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ENERGY FLOW IN THE SALT MARSH ECOSYSTEM OF GEORGIA[1]

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INTRODUCTION

Along the coast of the United States from northern Florida to North Carolina runs a band of salt marsh bordered on the east by a series of sea islands and on the west by the mainland. The Marine Institute of the University of Georgia was established on one of these islands, Sapelo, and has tended to focus attention on the marsh. Several studies have provided data from which it is now possible to construct a picture of the energy flow through the organisms of this marsh.

Reasonably detailed studies of the energy flow, or trophic level production have been limited to a few natural ecosystems. These include Cedar Bog Lake, reported in the pioneer work of Lindeman (1942), and 2 fresh-water springs (Odum 1957, Teal 1958). There have been a number of studies of the energetics of laboratory populations (Richman 1958, Slobodkin 1959), and some theoretical comments upon energetics of populations and ecosystems (e.g. Patten 1959, Slobodkin 1960), but work on even the broad details of energy flow in natural ecosystems has lagged.

The present paper draws heavily upon the work of others. The authors are cited in the appropriate places but I wish here to express my appreciation for their cooperation.

The physical and chemical features of the marsh have been described (Teal 1958, Teal & Kanwisher 1961) but I will briefly define 5 regions into which the marsh was divided in many of these studies (Figure 1).

Creek bank: muddy and/or sandy banks of tidal creeks between low water and the beginning of *Spartina* growth.

Streamside marsh: an area 1-3 m wide of closely spaced, tall *Spartina* located just above the bare creekbank.

Levee marsh: *Spartina* of intermediate height spacing atop the natural levees bordering the creeks.

Short-*Spartina* marsh: flat areas behind the levees with short, widely spaced *Spartina*.

Salicornia marsh: sandy areas near land where plants other than *Spartina* occur, among which *Salicornia* is conspicuous.

The relative areas of these various marsh types were measured on aerial photographs (Table V) to enable calculation of averages for the marsh as a whole.

The marsh fauna

Animals living in the marsh must be able to survive or avoid the great changes in salinity, temperature and exposure. Salinity of water flooding the marshes varies from 20 to 30 o/oo with values as low as 12 o/oo recorded in heads of creeks just after heavy rains. Salinity of water

in the mud may be 5 o/oo in isolated areas where fresh water drains from the islands and 70 o/oo in isolated low areas during rainless summer periods. An average aquatic or soil animal must be able to withstand variations from 20 to 30 o/oo but probably escapes greater extremes by burrowing in the mud and/or migrating short distances.

The limited number of animals which have adapted to these extremes are relatively free from competing species and enemies. For example, mussels living in the marsh are bothered by neither snails nor echinoderms, which take great toll of the estuarine bivalves living only a few meters away. Ants and grasshoppers are each represented by only one common species, *Cremato-gaster clara* and *Orchelimum fidicinium* respectively, which is quite abundant in marsh areas optimal for it. Once adapted to the marsh, the lack of competition from similar animals has perhaps allowed them to occupy a broader niche and

TABLE 1. Known macro-fauna of a Georgia salt marsh listed by groups according to distribution and origin

(1a) Terrestrial species living in marsh
  Orchelimum fidicinium Rehn & Hebard
  Ischnodesmus sp.
  Prokelisia marginata (Van Duzee)
  Liburnia detecta Van Duzee
  Tabanus spp.
  Culicoides canithorax Hoffman
  Dimicoenia spinosa (Loew)
  Plagiopsis aneo-nigra (Loew)
  Parydra vanduzeei (Creeson)
  Chaetopsis aenea (Wiedermann)
  Chaetopsis apicalis Johnson
  Haplodictya setosa (Coquillett)
  Mordellid sp.
  Crematogaster clara Mayr
  Camponotus pylartes fraxinicola M. R. Smith
  Hyctia pikei Peckham
  Seriolus sp.
  Lycosa modesta (Keyserling)
  Philodromus sp.
  Grammonata sp.
  Hyctia brina (Hentz)
  Eustala sp.
  Singa keyserlingi McCook
  Tetragnatha vermiformis Emerton
  Dictyna sp.
  Rallus longirostris Boddaert
  Termatodytes palustris (Wilson)
  Ammospiza caudacuta (Gmelin)
  A. maritima (Wilson)
  Oryzomys palustris (Harlan)
  Procyon lotor (Linne)
  Mustela vison Schreber
(1b) Terrestrial or fresh-water species only on landward edge of marsh
  Pachydiplax longipennis Burmeister
  Pantala flavescens Fabrisius
  Erythrodiplax verenice Drury
  Anax junius Drury
  Erythemis simplicicollis Say
  Orphylella sp.
  Platunus cincticollis (Say)
  Kinesternum s. subrubrum (Lacepede)
  Lutra canadensis (Schreber)

