Studies on the littoral seaweed epifauna of St Croix Island 2. Composition and summer standing stock

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The fauna associated with the littoral seaweeds of St Croix Island has been investigated in terms of numbers and biomass (grams and kilojoules). The seaweeds support an abundant and diverse epifauna dominated by crustaceans, nematodes, annelids, molluscs and mites. The summer standing stock of epifauna from the seaweeds occurring in three different metre wide vertical strips of shore was determined and found to total 2,1—4,6 × 10^6 individuals (equivalent to 85—117 g dry mass or 1,2—1,7 × 10^3 kJ). The nature of the seaweed micro-environment influences the epifauna and algal turfs and tufted seaweeds supported more epifauna than seaweeds with flattened thalli. A model depicting feeding relationships and the role of seaweed epifauna in the littoral zone is given and suggests that epifauna feed on detritus, plankton, algae or other epifauna and are in turn preyed upon, selectively or non selectively, by littoral macrofauna and transient predators.
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Die epifauna van littorale alge op St Croix Eiland is bestudeer in terme van getalle en biomassa (gram en kilojoules). Die alge het 'n volop en diverse epifauna wat gedomineer word deur Crustacea, Nematoda, Annelida, Molluska en Acarina. Die somerbiomassa van epifauna van die alge in 'n meter-wye trajek van die intergetysone was 2,1—4,6 × 10^6 individue (gelyk aan 85—117 g droë massa of 1,2—1,7 × 10^3 kJ droë biomassa) by drie plekke. Die tipe mikro-omgewing van die alge beïnvloed die epifauna, en ryker epifauna het voorgekom op grasagtige alge en bossieagtige alge as op dié met plat thalli. 'n Diagram word gegee van die trofiese verwantskappe van die epifauna en hulle rol in die intergetysone. Die epifauna vreet detritus, plankton, alge en ander epifauna en word op hulle beurt gevreet deur intergety-makrofauna en besoekende predatore.
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Rock surfaces in the littoral zone are occupied by a wide variety of benthos. Pools, crevices, stones and seaweeds provide additional microhabitats for other animals. The seaweed microhabitat can shelter the associated fauna from environmental hazards such as predators, wave action and dessication, act as a substrate for sessile animals or serve as a nursery for juveniles. Darwin (1902) noted the animal abundance in the kelp beds of South America and his observations were followed by pioneer research on the epifauna of kelp (Andrews 1925), *Enteromorpha* (Otto 1936) and intertidal seaweeds (Colman 1939; Dahl 1947; Wieser 1952). Subsequent research has covered the fauna associated with kelps, *Fucus, Saccorhiza,* pelagic *Sargassum, Cladophora, Caulerpa,* coralline algae, other intertidal algae and some animal groups specific to algae. In South Africa work on littoral seaweed epifauna has been neglected and the seaweed microhabitat is only briefly mentioned in guides to shore life (Barnard 1954; Day 1969; Griffiths 1976). Research into the west coast sublittoral kelp beds is, however, in progress and the standing stock of fauna associated with kelp holdfasts has been determined (Velimirov, Field, Griffiths & Zoutendyk 1977).

In the present study the faunal groups constituting the epifauna of the littoral seaweeds of St Croix Island in Algoa Bay have been distinguished and numbers and biomass of epifauna per gram dry mass of seaweed determined. The summer standing stock of epifauna supported by the algae in a metre wide vertical strip of shore has been calculated from transect surveys at three sites and a rough estimate for the total summer standing stock of epifauna for the littoral perimeter of St Croix has also been made.

