4.97	37.1 (3)	3.13	0.14		
<i>Dictyota flabellata</i>	C	4.95	26.2 (3)	3.65	0.02		
<i>Egregia menziesii</i> (stipe)	C	4.45	29.7 (3)	3.13	0.03	84.0 (18)	0.50
<i>Dictyopteris johnstonei</i>	C	4.37	32.5 (3)	2.95	0.15		
<i>Eisenia arborea</i> (blade)	C	4.35	26.4 (3)	3.20	0.14	84.2 (24)	0.51
<i>Sargassum agardhianum</i>	C	4.35	22.3 (3)	3.38	0.11	85.5 (20)	0.49
<i>Eisenia arborea</i> (stipe and holdfast)	O	4.34	35.5 (3)	2.80	0.07	84.2 (24)	0.44
<i>Pelvetia fastigiata</i> f. <i>gracilis</i> (stipe and holdfast)	C	4.28	20.1 (3)	3.42	0.06	72.0 (6)	0.96
<i>Pseudolithoderma nigra</i>	C	4.27	19.6 (3)	3.43	0.16		
<i>Halidrys dioica</i> (thick branch)	C	4.24	21.6 (3)	3.32	0.12	82.7 (26)	0.58
<i>Macrocystis pyrifera</i> (blade)	C	4.22	36.2 (3)	2.69	0.14	79.5 (15)	0.55
<i>Macrocystis pyrifera</i> (blade tips)	C	4.21	33.3 (3)	2.81	0.15	79.5 (15)	0.58
<i>Eisenia arborea</i> (stipe)	C	4.19	36.1 (3)	2.68	0.07	84.2 (24)	0.42
<i>Halidrys dioica</i> (branch tip)	C	4.18	24.1 (3)	3.17	0.12	82.7 (26)	0.55
<i>Scytosiphon lomentaria</i>	C	4.18	20.1 (3)	3.34	0.06		
<i>Pelvetia fastigiata</i> f. <i>gracilis</i> (stipe)	C	4.15	24.8 (3)	3.12	0.04	72.0 (6)	0.87
<i>Eisenia arborea</i> (blade)	O	4.15	35.3 (3)	2.68	0.16	84.2 (24)	0.42
<i>Zonaria farlowii</i>	C	4.09	25.7 (3)	3.04	0.08		
<i>Cystoseira neglecta</i>	C	4.07	24.5 (3)	3.07	0.06		
<i>Pelvetia fastigiata</i> f. <i>gracilis</i> (blade)	C	4.07	22.8 (3)	3.14	0.06	72.0 (6)	0.88
<i>Egregia menziesii</i> (holdfast)	C	4.04	23.4 (3)	3.10	0.03	84.0 (18)	0.50
<i>Colpomenia sinuosa</i>	C	3.92	55.9 (3)	1.73	0.08	83.0 (24)	0.29
<i>Macrocystis pyrifera</i> (holdfast)	C	3.86	28.4 (3)	2.76	0.04	79.5 (15)	0.57
<i>Egregia menziesii</i> (blade)	C	3.82	29.0 (3)	2.71	0.12	84.0 (18)	0.43

TABLE 5-1 (Continued)