(2a) Estuarine species limited in marsh to low water level
  Bouganvillia carolinensis (McCrady)
  Campanularid sp.
  Oerstedia dorsalis burger
  Nolella stipata Gosse
  Eteone alba Webster
  Autolytus prolifer (O. F. M.)
  Polydora ligni Webster
  Heteromastis filiformis (Claparede)
  Crassostrea virginica (Gmelin)
  Mercenaria mercenaria (Linne)
  Tagelus plebeius Solander
  T. divisus Spengler
  Mulinia lateralis Say
  Epitomium rupicolum (Kurtz)
  Balanus improvisus Darwin
  Microprotopus maculatoides Shoemaker
  Paracaprella sp.
  Crangon heterochelis (Say)
  Clibanarium vittatus (Bosc)
  Molgula manhattensis (DeKay)
(2b) Estuarine species in streamside marsh
  Nassarius obsoletus Say
  Chthamalus fragilis Darwin
  Neomysis americana (S. I. Smith)
  Leptochelia rapax Harger
  Cassidisca lumifrons (Richardson)
  Gammarus chesapeakensis Bousfield
  Melita nitida Smith
  Callinectes sapidus Rathbun
  Panopeus herbstii Milne-Edwards
  Eurypanopeus depressus (Smith)
  Malaclemys terrapin centrata (Latreille)
(2c) Estuarine species occurring well into marsh
  Neanthes succinea (Frey & Leuckart)
  Laeonereis culveri (Webster)
  Streblospio benedicti Webster
  Capitella capitata (Fab.)
  Orchestia grillus (Bosc.)
  O. Platensis Kroyer
(3a) Aquatic marsh species with planktonic larvae
  Manayunkia aestuarina (Bourne)
  Modiolus demissus Dillwyn
  Polymesoda caroliniana Bosc
  Littorina irrorata (Say)
  Littoridina tenuipes (Couper)
  Eurytium limosum (Say)
  Sesarma reticulatum (Say)
  S. cinereum (Bosc)
  Uca pugilator (Bosc)
  U. minax (LeConte)
  U. pugnax (S. I. Smith)
(3b) Aquatic marsh species living entirely within marsh
  Oligochaetes-3 spp.
  Melampus bidentatus Say
  Cyathura carinata (Kroyer)
  Orchestia uhleri Shoemaker

be more abundant than would otherwise be possible.

Table I lists the marsh fauna divided into several groups: (1) typically terrestrial insects and arachnids subdivided into those occurring throughout the marsh and those confined to the landward edge, (2) the aquatic species with their center of abundance in the estuaries and 2a confined to regions near low water, 2b occurring in the streamside marsh, or 2c occurring throughout the marsh, (3) marsh species derived from aquatic ancestors with their centers of distribution within the marsh which are subdivided into those with

planktonic larvae and those that spend their entire life cycle in the marsh.

The list shows that of the aquatic species, 33 or 60% are in groups 2a and 2b, estuarine forms that have managed to colonize the lowest portion of the salt marsh. They can survive only where periods of exposure at low tides are short. The individuals in the marsh are living at one edge of their species' distribution and their numbers are maintained by migrations from the surrounding waters. Those living above the mud are especially subject to damage by extremes of weather, and species that have penetrated farthest into the marsh are burrowers. The remaining aquatic species are either tolerant enough to inhabit the entire marsh although they are most common in the estuaries, group 2c, or are most common in the marshes themselves. But even among the latter, only 6 do not spend part of their life cycle in the estuaries. These are isopods, amphipods, oligochaetes and the pulmonate snail, *Melampus*, the last 2 of which are derived from fresh water or terrestrial rather than marine ancestors.

That part of the fauna derived from the land is at present the least well known, but the species so far encountered comprise nearly half of the marsh animals. They are, however, far less important in the energetics of the community than their aquatic counterparts, as will be seen below.

Most of the terrestrial species have made only slight adaptation to the marshes. They breath air and resist salinity changes and desiccation by means of their impervious exoskeleton. Most of the larger forms climb the marsh grass to escape

rising tides, but can climb under water to seek refuge from birds. Some insects, such as the ant, *Crematogaster*, are easily drowned, but live within *Spartina* stems and can effectively plug the entrance to their nests.

The distribution of marsh species can be seen in Figure 1. The data are from the samples reported in this paper taken at the sites indicated as well as other samples and general collecting. Most of the insect and spider samples are from Smalley (unpublished). Estuarine species occur mostly near low water and in drainage channels and are reduced on the levees which may dry out between spring tides. The aquatic marsh species are distributed relatively evenly throughout the marsh. Terrestrial species are common throughout the grassy areas, with more species present on the higher ground and in the taller marsh-grass.

The food web

The herbivorous faunas of many ecosystems can be divided into 2 groups, those which feed directly on living plants and those which feed on plants only after the plants have died and fallen to the ground (Odum and Smalley 1959). The marsh fauna may be grouped in a similar manner (Figure 2).

A group of insects lives and feeds directly upon the living *Spartina*: *Orchelium*, eating the tissues, and *Prokelisia*, sucking the plant juices. These and their less important associates support the spiders, wrens, and nesting sparrows. A different group lives at the level of the mud surface and feeds on the detritus formed by bacterial decomposition of *Spartina* and on algae. These mud dwelling groups function mostly as primary consumers, although the detritus also contains animal remains and numbers of the bacteria that help break the *Spartina* into small pieces. The carnivores preying on the algal and detritus group are principally mud crabs, raccoons, and rails.
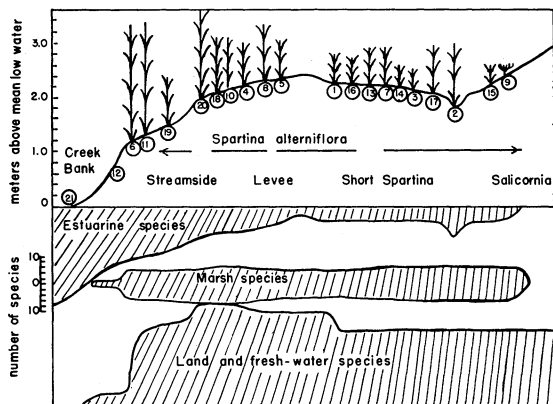
FIG. 1. Representative section of a Georgia salt marsh with horizontal scale distorted non-uniformly. Sample sites indicated by circled numbers. Site 2 represents the beginning of a drainage channel, not an isolated low spot. Symbols for grass are drawn to correct height for average maximum growth at those sites. The number of species of animals of 3 groups listed in Table I are plotted against sample sites. Names of marsh types used herein are also indicated.
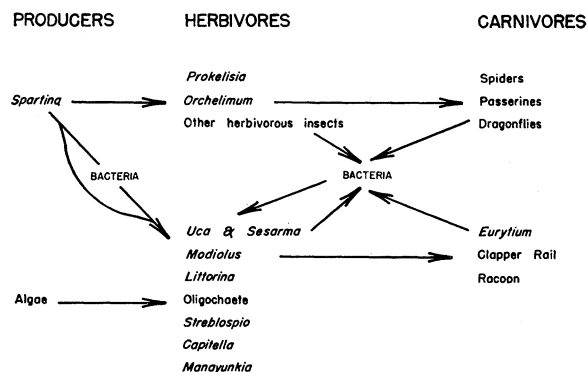
FIG. 2. Food web of a Georgia salt marsh with groups listed in their approximate order of importance.