Methods

Samples of littoral algae were collected from three transect sites, S, M and E, on St Croix (Beckley & McLachlan 1979) during the summer months of 1975/1976 and 1976/1977 for investigation of the associated fauna. The samples were taken by placing a polythene bag over a tuft of seaweed and swiftly detaching the plant from the rocks with a sharpened paint scraper. The samples were preserved in 5% formalin until arrival at the laboratory where each sample was washed into a 63 μm test sieve, the seaweed tuft separated into its constituent fronds and the holdfast pulled apart. Each piece of seaweed was thoroughly rinsed to dislodge associated fauna and the animals collected on the sieve carefully transferred to small plastic containers where they

Table 1 Mean number of animals per gram dry mass of seaweed at Transect S

	Enteromorpha	*Ulva rigida*	*Porphyra capensis*	*Gelidium pristoides*	*? Lyngbya* sp.	Algal turf	*Laurencia natalensis*	*Laurencia pumila/flexuosa*	Sublittoral algal turf
Number of samples	2	4	2	7	2	1	11	3	3
Protozoa									
Foraminifera	7					289	54	17	271
Coelenterata									
Anthozoa									2
Platyhelminthes									
Turbellaria									1
Nemertea				2					1
Nematoda	57	244	1	101	938	2 711	207	114	317
Annelida		34		8	81	118	232	198	448
Sipuncula									
Echiura	220	118			2				
Crustacea									
Ostracoda	18	11		12	34	276	240	75	320
Copepoda	671	4 160		40	165	842	268	115	419
Tanaidacea							18	3	113
Isopoda	124			8	1		30	17	24
Amphipoda	7	2	1	90	1	13	899	321	395
Nauplii larvae	392	8	686	2	4 538	92			20
Insecta									
Diptera									
Larvae									
Arachnida									
Aranae				1					
Acari				2		210	1	2	
Mollusca									
Gastropoda	4	23		13	5	39	89	48	206
Pelecypoda		2	1	55		26	36	11	117
Echinodermata									
Ophiuroidea							1	2	
Echinoidea							1	1	
Asteroidea									
Total number	1 500	4 602	689	344	5 765	4 616	2 076	924	2 654

were preserved in 10% formalin and a few drops of rose bengal staining solution. The 'clean' seaweed was dried in an oven at 90 °C for 24 h and then weighed. (Examination of the 'clean' seaweed under a dissecting microscope revealed the extraction technique to be very efficient with the number of animals adhering to the seaweed after extraction less than 1% of the total epifauna in the sample.)

Counts of animals for the faunal groups in each sample were expressed as numbers per gram dry seaweed and from replicates the average composition of the epifauna for each littoral seaweed was calculated.

The animals from numerous seaweeds were collected and pooled for biomass determination of the dominant epifaunal groups. Glass coverslips were cleaned, dried and weighed using a Sartorius microbalance accurate to one microgram (10^{-6}g). The animals, after being rinsed twice in distilled water, were placed on these coverslips, dried for 24 h at 90 °C and then weighed. A Phillipson microbomb calorimeter calibrated with benzoic acid was used to determine the energy content of the dominant epifaunal groups. Samples for energy determinations were rinsed in distilled water and dried in crucibles for 24 h at 60 °C prior to combustion.

Results

Littoral seaweed epifauna on St Croix Island was found to be very abundant and to consist of many faunal groups. Tables 1, 2 and 3 give the mean numbers of animals per gram dry mass of seaweed at each transect. Numbers per gram dry mass of seaweed ranged between 13 and 6 087 with a mean of 1 800 animals. Nematoda and Crustacea were the two most abundant groups and together constituted about 80% of the total number of animals on each seaweed. Species identifications were not made during the present study but amongst the nematodes predatory, plant