Major Groups and Taxa	Location	kcal/g ash-free dry weight	% ash (N)	kcal/g dry weight	C.I. (N=3)	% H ₂ O (N)	kcal/g wet weight
Phaeophyta (Continued)							
<i>Macrocystis pyrifera</i> (stipe)	C	3.72	30.1 (3)	2.60	0.08	79.5 (15)	0.53
<i>Eisenia arborea</i> (holdfast)	C	3.68	37.4 (3)	2.30	0.14	84.2 (24)	0.36
<i>Ralfsia</i> sp.	C	3.54	44.7 (3)	2.80	0.09	70.1 (2)	0.84
Rhodophyta							
<i>Gelidium purpurascens</i>	C	5.06	24.5 (3)	3.82	0.06	70.4 (12)	1.13
<i>Rhodymenia pacifica</i>	C	4.76	23.1 (3)	3.66	0.13		
<i>Laurencia pacifica</i>	C	4.73	26.5 (3)	3.48	0.08	89.9 (25)	0.35
<i>Corallina officinalis</i> var. <i>chilensis</i>	O	4.73	84.7 (11)	0.72	0.16	55.6 (37)	0.32
<i>Gelidium pusillum</i>	O	4.63	21.4 (3)	3.64	0.08	83.9 (19)	0.58
<i>Pterocladia capillacea</i>	O	4.55	15.3 (3)	3.85	0.15	74.0 (33)	1.00
<i>Pterocladia capillacea</i>	C	4.34	8.4 (3)	3.98	0.03	74.0 (33)	1.04
<i>Plocamium cartilagineum</i>	C	4.33	22.5 (3)	3.35	0.04	85.7 (4)	0.48
<i>Hydrolithon decipiens</i>	C	4.32	89.4 (3)	0.46	0.07		
<i>Gelidium coulteri</i>	C	4.21	9.3 (3)	3.82	0.22	77.0 (11)	0.87
<i>Gelidium robustum</i>	C	4.19	14.3 (3)	3.59	0.13	70.4 (12)	1.06
<i>Gigartina canaliculata</i>	C	4.18	22.2 (3)	3.25	0.09	79.8 (37)	0.66
<i>Haliptylon gracile</i>	C	4.15	76.7 (7)	0.97	0.13	61.9 (15)	0.37
<i>Rhodoglossum affine</i>	C	4.11	32.4 (3)	2.78	0.25	80.4 (13)	0.55
<i>Rhodymenia californica</i> f. <i>californica</i>	C	4.07	18.9 (3)	3.30	0.20	84.5 (8)	0.51
<i>Gigartina spinosa</i>	C	4.04	27.5 (3)	2.93	0.08	83.0 (16)	0.50
<i>Corallina officinalis</i> var. <i>chilensis</i>	C	3.86	84.7 (11)	0.59	0.04	55.6 (37)	0.26
<i>Lithothrix aspergillum</i>	C	3.25	79.1 (13)	0.68	0.17	66.9 (31)	0.23
Spermatophyta							
<i>Phyllospadix torreyi</i>	C	4.27	19.5 (3)	3.44	0.20	77.7 (12)	0.77

TABLE 5-2

CALORIC AND ASSOCIATED VALUES OF DOMINANT CONSUMERS NEAR WILSON COVE, SAN CLEMENTE ISLAND, CALIFORNIA, ON 14 DECEMBER 1974

Species collected from the sewage-affected area are indicated by O, those from the unpolluted control area by C, and C.I. = \pm the 95% confidence interval for the kcal/g dry weight measurements (N=3 combustions).