The species of the detritus-algae feeding group that are important in the economy of the marsh are the fiddler crabs, oligochaetes, *Littorina,* and the nematodes among the deposit feeders, and *Modiolus* and *Manayunkia* among the suspension feeders. Thus, the community consists of 2 parts, one deriving its energy directly from the living *Spartina* and the other deriving its energy from detritus and algae.

ENERGY FLOW BY TROPHIC GROUPS

Methods

Some populations were sampled completely enough that production could be measured directly, e.g. *Spartina* and grasshoppers. In other cases production could not be determined from the sampling but was estimated either from turnover time, in which case production equals one maximum population per turnover period, or by assuming that the ratio between respiration and production for the group in question is 0.25 to 0.30 as has been found for other groups (Teal 1958, Slobodkin 1960). Respiration in air was the measure of energy degradation. Some of the mud dwelling forms live in completely anaerobic conditions (Teal & Kanwisher 1961), e.g. nematodes, and the energy degradation under anaerobic conditions is assumed to be equal to that in air. This is supported only by the observation of Wieser and Kanwisher (1961) that nematodes from anaerobic muds are as active under anaerobic conditions as under aerobic.

Primary production

The only higher plant of importance on the salt marsh is *Spartina alterniflora.* It grows over the entire marsh, is eaten by insects, then dies, decomposes and as detritus furnishes the food for much of the remaining fauna of the marsh. Smalley (1959) measured production of *Spartina* by harvesting and weighing plants at monthly intervals. Teal and Kanwisher (1961) measured respiration. Since the net production was determined by short-term harvesting, it is necessary to add the 305 kcal/m² yr consumed by the insects (see below) to arrive at the true net production. Table II shows that net production of *Spartina* comes to only 19% of gross production. There are indications (Odum 1961) that the production values are underestimated, but not the standing crops upon which respiration values are based. Furthermore, the *Spartina* used to measure respiration was collected in spring. If there is appreciable acclimation to temperature by this species, then summer values will be lower and winter values higher than indicated, but as summer con-

TABLE II. Data for *Spartina* in Georgia salt marhes. Production figures from Smalley (1959), respiration rates from Teal and Kanwisher (1961)

Season		Short Spartina 42% of total area	Levee-Streamside 58% of total area
Winter 2 mo at 10°	Standing crop Respiration	300 fresh g/m² 235 kcal/m²	750 fresh g/m² 580 kcal/m²
Spring 3 mo at 17.5°	Standing crop Respiration	600 g/m² 1250 kcal/m²	1350 g/m² 2800 kcal/m²
Summer 4 mo at 26°	Standing crop Respiration	705 g/m² 6450 kcal/m²	3225 g/m² 29600 kcal/m²
Autumn 3 mo at 20°	Standing crop Respiration	900 g/m² 3240 kcal/m²	1800 g/m² 6480 kcal/m²
Production		2570 kcal/m² yr	8970 kcal/m² yr

Marsh average: net product on = 6590 kcal/m² yr
respiration = 28000 kcal/m² yr
────
gross production = 34580

tributes twice as much (4 vs. 2 months), an adjustment would lower the total figure for respiration. But assuming perfect summer acclimation would bring net production to only 24% of gross production.

In addition to *Spartina,* the algae living on the surface of the marsh mud contribute 1800 kcal/m² yr gross production and not less than 1620 kcal/m² yr net production (Pomeroy 1959).

Decomposition of *Spartina*

Before the *Spartina* is available to most of the marsh consumers it must be broken down by bacteria. Part of the *Spartina* crop decomposes in place on the marsh, especially that portion in the Short Spartina areas not subject to strong tidal currents. *Spartina* from the streamside marsh, however, is swept off by the water and carried back and forth until it is either decomposed in the water, stranded, or carried out to sea. Material stranded on the beach and representative of that carried out of the system consists mostly of stalks. The leaves have decomposed before leaving the marsh-estuarine system.

Burkholder and Bornside (1957) found that when marsh grass was confined in cages in a tidal creek over the winter, one-half of the dry weight was broken up and washed away after 6 months, by which time only the stems remained.