Table 2 Mean number of animals per gram dry mass of seaweed at Transect M

	Porphyra capensis	*Lyngbya semiplena*	*Ulva rigida*	*Chaetangium erinaceum*	*Enteromorpha* sp.	*Gelidium pristoides*	*Jania* sp.	Algal turf	*Gigartina paxillata*	*Corallina* sp.	*Cheilosporum cultratum*	*Hypnea spicifera*	*Laurencia pumila/ flexuosa*	*Plocamium corallorhiza*
Number of samples	2	2	2	3	2	8	5	1	2	2	2	2	2	2
Protozoa														
Foraminifera		11	17			1	1	62		19	8	134	11	55
Coelenterata														
Anthozoa							1							
Platyhelminthes														
Turbellaria							1		1					3
Nemertea						3	1	14	1			5	1	11
Nematoda	2	321	179	22	16	393	47	3 370	28	71	207	399	317	974
Annelida			8		1	32	47	457	10	6	147	117	81	315
Sipuncula						1								
Echiura														
Crustacea														
Ostracoda			3	1		19	13	235	5	134	46	29	8	12
Copepoda		11	746	6	7	181	91	1 107	37	113	146	448	118	381
Tanaidacea				1		1						1		2
Isopoda			3	1		6	4	14	6	11	9	32	12	31
Amphipoda	8		138	23	10	9	7		11	4	188	40	17	73
Nauplii larvae	1		3	1		10	1	35	2	8		19	19	506
Insecta														
Diptera				2								1		1
Larvae														
Arachnida														
Aranae														
Acari	1	31	27	52	2	7	4	270	3	10	7	76	7	19
Mollusca														
Gastropoda			6	3		9	6	76	5	34	3	85	3	22
Pelecypoda	1		3	2		53	32	83	2	3	4	10		14
Echinodermata														
Ophiuroidea														
Echinoidea							1							
Asteroidea							1	1						
Total number	13	376	1 133	114	36	725	258	5 724	111	413	765	1 396	594	2 419

feeding and deposit feeding forms could be distinguished. Ostracoda, calanoid and harpacticoid Copepoda, Tanaidacea, the isopod suborders Flabellifera, Asellota and Anthuridae, gammarid and caprellid Amphipoda and numerous nauplii larvae constituted the crustracean epifauna. Oligochaeta, Syllidae, Nereidae, Sabellidae and polychaete larvae were the most abundant annelids and other vermiform animals included Turbellaria, Nemertea, Sipuncula and Echiura. The mollusc epifauna was made up of prosobranch and opisthobranch Gastropoda and numerous bivalves. Marine mites were abundant on some seaweeds, many different Foraminifera were distinguished and some insects and echinoderms were also found. Porifera, Hydrozoa and Bryozoa were associated with most lower shore algae but could not be counted.

Mean biomass values for the animal groups associated with littoral algae are given in Table 4 and a wide range is evident. Biomass values reduce the importance of smaller animals such as nematodes, copepods and ostracods in the epifauna and accentuate the contribution of larger animals, such as annelids, isopods, amphipods and molluscs, to the total epifauna biomass. The energy values of nine epifaunal groups are also given in Table 4. Isopoda have the lowest energy value (5,92 $J.mg^{-1}$), insect larvae the highest (27,66 $J.mg^{-1}$), and all the other groups were found to have values between 10 and 20 $J.mg^{-1}$. Groups for which energy values could not be determined were ascribed the reference value of 12,56 $J.mg^{-1}$ given by Odum (1971).

The summer standing stock of algal epifauna at each transect was calculated from the mean percent coverage of algae and the mass of algae in grams per percent coverage (Beckley & McLachlan 1979), the epifauna numbers per