Major Groups and Taxa	Location	kcal/g ash-free dry weight	% ash (N)	kcal/g dry weight	C.I. (N=3)	% H ₂ O (N)	kcal/g wet weight
Arthropoda							
Crustacea							
<i>Chthamalus fissus/dalli</i>	O	6.73	90.4 (16)	0.65	0.26	44.5 (18)	0.36
<i>Tetraclita squamosa rubescens</i>	O	5.97	94.1 (15)	0.35	0.24	33.7 (31)	0.23
<i>Pachygrapsus crassipes</i>	O	5.49	47.8 (3)	2.86	0.13	82.1 (20)	0.51
<i>Pachygrapsus crassipes</i>	C	5.16	47.3 (3)	2.72	0.27	82.1 (20)	0.49
<i>Pollicipes polymerus</i>	C	4.90	75.0 (29)	1.22	0.26	49.0 (19)	0.62
<i>Tetraclita squamosa rubescens</i>	C	4.77	94.1 (15)	0.28	0.02	33.7 (31)	0.19
<i>Pagurus samuelis</i>	C	4.77	50.7 (3)	2.35	0.12	40.2 (28)	1.40
<i>Chthamalus fissus/dalli</i>	C	4.46	90.4 (16)	0.43	0.10	44.5 (18)	0.24
Cnidaria							
Anthozoa							
<i>Anthopleura elegantissima</i>	O	6.48	31.5 (3)	4.44	0.11	70.0 (3)	1.33
Mollusca							
Gastropoda							
<i>Acmaea (Collisella) strigatella</i>	C	7.01	77.4 (10)	1.58	0.15	40.4 (11)	0.94
<i>Acmaea (Collisella) limatula</i>	O	5.86	85.0 (39)	0.88	0.21	61.1 (11)	0.34
<i>Lottia gigantea</i>	O	5.83	86.0 (13)	0.82	0.15		
<i>Lottia gigantea</i>	C	5.69	86.0 (13)	0.80	0.10		
<i>Acmaea (Collisella) limatula</i>	C	5.60	85.0 (39)	0.84	0.21	61.1 (11)	0.33
<i>Acmaea (Collisella) scabra</i>	C	5.58	86.6 (16)	0.75	0.05	41.3 (20)	0.44
<i>Acmaea (Collisella) digitalis</i>	O	5.44	86.0 (22)	0.76	0.05	44.4 (3)	0.42
<i>Haliotis cracherodii</i>	C	5.39	68.0 (4)	1.72	0.04	40.0 (4)	1.03
<i>Norrisia norrisi</i>	C	5.35	89.0 (9)	0.59	0.11	11.1 (6)	0.52
<i>Acmaea (Collisella) digitalis</i>	C	5.34	86.0 (22)	0.75	0.27	44.4 (3)	0.42
<i>Littorina planaxis</i>	C	5.32	82.2 (6)	0.95	0.42	33.5 (12)	0.63
<i>Haliotis fulgens</i>	C	5.05	76.0 (2)	1.21	0.18	45.6 (7)	0.66
<i>Tegula funebris</i>	C	4.87	88.0 (41)	0.58	0.03		
<i>Littorina scutulata</i>	C	4.79	86.1 (9)	0.67	0.39	27.7 (13)	0.48
<i>Serpulorbis squamigerus</i>	O	4.67	92.0 (3)	0.37	0.12		

TABLE 5-3

PERCENT DIETARY COMPOSITION OF THE PREDOMINANT OUTFALL (O) AND CONTROL (C) INVERTEBRATE POPULATIONS (BASED ON A MEAN OF SIX INDIVIDUALS PER SITE)