Pieces of dead standing *Spartina* were collected in mid-winter when decomposition was starting. Algae were not present, hence oxygen consumption was a measure of bacterial activity. From the initial rate of decomposition measured at 15° C, it was estimated that leaves submerged at every tide would be completely consumed in 2 months, stems in 3½ months. Leaves and stems that dry
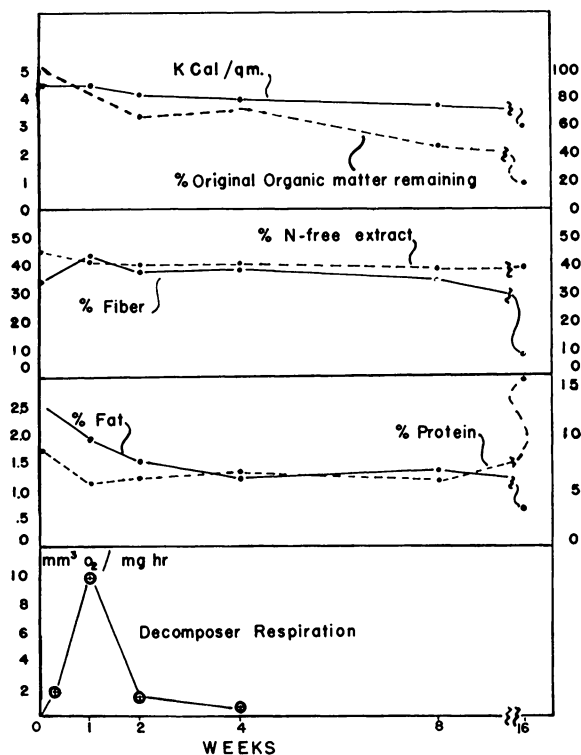
FIG. 3. Decomposition of marsh grass in sea water showing changes in oxygen consumption and composition of grass-bacteria mixture. Line between 8-week point and break shows correct slope.

out in periods between spring tides would last about twice as long.

To find out what changes in composition occur during the breakup of *Spartina,* 10 g of finely-dropped air-dried marsh grass were placed in 500 ml flasks with 200 ml sea water, inoculated with 1 ml of marsh mud and placed on a shaker in the dark at 20° C. The oxygen content of the flasks was not measured but in no case did the material go completely anaerobic. After periods of 0, 2, 7, 14, 28, 56 and 112 days samples were removed. Oxygen consumption of 2 samples was measured and the material from 4 flasks was lumped for analyses of moisture, fat, protein, crude fiber, nitrogen-free extract, ash and caloric content made by Law and Company, Atlanta, Georgia. The results are shown in Figure 3.

Respiration in the flasks rapidly reached a maximum as bacteria grew on the material liberated from crushed cells by the chopping. In 2 weeks this phase passed and bacterial action remained low for the remainder of the experiment. The initial phase is reflected in the decrease in fat and protein percentages but, while fat continued to decline slowly, protein concentration increased gradually until at 16 weeks it was twice as high

as at the beginning. At the same time carbohydrates (N-free extracts) remained constant but fiber, principally cellulose, declined to less than $\frac{1}{4}$ of its initial value. The caloric content declined by 33%. During the period 82% of the organic matter was consumed.

If this is representative of what happens to the *Spartina* as it is changed from standing marsh grass to detritus then, although the total amount of material is decreased, the animal food value of what remains is increased. Bacteria attack the grass substances and convert a portion into bacterial protoplasm and in this process cellulose in the bacterial-detritus mixture decreases most swiftly and protein least swiftly.

The magnitude of the bacterial metabolism was calculated with figures for respiration of plankton in the estuarine waters and bacteria in the marsh sediments and on the standing *Spartina.* Ragotzkie (1958) found that plankton respiration averaged 1600 kcal/m^2 yr in estuarine waters. Since the turbidity of the water is high, there is very little phytoplankton and I assumed that all of this respiration represents bacterial action upon *Spartina* detritus. Since a planimetric survey of charts and aerial photos of the region showed that there is twice as much marsh as estuarine area in the system, this represents 800 kcal/m^2 yr of marsh. From Teal and Kanwisher (1961) we find that the bacteria in the marsh sediments degrade 2090 kcal/m^2 yr. The average respiration of bacteria on standing, dead *Spartina* is about 60 mm^3/gm hr, which, multiplied by the biomass of that *Spartina* (Smalley 1959) comes to 1000 kcal/ m^2 yr. Thus the activities of bacteria account for 3890 kcal/m^2 yr averaged over the marsh area. This amounts to 59% of the available *Spartina.*

Besides bacteria, colorless blue-green algae are also active in the degradation of *Spartina.* Bits of partly decomposed *Spartina* were often found within the mud which was usually black just around them. Within these bits were often numerous filaments of what were apparently *Thioploca* and *Beggiatoa* or *Oscillatoria.* The algae were alive and active, living in a lightless, highly reduced environment as has been discussed by Pringsheim (1949).

Herbivorous insects

The salt marsh grasshopper and the plant hopper are the only important animals in this category. The grasshoppers respire 18.6 kcal and produce 10.8 kcal of tissue per m^2 per year which adds to an assimilation of 29.4 kcal/m^2 yr (Smalley 1960). The corresponding plant hopper figures are: respiration 205 kcal/m^2 yr, produc-

TABLE III. Summary of energy-flow for detritus-algae feeders in Georgia salt marsh

	Respiration	Production	Assimilation	Production Assimilation
Crabs.......	171	35	206	17%
Annelids.....	26	9	35	25%*
Nematodes...	64	21	85	25%*
Mussels......	39	17	56	30%
Snails........	72	8	80	10%
Totals....	372	90	462	19.5%

* Assumed as means of calc. P.

tion 70 kcal/m² yr and assimilation 275 kcal/m² yr (Smalley 1959). Production of plant hoppers was not measured but calculated on the assumption that the ratio of production to assimilation equals 25%. The grasshoppers assimilate only about 30% of what they ingest which means they produce nearly 70 kcal/m² yr of fecal matter which can probably serve as food for some of the other marsh inhabitants.

Detritus-algae feeders

Table III gives a summary of the results for the various groups of animals that feed at the surface of the mud-eating Spartina-detritus, algae and to a lesser but unknown extent each other. The groups are considered in turn below.