Table 3 Mean number of animals per gram dry mass of seaweed at Transect E

	Lyngbya semiplena	*Gelidium pristoides*	*Ulva rigida*	*Bryopsis* sp.	*Gigartina paxillata*	*Corallina* sp.	*Laurencia pumila/ flexuosa*	*Pterosiphonia cloiophylla*	*Cheilosporum cultratum*	*Plocamium corallorhiza*	*Hypnea spicifera*
Number of samples	2	2	2	2	3	2	2	2	2	2	2
Protozoa											
Foraminifera			4	16	1	1	7		2		420
Coelenterata											
Anthozoa									1		
Platyhelminthes											
Turbellaria		1			1		1				
Nemertea		1	15		1	2	7	8	1	2	10
Nematoda	18	626	2 566	1 234	85	30	367	716	137	1 177	3 160
Annelida		4	181	31	27	23	254	279	45	326	365
Sipuncula											
Echiura											
Crustacea											
Ostracoda	1	5	12	17	2	16	10	121	6	32	40
Copepoda	3	82	321	806	64	52	503	1 214	167	553	1 682
Tanaidacea					1		1	8	2	7	
Isopoda		1	5	2	10	1	25	134	11	58	74
Amphipoda		653	11	7	13	18	320	788	40	691	30
Nauplii larvae		1 343	1	33	3	10	6	679	96	23	91
Insecta											
Diptera					1						
Larvae	3	27	3								
Arachnida											
Aranae											
Acari	5	621	10	18	5	3	32	21	9	99	76
Mollusca											
Gastropoda		8	22	7	1	2	6	14	1	153	87
Pelecypoda		75	56	8	1	3	5	7	1	3	52
Echinodermata											
Ophiuroidea											
Echinoidea						1					
Asteroidea											
Total number	30	3 447	3 207	2 179	216	162	1 544	3 989	519	3 124	6 087

gram of seaweed and the biomass and energy content of the epifauna. Tables 5, 6 and 7 show the progression of calculations to arrive at summer standing stock values per mean square metre of rocky shore at the three sites. At transect S the largest portion of the epifauna standing stock is associated with the abundant algal turf on the lower shore. At transect M large epifauna stocks are supported by the algal turf and *Cheilosporum cultratum* whilst on the lower shore of transect E where *Pterosiphonia cloiophylla, Laurencia pumila/flexuosa, Plocamium corallorhiza* are all abundant large stocks of epifauna are found. The three transects support standing stocks of the same order of magnitude per square metre, with transect S having greatest numbers and biomass.

Transects S, M and E respectively have rocky surfaces totalling 6,0 m, 10,25 m and 9,5 m in length (Beckley & McLachlan 1979). The total numbers of epifauna associated with the seaweeds occurring in a metre wide vertical strip of shore during summer are therefore $4,6 \times 10^6$, $3,8 \times 10^6$ and $2,1 \times 10^6$ with standing stock biomass values totalling 84,7 g, 116,8 g and 94,3 g or $1,23 \times 10^3$ kJ, $1,73 \times 10^3$ kJ and $1,15 \times 10^3$ kJ for transects S, M and E respectively. From the means of the above figures and a measured value of 3 180 metres for the littoral perimeter of the island a crude estimate of total summer standing stock of littoral seaweed epifauna on St Croix is thus in the order of $1,1 \times 10^{10}$ animals with a dry biomass of 314 kg or $4,4 \times 10^6$ kJ.

Discussion

The present study has shown that seaweeds on St Croix

Table 4 Biomass and energy values for seaweed epifauna

Taxon	Mean Biomass (μg)	No. determinations	S.D.	J.mg^{-1}	No. determinations	S.D.
Foraminifera	36,8	3	25,5	—	—	—
Anthozoa	363,0	1	—	—	—	—
Turbellaria	336,0	1	—	—	—	—
Nemertea	88,0	1	—	—	—	—
Nematoda	5,7	5	1,9	19,13	1	—
Annelida	93,9	4	43,2	17,38	2	0,11
Ostracoda	8,5	3	3,7	—	—	—
Copepoda	4,7	3	0,5	13,63	1	—
Tanaidecea	45,6	2	9,8	—	—	—
Isopoda	288,6	4	94,0	5,92	5	0,61
Amphipoda	154,1	7	28,2	10,91	3	0,30
Nauplii larvae	1,3	2	0,8	—	—	—
Insect larvae	328,0	1	—	27,66	1	—
Aranae	14 000	1	—	—	—	—
Acari	15,3	3	6,1	10,28	1	—
Gastropoda	244,7*	4	86,0	12,97*	2	0,72
Pelecypoda	311,0*	4	132,6	18,29*	2	0,30
Ophiuroidea	627,0	1	—	—	—	—
Echinoidea	1 712,0	1	—	—	—	—

* Shells removed by treatment with dilute hydrochloric acid.