		DIETARY COMPONENTS																									
		Detritus	Blue-green algae	Diatoms	<i>Ulva californica</i>	<i>Enteromorpha</i> sp.	<i>Macrocystis pyrifera</i>	Bacteria	Juvenile Phaeophyta	Ectocarpoid forms	<i>Peyssonnetia</i> sp.	Articulated corallines	<i>Ralfsia/Pseudolithoderma</i>	Laminarianian forms	Marine mite (Halacaridae)	Sponge spicules	Rock	Chlorophyte forms	Copepods	<i>Gelidium pusillum</i>	Juvenile Rhodophyta	<i>Pterocladia/Gelidium</i>	Gigartinalian forms	Marine worms	Crustose corallines	<i>Cryptopleura</i> sp.	<i>Polysiphonia</i> spp.
<i>Acmaea (Collisella) digitalis</i>	O	78.2	4.6	0.2	0.8	8.6	6.5			0.9						0.2											
	C	90.4	4.8	4.2	0.6		<0.1																				
<i>Acmaea (Collisella) limatula</i>	O	74.5	19.6	4.4		0.2			1.3					<0.1													
	C	81.7	7.0	10.8			<0.1		0.1			0.5														<0.1	
<i>Acmaea (Collisella) scabra</i>	O	43.0	50.5	6.6			<0.1																				
	C	88.1	4.3	7.2			<0.1					0.5													<0.1		
<i>Acmaea (Collisella) strigatella</i>	O	-	-	-																							
	C	87.8	4.2	7.6																							
<i>Haliotis cracherodii</i>	O	81.2	4.9	6.4			0.6	5.6	0.4		<0.1	0.7	0.6							<0.1	<0.1	<0.1	<0.1	<0.1		<0.1	<0.1
	C	75.6	5.3	1.9		4.0	<0.1	<0.1			7.8	2.4	3.9		<0.1							1.2				<0.1	<0.1
<i>Littorina planaxis</i>	O	99.9	0.2	<0.1			<0.1																				
	C	100.0	0.1	<0.1			<0.1																				
<i>Littorina scutulata</i>	O	99.7	0.4	0.1			0.1					<0.1				0.1											
	C	99.7	0.2	0.2																							
<i>Lottia gigantea</i>	O	49.1	28.4	22.2			<0.1							0.3													
	C	42.3	22.7	34.9			<0.1			0.1				<0.1													
Grazers (grand mean)	O	75.1	15.5	5.7	0.1	1.3	1.0	0.8	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1				<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
	C	83.2	6.1	8.4	<0.1	0.5	<0.1	<0.1	<0.1	<0.1	1.0	0.4	0.5	<0.1	<0.1	<0.1						0.2			<0.1	<0.1	<0.1
<i>Anthopleura elegantissima</i>	O	78.2	1.2	3.3	7.5		8.3		0.5		0.8						0.2	<0.1					<0.1				
	C	-	-	-	-		-		-		-						-	-					-				
<i>Chthamalus fissus</i>	O	100.0	<0.1	<0.1																							
	C	100.0	<0.1	<0.1			<0.1																				
<i>Serpulorbis squamigerus</i>	O	93.5	2.0	4.2			<0.1									0.3											
	C	91.1	3.5	4.8			<0.1				<0.1					0.4											
<i>Tetraclita squamosa rubescens</i>	O	100.0	<0.1	<0.1			<0.1																				
	C	96.7	1.6	1.7																							
Suspension feeders (grand mean)	O	92.9	2.1	1.9	1.9		2.8	<0.1	0.1		0.2						<0.1	<0.1					<0.1				
	C	95.9	1.7	2.2			<0.1				<0.1																
<i>Pachygrapsus crassipes</i>	O	63.0	13.0	9.8	12.2	0.6	1.3		0.2																		
	C	53.1	3.8	16.4	1.5	0.3	0.4		3.8	0.5	17.7	2.1				0.5										0.5	

from the control area); the mean calorific value for macro-invertebrates was 5.43 kcal/g AFDW (Table 5-2). No ranking by phylum or trophic level was possible according to these data. It is readily observable in Table 5-2 that, in most cases, outfall populations of a given species were higher in calorific content than were control populations.

GUT ANALYSES

The overall dietary composition of the major consumer populations from both the outfall and control areas is presented by feeding mode in Table 5-3. *Pachygrapsus crassipes* specimens taken from the outfall area were found to utilize more sewage particulates and opportunistic forms of primary producers than those specimens from control areas whose diet was more diverse and included calcareous algae as important constituents. Other grazers, such as *Acmaea (Collisella) scabra*, *A. (Collisella) limatula*, and *Lottia gigantea*, were found to preferentially utilize high energy disclimax forms of algae in the outfall system. There was little difference in the gut contents of control vs. outfall populations of *Serpulorbis squamigerus*, *Littorina planaxis*, and *L. scutulata*.

DISCUSSION

CALORIMETRY

The data generated by the calorimetry program are given in Tables 5-1 and 5-2. The most meaningful values for comparing between taxa and habitats are those for kcal/g AFDW, for reasons explained by Paine and Vadas (1969), Paine (1971), and Cummins and Wuycheck (1971). Our calorific values for macrophytes (Table 5-1) agree closely with those published for colder water forms by Paine and Vadas (1969). These workers noted the tendency for each phylum to be characterized by a different modal value (i.e., green algae, 4.92 kcal; reds, 4.39 kcal; browns, 4.50 kcal). Although the means are slightly lower, the same trend is shown by our data (i.e., greens, 4.78 kcal; reds, 4.39 kcal; blue-greens, 4.38 kcal; browns, 4.22 kcal).