Crabs

Uca pugilator, U. pugnax, and *Sesarma reticulatum* are the most conspicuous consumers in the marsh. One or more of these species is present in all parts of the marsh. They feed on the surface of the mud for the most part, picking up clawfuls of mud, sorting it with their mouthparts, spitting the rejected material into a claw and depositing it back on the mud and swallowing the remainder. If the spit is compared with the undisturbed mud surface, it is apparent that most of the sorting consists of rejecting larger particles. Spit from *U. pugilator* which live on sand consists of sand from which the smaller particles, the algae and detritus, are gone. In spit from *U. pugnax* feeding on mud rich in diatoms and nematodes most of the larger diatoms and nematodes were no longer distinguishable but the average particle size of the spit was larger than that of the mud and contained many bits of diatom shells. Apparently the large diatoms and nematodes were crushed and then the finer particles were swallowed and the larger ones rejected.

By comparing the amount of feces produced in a few hours by freshly collected animals with the normal rates of respiration and growth, the portion of the ingested food actually assimilated was

estimated. Four measurements during the winter on groups of from 5 to 16 animals gave values from 23 to 31%. One measurement on 57 crabs in August gave a value of 75%. Algae and detritus are scarcer in summer than winter on the areas where these crabs were collected and apparently they assimilate a larger part of the digestible material when it is scarce. A parallel situation is found in copepods (Marshall and Orr 1955).

In areas of dense crab populations the entire surface of the marsh is worked over between successive high tides. The feces produced by the crabs feeding on muddy substrates contain about one-third more calories per gram than the mud; feces produced by crabs on sand about 10 times as many calories as the sand. Both by the working over of the marsh surface and the concentration of organic matter in their feces the crabs will have considerable influence upon other organisms, especially the nematodes, annelids and bacteria.

The crab populations were sampled by placing metal rings, 30 cm high, on the marsh while the tide was in and the animals were in or near their burrows, returning at low tide and removing

TABLE IV. Crab populations in g/m² in Georgia salt marshes followed by standard errors. Sizes: s=0-150 mg; m=150-500 mg; 1=>500 mg

Marsh type	Size	Winter	Spring	Summer	Autumn	Species
Creek bank	s	0	?	4.89±1.04	0	*Uca pugilator*
	m	0	0	3.67±0.75	0	
	1	0	0	33.1 ±5.6	0	
Stream-side	s	0	0	4.8 ±2.8	0	*Sesarma reticulatum*
	m	0.7 ±0.4	3.65±1.15	7.35±1.15	*	
	1	10.2 ±1.5	*	*	*	
Stream-side	s	0	0	2.6 ±1.6	0	*Eurytium limosum*
	m	0	0	2.85±0.45	*	
	1	8.7 ±1.44	*	*	*	
Levee	s	0.5 ±0.3	?	0.8 ±0.8	0.41±0.14	*Sesarma reticulatum*
	m	0.5 ±0.5	0.2 ±0.2	2.34±0.45	1.4?	
	1	12.4 ±4.35	12.4 ±4.33	22.1 ±0.8	17.0?	
Levee	s	0.81±0.36	2.27±0.68	5.74±0.93	2.47±0.67	*Uca pugnax*
	m	3.0 ±1.5	9.8 ±2.1	7.14±0.65	5.0?	
	1	16.7 ±3.4	32.5 ±9.0	54.3 ±9.5	35.5?	
Levee	1	15.6 ±2.9	*	*	*	*Eurytium limosum*
Short Spartina	s	1.0 ±0.45	0	3.16±0.71	1.0 ±0.45	*Uca pugnax*
	m	2.30±0.60	1.95±0.65	5.00±0.85	3.65?	
	1	16.25±3.90	9.5 ±2.0	12.2 ±1.70	14.25?	
Salicornia-Distichlis	s	?	?	1.91±0.43	8.13±1.17	*Uca pugilator*
	m	3.6 ±0.5	*	*	*	
	1	114.9 ±20.4	*	*	*	

? indicates no samples were taken, numbers if entered are interpolations. When data for several seasons were pooled, the mean appears, followed by asterisks for other seasons involved in the average.

TABLE V. Respiration of Georgia salt marsh crabs by marsh type. Values are kcal/m²/season

Marsh type	Species	Winter	Spring	Summer	Autumn	Total	% by adults
Creek bank.	U. pl.	0	0	69.5	0	69.5	66%
Streamside..	S. r.	2.9	10.5	66.6	17.4	97.3	37%
Levee......	S. r.	3.8	8.6	49.4	17.0	78.7	81%
	U. px.	5.9	50.0	139.6	51.2	246.6	67%
Short spartina..	U. px.	5.5	11.6	48.0	23.3	88.4	56%
Salicornia...	U. pl.	37.3	80.6	170	100	388	90%

everything within the ring, separating, counting and weighing the crabs. Rings of ⅕ m² were used for adults which were picked out by hand but rings of only 0.018 m² were used for the young, which had to be separated by sieving. Crabs of more than 150 mg were ignored in the small samples and vice versa.

The sampling results are shown in Table IV. In general the biomass of crabs follows the same distribution as the numbers of species of marsh animals (Fig. 1). The *U. pugilator* on the creek bank are apparently completely killed during the autumn and replaced the following spring. It seems unlikely that they migrate as they are confined to sandy substrates (Teal 1958) and the Streamside, Levee and Short Spartina marshes are uniformly muddy (Teal and Kanwisher 1961). The values for the Salicornia marsh must be divided by 4 since only about ¼ of the area is occupied by plants and crab burrows, the rest being open sand flats not included in the samples where the crabs feed but do not live.