Table 5 Summer standing stock of seaweed epifauna at Transect S

	Mean % cover of algae	Algae g.m^{-2}	Epifauna numbers g^{-1} alga	Epifauna numbers m^{-2}	Epifauna mg.g^{-1} alga	Epifauna g.m^{-2}	Epifauna J.g^{-1} alga	Epifauna kJ.m^{-2}
Enteromorpha sp.	2,71	2,03	1 500	3 045	42,7	0,087	302,5	0,614
Porphyra capensis	0,21	0,97	689	668	1,4	0,001	19,0	0,018
Ulva rigida	2,29	8,94	4 602	41 142	31,0	0,277	440,2	3,935
Gelidium pristoides	3,75	18,60	334	6 212	52,4	0,975	726,9	13,520
? Lyngbya sp.	2,92	4,67	5 765	26 923	21,4	0,100	339,7	1,587
Turf	18,75	142,50	4 616	657 780	66,4	9,462	1 033,2	147,231
Laurencia natalensis	5,0	15,20	2 076	31 555	211,6	3,216	2 558,8	38,894
Lithothamnia	5,63	—	—	—	—	—	—	—
Others	1,25	—	—	—	—	—	—	—
Total per mean m^2 of shore	42,51%	192,91g	—	767 325	—	14,118g	—	205,799 kJ.

Island provide a micro-habitat for a diverse and abundant epifauna comprising many systematic groups. The epifauna on St Croix corresponds closely with that found by other workers in Britain, Europe, America, India and New Zealand (Colman 1939; Wieser 1952; Glynn 1965; Dommasnes 1969; Hicks 1971; Sarma & Ganapati 1972; Morton & Miller 1968; Jansson 1974).

Variation in the composition and abundance of the epifauna amongst the littoral seaweeds on St Croix is due to the different micro-environments provided by each seaweed species. Though the distribution of littoral organisms is influenced by tidal levels, exposure to wave action and the general littoral environment, Wieser (1952) and Sarma and Ganapati (1972) concluded that the most significant factor for epifauna is the micro-environment offered by the seaweed. This micro-environment is determined largely by the size, structure, colour and developmental state of the seaweed, the presence or absence of epiphytes and the amount of sediment and detritus accumulated about the seaweed.

Porphyra capensis, a distinctly seasonal upper shore seaweed with a flattened sheetlike thallus and a tiny holdfast, offers little protection to animals and was found to support limited epifauna. *Gelidium pristoides*, a densely tufted midshore seaweed, provides a more favourable microenvironment for associated animals and much epifauna occurred amongst the fronds and holdfast. *Laurencia natalensis, Laurencia pumila/flexuosa, Hypnea spicifera, Pterosiphonia cloiophylla* and *Plocamium corallorhiza*, with their branching fronds and dense holdfasts, also supported much epifauna. The coralline algae, *Jania* sp., *Corallina* sp. and *Cheilosporum cultratum* supported low epifauna numbers per gram seaweed because of their relatively high mass values due to their great ash contents (Beckley & McLachlan 1979). The algal turfs of St Croix consists of numerous stunted and epiphytic algae amongst which sediment and detritus accumulate and consequently numerous interstitial nematodes, harpacticoids and ostracods were found amongst them. Sarma and Ganapati