Much of the variation in Table 5-1 is most likely due to differences in life-form strategies. Paine and Vadas (1969) first emphasized that within a given algal phylum the following ranking of species by life histories from high to low kcal/g AFDW holds: ephemeral > annual > perennial. We are more inclined to interpret the above trend in terms of life-form strategies where those macrophytes with relatively more structural tissues (presumably selected for by competition for space and light, predation, or physical shearing stress), and hence relatively less energy allocated to growth and reproduction, result in lower total calories per unit weight. On the other hand, fugitive or opportunistic species selected for fast growth and higher productivity (see Littler and Murray, 1974) and containing little predator or competitor defenses tend to have relatively high calorific values. Contrary to the interpretation of Paine and Vadas (1969), we see those forms which have high production rates and associated large surface to volume ratios (see Odum, Kuenzler, and Blunt, 1958; Littler and Murray, 1974) to be highly correlated with elevated calorific values.

We also examined the various portions of the more structurally complex forms to determine whether or not the rapidly growing regions were richer in energy. The blades of *Eisenia arborea* contained higher values than did the stipe or the holdfast (4.35 vs. 4.19 vs. 3.68 kcal/g AFDW), as was the case for *Macrocystis pyrifera* (blade, 4.22; blade tips, 3.93; holdfast, 3.86; stipe, 3.72 kcal/g AFDW). However, the reverse trend was recorded for *Egregia menziesii* (stipe, 4.45; holdfast, 4.04; blade, 3.82) and *Pelvetia fastigiata* f. *gracilis* (stipe plus holdfast, 4.28; stipe, 4.15; blade, 4.07). Thalli of *Eisenia arborea* from the sewage-polluted area showed the reverse of the trend determined for thalli from the control area (i.e., stipe plus holdfast, 4.34; blade, 4.15 kcal/g AFDW). Therefore, our data agree with those of Paine and Vadas (1969) who concluded that the rapidly growing portions of a brown alga's thallus show no consistent evidence of being energetically richer than the slower growing portions. The crustose saxicolous and saccate cushion-like forms all showed quite low calorific values (e.g., *Hydrolithon decipiens*, 4.32; *Pseudolithoderma nigra*, 4.27; *Colpomenia sinuosa*, 3.92; *Ralfsia* sp., 3.54 kcal/g AFDW). These data support the suggestion of Paine and Vadas (1969) that encrusting forms which are easily accessible to all herbivores may have evolved reduced palatability through selection for thallus constituents with lower calorific values. Our low data (even when corrected for endothermy) for coralline algae (i.e., *Hydrolithon decipiens*, 4.32; *Haliptylon gracile*, 4.15; *Corallina officinalis* var. *chilensis*, 3.86; *Lithothrix aspergillum*, 3.25) support the interpretation

of Larkum, Drew, and Crossett (1967) and Paine and Vadas (1969) that calcification and low calorific values may be of survival importance under conditions of high grazing pressure, by reducing the energetic return per unit effort to the consumer.

The calorific program for macro-invertebrates produced the data given in Table 5-2. In contrast to our observations above for macrophytes, those noted by Paine and Vadas (1969) for marine algae, and others recorded for alpine tundra plants by Bliss (1962), the animal phyla near Wilson Cove did not show tendencies for characteristically high or low calorific values. This last observation has also been made on other animal phyla by Slobodkin and Richman (1961) and Cummins and Wuycheck (1971); these last authors compared most of the published calorific values and observed no relationship between trophic level and calorific content. However, egg-bearing animal consumers and female organisms showed (Cummins and Wuycheck, 1971) relatively high calorific values related to differential fat reserves.

The most striking feature of our invertebrate calorific values was the observation that, in nearly every case, outfall populations of the species examined had higher energy contents than control populations (Table 5-2). This was especially pronounced for *Chthmalus fissus/dalli* (outfall, 6.73, vs. control, 4.46 kcal/g AFDW), *Tetraclita squamosa rubescens* (outfall, 5.97, vs. control, 4.77 kcal/g AFDW), and *Pachygrapsus crassipes* (outfall, 5.49, vs. control, 5.16 kcal/g AFDW). Paine and Vadas (1969) reported a similar relationship for algae from polluted waters, which showed 7-14% higher energy content than the same species from clean waters. These workers suspected that possible causes for the higher energy content in species from the enriched environment might be (1) the presence of a bacterial epifauna, (2) the shallower depths of collection, or (3) the accumulation of energy-rich compounds such as oils. We can eliminate the first and second of these possibilities 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 the first hypothesis that the enhancement of these populations may be due to the utilization of sewage matter as an energy source.