Table V lists values for respiration of the crabs by marsh types. Respiratory rates are from Teal (1959). The last column gives an idea of the relative importance of the large and small individuals to the population's energy degradation.

By assuming that the crab populations replace themselves annually the energy flow figures in Table VI were calculated.

TABLE VI. Energy flow of detritus-eating crabs in a Georgia salt marsh. Data in kcal/m²/yr

Marsh type	Relative area	Respiration	Production
Creek-bank......	10%	70	28
Streamside......	10%	97	19
Levee...........	35%	325	65
Short Spartina....	40%	88	14
Salicornia........	5%	97	20

Average respiration	171
Average production	35
Average assimilation	206
Production efficiency	17%

TABLE VII. Summary of annelid sampling in Georgia salt marsh

Marsh type	Nov-Dec Sample		Jul-Aug Sample	
	N	g/m²	N	g/m²
Creek bank.........	8	2.0 ±2.0	7	0.95 ±0.25
Streamside.........	15	2.9 ±0.6	10	1.0 ±0.53
Levee..............	35	1.8 ±0.28	38	2.2 ±0.32
Short Spartina.......	39	2.2 ±0.95	8	0.5 ±0.12
Salicornia..........	5	0.2 ±0.2	2	0.0
Marsh average.......		2.01 ±0.46		1.16 ±0.14

Annelids

The annelids in the marsh are mostly deposit feeders, feeding either from fixed burrows or working their way through the sediments like the oligochaetes, although *Manayunkia* is a filter-feeder. Although *Neanthes,* because of its jaws, might be thought to be predaceous, guts examined at different seasons revealed only diatoms, detritus, and mud and sand.

The annelids were sampled once in November-December and once in July-August. Five samples were taken with a plastic coring tube at spots chosen by taking a pair of random numbers, one indicating the distance north and the other, the distance east of a stake marking the southwest corner of a square meter plot selected at random from the marsh as a whole. The sites are indicated in Fig. 1 and may be seen on an aerial photograph of the marsh in Teal and Kanwisher (1961). Each core was divided into 3 parts at 2 cm intervals and the portion below 6 cm discarded. The annelids were removed by gentle washing in sea water in a sieve with 16 meshes/cm. All samples were examined within 24 hours of collection. Biomass was calculated by multiplying the average weight of each species by the number found in the sample. Average weights were determined for the more common species by weighing on a quartz helix as well as by measuring length and width and calculating the weight based on a specific density equal to sea water. The methods agreed within 15%. Insect larvae collected with the annelids are included in the figures (Table VII).

Table VIII shows the numbers of the most common annelids and insect larvae from selected representative sites. *Capitella,* the oligochaetes, *Streblospio* and *Manayunkia* made up most of the biomass, usually in that order. Two of these, *Capitella* and *Streblospio,* are characteristic not of the marshes but of the estuaries, indicating that the annelids have had to make relatively little adaptation to marsh life. In general they are most

TABLE VIII. Numbers of selected annelids and insect larvae/0.01 m² in representative marsh types in a Georgia salt marsh

Site	21	6	19	10	8	4	1	7	3
Winter Series									
Capitella capitata........	0	10	30	70	50	30	0	10	0
Steblospio benedicti......	50	150	80	40	50	0	20	30	0
Neanthes succinea.......	0	10	0	0	0	0	0	0	10
Manayunkia aestuarina..	0	0	40	90	0	290	0	0	0
oligochaete.............	10	10	170	80	30	80	40	40	0
dipteran larvae........	0	0	10	0	10	10	0	0	0
Summer Series									
Capitella capitata........	30	26	14	56	136	38	12	30	0
Streblospio benedicti......	14	38	40	6	4	0	4	0	0
Neanthes succinea.......	0	0	0	0	2	0	0	0	0
Manayunkia aestuarina..	8	10	12	52	0	60	0	0	0
oligochaete.............	78	10	60	88	88	66	30	32	20
dipteran larvae........	2	0	0	0	0	2	0	0	0

numerous in the most productive parts of the marsh as are other animals, except that they are somewhat scarcer on the highest and thus the driest parts of the levees.

Energy flow for the annelids was calculated on the basis of an average respiration rate of 400 mm³/gm hr (Zeuthen 1953) and a production equal to 25% of assimilation. The latter results in a turnover time of 1.6 months which is reasonable since the animals are between 20µ gm and 200µ gm in weight.

Nematodes

Using the relative areas of various marsh types from Table V, and the weights of nematodes from Teal and Wieser (1961) I calculate that there are about 2.76 g fresh weight/m². The samples were all taken in spring so it must be assumed that the nematode biomass does not change appreciably throughout the year. Wieser and Kanwisher (1961) found that there was only slightly more than a 2-fold variation in a marsh at Woods Hole, Mass. where the climate is considerably colder and more variable. Using the average respiratory rate of 540 mm³/fresh gm/hr (Teal and Wieser 1961) the nematodes would respire an average of 64 kcal/m² yr. Assuming their production to equal 25% of assimilation, production would be 21 kcal/m² yr which would amount to a turnover of the population every 1.6 months. This may be compared with turnovers of 1 year and 1 month quoted by Wieser and Kanwisher (1961) and Nielsen (1949) respectively.

Snails and Mussels

The mussels (Kuenzler 1961) respire on the average 39 kcal/m² yr and produce 17 kcal/m² yr. The small snails of the current year class had a production equal to 14% of their assimila-

tion but Smalley's population data did not provide a production value for the adults which grew very slowly. Since there is some growth of adult snails as well as the formation of gametes, which amounts to ⅙ of the total production of the mussels (Kuenzler 1961), the snail production must be something less than 14%, and 10% is used here.