Table 6 Summer standing stock of seaweed epifauna at Transect M

	Mean % cover of algae	Algae g.m^{-2}	Epifauna numbers g^{-1} alga	Epifauna numbers m^{-2}	Epifauna mg.g^{-1} alga	Epifauna g.m^{-2}	Epifauna J.g^{-1} alga	Epifauna kJ.m^{-2}
Porphyra capensis	3,05	14,15	13	184	1,5	0,021	18,6	0,263
Lyngbya semiplena	2,19	4,20	374	1 571	2,8	0,012	45,9	0,192
Ulva rigida	5,61	10,77	1 133	12 202	30,9	0,333	366,0	3,942
Enteromorpha sp.	0,49	0,37	36	13	1,7	0,001	20,0	0,020
Chaetangium erinaceum	0,98	3,45	114	393	6,7	0,023	89,6	0,309
Gelidium pristoides	4,63	22,96	725	16 646	28,5	0,654	469,7	10,784
Jania sp.	2,32	24,87	258	6 416	23,2	0,577	363,1	9,030
Turf	15,37	44,57	5 724	255 119	127,0	5,660	2 053,1	91,507
Gigartina paxillata	0,24	1,88	111	209	15,6	0,029	232,2	0,437
Corallina sp.	0,85	11,70	413	4 832	32,1	0,376	199,2	2,331
Cheilosporum cultratum	4,39	59,00	765	45 135	50,0	2,950	656,2	38,716
Hypnea spicifera	0,37	1,07	1 396	1 494	61,8	0,066	792,5	0,848
Laurencia pumila/flexuosa	6,34	24,35	594	14 464	17,5	0,426	252,7	6,153
Plocamium corallorhiza	2,80	3,81	2 419	9 216	70,8	0,270	1 024,2	3,902
Lithothamnia	11,59	—	—	—	—	—	—	—
Others	0,73	—	—	—	—	—	—	—
Total per mean m^2 of shore	61,95%	227,15g	—	367 894	—	11,398g	—	168,434 kJ.

(1972) noted that an increased sediment content caused an increase in interstitial forms and a decrease in the number of creeping and burrowing forms and Moore (1972), investigating the sediment factor in relation to the fauna of kelp holdfasts, also concluded that the sediment regime can be expected to have different (perhaps contrary) effects on the different components of the epifauna.

The estimate of total summer standing stock of seaweed epifauna on St Croix emphasizes that animals associated with algae are a significant and integral part of the littoral zone ecosystem. To view the role of the epifauna in perspective a model depicting probable food relationships between the components of the littoral zone ecosystem is given in Fig. 1. Seaweeds and their epifauna and epiphytes are linked to constitute one major component whilst macrofauna (molluscs, barnacles, etc.) form another major component. The animals associated with seaweeds have a variety of food sources at hand and can feed on the seaweed tissues themselves, small epiphytes and/or other epifauna (Morton & Miller 1968). In addition, epifauna can utilize the plankton and detritus in the inshore water as food during high tide or feed on detritus accumulated amongst the seaweeds (Glynn 1965). Some littoral macrofauna and transient predators such as reef fish (eg. *Sarpa salpa* and *Diplodus sargus*) and birds (eg. *Haematopos moquini*) may selectively feed on the epifauna by picking out suitable prey organisms or non-selectively by ingesting the seaweed and thus obtaining the associated fauna as well. From seaweed energy values (Beckley & McLachlan 1979) and energy values of fauna associated with seaweeds it has been determined that the energy content of the fauna can be equivalent to as much as 35% of the seaweed energy value. This added animal food supply must be regarded as important because of the greater digestibility of animal tissues. 'Herbivorous' animals (notably reef fish) grazing on seaweeds can thus receive considerable food energy from the