The second hypothesis, concerning the stress-maintenance of a high energy algal disclimax community which augments a gastropod-dominated grazing subweb, is also supported by our data, but not as strongly. For example, outfall populations of the grazers *Acmæa (Collisella) limatula*, *Lottia gigantea*, and *A. (Collisella) digitalis* all had slightly higher energetic contents than corresponding control populations (Table 5-2), and the same tendency was observed for all of the algal species, i.e., *Eisenia arborea* (both blade and stipe portions separately), *Corallina officinalis* var. *chilensis*, and *Pterocladia capillacea*. Blue-green algae from the control area represent a different taxon and cannot be compared with those from the outfall. The algae from the outfall area often contained epiphytic bacteria and fungal hyphae which probably contributed to the calorific differences.

GUT ANALYSES

The gut content data for the 13 predominant macro-consumers, 11 of which were taken from both outfall and control areas, are given in Table 5-3. We could not distinguish sewage particulates from other detritus so it was assumed that those organisms utilizing sewage as an energy source would show elevated detritus values in the outfall area. This seems to be the case for the outfall population of *Pachygrapsus crassipes*, whose diet included 18% more detritus than control populations. This rock crab, in accordance with our second hypothesis, also was apparently utilizing the opportunistic, high-energy algal forms (Table 5-1) *Ulva californica* and blue-greens, which presumably (see Chapter Two) are maintained by environmental stress from the effluent. The diet of *P. crassipes* was more diverse in the control area where articulated coralline algae were important constituents. The omnivorous suspension feeder *Anthopleura elegantissima* occurs only rarely outside of the outfall fringe zone; consequently, comparisons with a control population were not made. However, we have examined its gut contents in the field and have regularly found sewage to be a major component.

The grazers, which our second hypothesis predicts should be utilizing high-energy disclimax algal forms, can be seen in several instances to follow the prediction. For example, *Acmæa (Collisella) digitalis* (one specimen) was utilizing considerable *Enteromorpha* sp., while the diets of *A. (Collisella) limatula*, *A. (Collisella) scabra*, and *Lottia gigantea* consisted of relatively large quantities of blue-green algae near the outfall. Two of the six specimens of *Acmæa (Collisella) digitalis* (Table 5-3), a limpet which occurs higher in

the intertidal than other limpets and, consequently, nearer the outfall terminus, were found to be feeding on considerably more bacteria than other gastropods. Littorine snails were taken along the shoreline above the sewage affected zone; hence, there was (as expected) little difference in dietary composition between control and outfall populations.

Of the suspension feeders examined, our first hypothesis predicts that *Serpulorbis squamigerus*, a species greatly enhanced in the fringe zone, would contain a relatively high detritus content from the outfall. In fact, because this gastropod is primarily a detritivore owing to its manner of feeding, its gut contents would be expected to consist predominantly of detritus in both polluted and control habitats; this was indeed the case (Table 5-3). We regularly made qualitative assessments of the gut volumes for all specimens. These observations indicated that the control populations of five species [i.e., *Acmaea (Collisella) digitalis*, *Chthamalus fissus/dalli*, *Littorina planaxis*, *L. scutulata*, and *Pachygrapsus crassipes*] consistently had much larger quantities in their guts, while other consumers had about the same gut volumes in both areas. This difference indicates that organisms with a high degree of diet selectivity, such as *P. crassipes*, may have to consume less food volume to meet their energetic requirements in an enriched environment. Gut contents were included in the combustion procedures and no doubt influenced the calorific values obtained. Thus, it would seem that a reduction in gut volume, with its relatively lower energy compared to living tissues, along with the probably higher lipid content contained in the outfall diet, would, in relatively small part, account for some of the increased kcal/g AFDW observed.

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WILSON COVE, SAN CLEMENTE ISLAND

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