Secondary consumers

The population data for the mud crab, *Eurytium limosum*, were presented in Table III. An average respiration value of 21.9 kcal/m² yr was derived from data of Teal (1959) and a production of 5.3 kcal/m² yr was calculated in the same manner as for the other crabs. For the Clapper Rails, a production of 0.1 kcal/m² yr was calculated from the data of Oney (1954) for population and mortality, and an average respiration of 1.6 kcal/m² yr was calculated on the basis of the weight-metabolism curve of warm blooded animals in Hemmingsen (1950). So figured the total assimilation of the carnivores comes to 30.6 kcal/m² yr divided into 25.1 kcal/m² yr respiration and 5.5 kcal/m² yr production. The raccoons in the marsh have not been studied but on the basis of general observation during 4 years when I was in the marsh nearly every week, they are considered to have an assimilation equal to that of the rails.

As yet there is no study of the carnivorous birds and spiders that feed on the marsh insects. For purposes of this calculation they are assumed to take the same portion of their prey as do the predators feeding on the detritus-algae eaters.

COMMUNITY ENERGY FLOW

Figure 4 shows the energy flow for the marsh system calculated in the preceding sections. The value for light input is from Kimball (1929). The amount of light that is actually intercepted by the plants is unknown but it is obvious from colored aerial photographs that a considerable portion of the mud is exposed especially in the parts of the marsh not close to a creek. Nevertheless, gross production is 6.1% of the incident light energy. This may be compared with values of from 0.1 to 3.0% reported for various fresh-water and marine areas (Odum and Odum 1959, 1955). The salt marsh occupies a highly advantageous position where nutrients are plentiful and circulation is supplied by the tides.

However, as noted above, a large part of the gross production is metabolised by the plants themselves and net production over light is a little less than 1.4%. This is still high compared to other
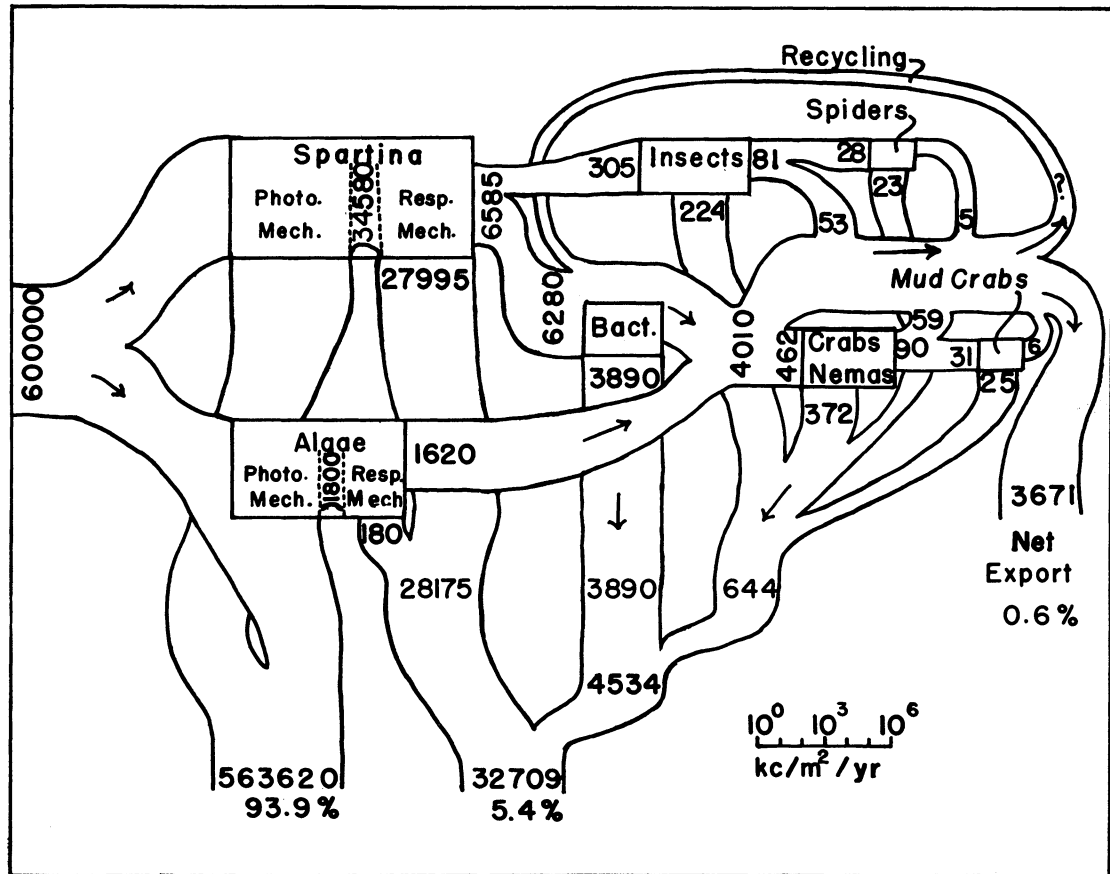
Fig. 4. Energy-flow diagram for a Georgia salt marsh.

systems although values as high as 6.0% have been reported for pine plantations (Ovington 1959).

The herbivorous insects assimilate 4.6% of their potential food, the net production of *Spartina*. They eat the plants directly and there is no significant time lag between production and consumption, since Georgia is far enough south that the *Spartina* grows to some extent throughout the year. The grasshoppers feed on it during the summer whereas the leaf hoppers are most abundant during the cooler seasons.