Table 7 Summer standing stock of seaweed epifauna at Transect E

	Mean % cover of algae	Algae g.m^{-2}	Epifauna numbers g^{-1} alga	Epifauna numbers m^{-2}	Epifauna mg.g^{-1} alga	Epifauna g.m^{-2}	Epifauna J.g^{-1} alga	Epifauna kJ.m^{-2}
Lyngbya semiplena	1,05	2,02	30	61	1,2	0,002	30,6	0,062
Gelidium pristoides	0,26	1,29	3 447	4 447	151,1	0,195	2 003,1	2,801
Ulva rigida	2,11	4,05	3 207	12 988	61,7	0,250	1 058,8	4,288
Bryopsis sp.	0,26	1,39	2 179	3 029	20,6	0,029	331,3	0,461
Gigartina paxillata	7,50	58,80	216	12 701	9,5	0,559	114,1	6,709
Corallina sp.	2,24	30,82	162	4 993	9,1	0,281	125,1	3,856
Laurencia pumila/flexuosa	5,26	20,20	1 544	31 189	89,7	1,812	1 137,1	22,969
Pterosiphonia cloiophylla	6,45	20,64	3 989	82 333	205,1	4,233	2 291,4	47,294
Cheilosporum cultratum	4,21	56,58	519	29 365	16,7	0,945	206,1	11,661
Plocamium corallorhiza	3,68	5,00	3 124	15 620	203,7	1,019	2 483,2	12,416
Hypnea spicifera	1,48	4,26	6 087	25 931	141,1	0,601	2 020,9	8,609
Lithothamnia	2,37	—	—	—	—	—	—	—
Others	2,49	—	—	—	—	—	—	—
Total per mean m^2 of shore	39,36%	205,05g	—	222 657	—	9,926g	—	121,126 kJ.

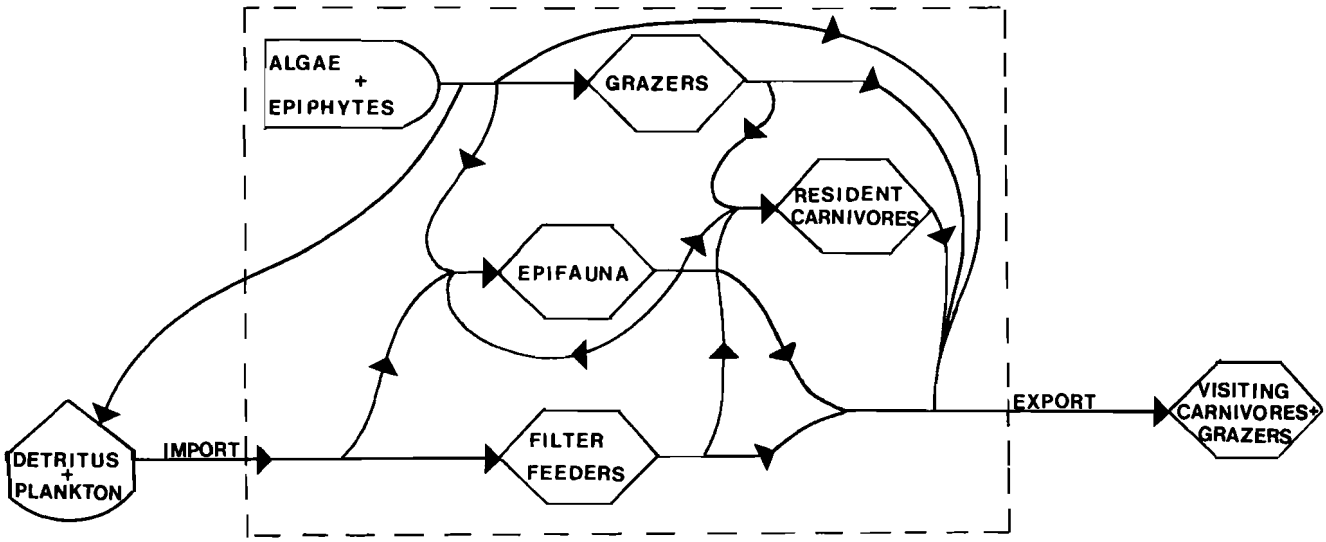

Fig. 1 A model depicting food relationships between the main components of the rocky shore environment.

associated fauna and in most cases are probably really omnivores.

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