The relation between production and consumption for the algae-detritus feeders is more complex. Mud algae production is rather constant throughout the year (Pomeroy 1959) and algal turnover is much more rapid than *Spartina* turnover. When the algae-detritus feeders utilize algae there is little or no time lag between production and primary consumption, but when they feed on *Spartina* detritus and the associated bacteria, there is a definite time lag. Detritus is produced throughout the year as the older leaves die and are broken up, but most of the *Spartina* dies in autumn and winter after seed formation. Low winter temperatures

retard formation of detritus and spread the supply out into the spring. At the beginning of summer, a new supply forms as the leaves of the spring growth die and decay. Whatever the actual time relationships may be, it is certain that there is considerable delay before detritus feeders can use the *Spartina* and the longer the delay, the less food remains.

These animals compensate for the variations in detrital supply by eating algae. The most conspicuous and abundant consumers of the marsh, the fiddler crabs, have perhaps the most omnivorous food habits. They can survive on detritus, algae, bacteria or animal remains (Teal 1958), i.e. they have a very unrestricted diet.

Odum and Odum (1959) and MacArthur (1955) have suggested that the fluctuations characteristic of certain communities may be correlated with the presence of few species as in arctic or desert areas. In the salt marsh we have a system with few species but one which seems to exhibit considerable stability. In the 5 years during which these studies were carried on there were no noticeable changes in population size in any of the

important animals. (The microfauna of the soil is probably relatively little affected by the weather extremes which make life difficult for the larger animals and are not considered in this argument.)

Stability is a valuable asset for an ecosystem as it minimizes disturbance which might lead to partial or total extinction. Stability will therefore have selective value and ecosystems will tend to develop more stable configurations with time (Dunbar 1960). Salt marsh faunas and floras have had long periods in which to develop and although they have been greatly affected by the considerable changes in sea level which occurred during the Pleistocene they may not be considered as youthful as arctic areas. There has therefore been sufficient time for stability to develop and for species to adapt to the marsh conditions.

MacArthur (1955) shows that a community may achieve stability by having either many species with restricted diets or fewer species with broad diets. The former alternative will permit greater efficiency and, other things equal, will be the one selected. The salt marsh has, however, the 2nd alternative. Among the detritus-algae feeders there are only a few important species and they all have a very unrestricted diet. There are also only a few species among the carnivores that prey on the detrital feeders and they also have an unrestricted diet. Among the insects there are only 2 important species and though they feed only on *Spartina,* this is the only higher plant growing on most of the marsh and so the only food available. These 2 insects are not especially restricted in other ways; they feed on various parts of the plants and in various degrees of exposure. The situation among the spiders and carnivorous insects has not been adequately investigated but there seem to be more species in these groups and perhaps more specialization in their niches.

There are 2 principal reasons why the salt marsh should have the less efficient alternative of the 2 paths to community stability. There is only one higher plant on the marsh and consequently a lack of variety of possible niches such as could be found in a forest at the same latitude. Possibly even more important is the restriction of biomass by the removal of much of the marsh production by the tidal currents. As Hutchinson (1959) has pointed out, if the total biomass is restricted, "then the rarer species in a community may be so rare that they do not exist." With these 2 limitations of the possible numbers of species that can survive in the marsh community, the only road to stability is the development of broad, unrestricted food habits such as is found in the marsh.

TABLE IX. Summary of salt marsh energetics

Input as light	600,000 kcal/m²/yr
Loss in photosynthesis	563,620 or 93.9%
Gross production	36,380 or 6.1% of light
Producer Respiration	28,175 or 77% of gross production
Net Production	8,205 kcal/m²/yr
Bacterial respiration	3,890 or 47% of net production
1° consumer respiration	596 or 7% of net production
2° consumer respiration	48 or 0.6% of net production
Total energy dissipation by consumers	4,534 or 55% of net production
Export	3,671 or 45% of net production

Table IX gives a summary of the energy flow for the system. The producers are the most important consumers in the marsh followed by the bacteria which degrade about ⅐ as much energy as the producers. The animals, both primary and secondary consumers, are a poor 3rd degrading only ⅐ as much energy as the bacteria. As far as the consumers are concerned, the situation in the salt marsh is not very different from that in other systems. But the high consumption by the producers is unusual. In a stable system such as a so-called "climax forest" consumption equals production and there is no accumulation of organic matter, but the trees are relatively unimportant consumers. Ovington (1957) gives data indicating that in mature pines respiration is something less than 10% of production. The fact that salt marsh *Spartina* respires over 70% of its production may be associated with existence in an osmotically difficult situation.

In spite of the high rate of producer respiration, net production in the salt marsh is 1.4% of incident light which is higher than in most systems studied (Teal 1957). Table IX shows that 45% of this production is lost to the estuarine waters. The fauna of the estuaries has not been quantitatively studied but the numbers of shrimp and crabs taken by the local fishery give evidence of their abundance. Since the waters of these estuaries are so turbid and well mixed that the phytoplankton spend most of their time in the dark and their net production is zero (Ragotzkie 1958), the estuarine animals must be living on the exported marsh production. There is about ½ as much estuarine as marsh area behind the sea islands and since 45% of the marsh production is exported to the estuaries, there can be 1.6 times as much consumer activity in the latter region as in the former.

The tides are of supreme importance in controlling the environment of the salt marshes. They limit the number of species that can occupy the system and so make it simple enough to be studied

in the detail reported here. They are responsible for the high production of *Spartina,* as witnessed by the luxuriant growth along the tidal creeks as compared with that on the Short Spartina areas. At the same time the tides remove 45% of the production before the marsh consumers have a chance to use it and in so doing permit the estuaries to support an abundance of animals.

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