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THE ROLE OF TWO INVERTEBRATE POPULATIONS,
LITTORINA IRRORATA AND ORCHELIMUM FIDICINUM,
IN THE ENERGY FLOW OF A SALT MARSH ECOSYSTEM

by

ALFRED EVANS SMALLEY

B.S., The Pennsylvania State University

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by

ALFRED EVANS SMALLEY

Approved:

Eugene P. Odum
Major Professor

W. B. Balch
Chairman, Reading Committee

Approved:

Gerald B. Huff
Dean, Graduate School

May 6, 1959
Date

TABLE OF CONTENTS

LIST OF TABLES.....	v
LIST OF FIGURES.....	viii
INTRODUCTION.....	1
ACKNOWLEDGEMENTS.....	3
METHODS	
Measurement of Production.....	4
Measurement of Respiration.....	6
Measurement of Ingestion.....	10
MARSH MORPHOLOGY AND ITS RELATION TO VEGETATION.....	11
THE NET PRODUCTION AND SEASONAL GROWTH CYCLE OF <u>SPARTINA</u> <u>ALTERNIFLORA</u>	21
THE ENERGY FLOW OF TWO INVERTEBRATE COMPONENTS OF THE SALT MARSH ECOSYSTEM. <u>LITTORINA IRRORATA</u> : AN AUFWUCHS-DETRITUS FEEDER	
Methods of Determining Population Density.....	29
Life History and Behavior	
General distribution.....	30
Reproduction.....	31
Early life in the marsh.....	32
Distribution in different marsh types.....	33
Population Density.....	35
Population Density and the Growth Rate of Snails.....	40
Mortality.....	44
Production.....	46

Energy Utilization.....	51
Ingestion.....	53
<u>ORCHELIMUM FIDICINIUM</u> : A PRIMARY CONSUMER.....	54
Population Density.....	54
Mortality and Production.....	56
Energy Utilization.....	62
Ingestion.....	65
DISCUSSION AND CONCLUSIONS	
Population Phenomena and Energy Flow.....	68
Seasonal Activity of <u>Littorina</u> and <u>Orchelimum</u> and <u>Spartina</u> production.....	70
Efficiency of Energy Utilization in <u>Orchelimum</u> and <u>Littorina</u>	74
Energy Flow as an Index to Animal Activity.....	78
SUMMARY.....	81
LITERATURE CITED.....	85
APPENDICES	
Appendix 1: Rankits for <u>Spartina</u> clip samples.....	87
Appendix 2: Population estimates of <u>Littorina</u>	90
Appendix 3: Population estimates of <u>Orchelimum</u>	97
Appendix 4: Calculation of production, and respiratory rates in <u>Littorina</u>	99
Appendix 5: Calculation of production, and respiratory rates in <u>Orchelimum</u>	111
Appendix 6: Data for calculation of ingestion rates of <u>Orchelimum</u>	122
Appendix 7: The relation of respiration to temperature in <u>Littorina</u> and <u>Orchelimum</u>	124

LIST OF TABLES

TABLE	PAGE
1. Analysis of the fraction of <u>Spartina</u> leaves which are available to <u>Orchelimum</u> , and its oxycaloric coefficient....	9
2. Net production of <u>Spartina</u> on the high marsh.....	24
3. Net production of <u>Spartina</u> on the streamside-levee marsh...	25
4. <u>Spartina</u> production in clipped quadrats.....	27
5. Caloric content of <u>Spartina</u>	28
6. Size distribution of <u>Littorina</u> in two marsh types.....	34
7. Size distribution of small <u>Littorina</u> in October, 1956.....	38
8. Size distribution of small <u>Littorina</u> in July, 1957.....	39
9. Size of <u>Littorina</u> in three sections along the sampling transect.....	41
10. Population density of <u>Littorina</u> in three sections along the sampling transect.....	42
11. Caloric content of <u>Littorina</u>	49
12. Energy flow of a population of <u>Littorina</u>	50
13. Estimates with a portable cage of the grasshoppers per unit area captured with a sweep net.....	57
14. Population density of <u>Orchelimum</u> in 1957.....	58
15. Proportion of different size classes in an <u>Orchelimum</u> population.....	59
16. Caloric content of <u>Orchelimum</u> and <u>Orchelimum</u> feces.....	63

17. Ingestion rates of <u>Orchelimum</u>	66
18. Some efficiencies of <u>Littorina</u> and <u>Orchelimum</u>	76
19. Population density of the 1955 year class of <u>Littorina</u> ...	91-92
20. Population density of adult <u>Littorina</u>	93-94
21. Population density of the 1956 and 1957 year class, and small <u>Littorina</u> of undetermined age.....	95-96
22. Numbers and dry weight of <u>Orchelimum</u> taken in sweep samples.....	98
23. Mean length and weight of snails of the 1955 year class....	101
24. Monthly production of the 1955 year class of <u>Littorina</u>	103
25. Oxygen consumption rates for various size classes of <u>Littorina</u>	105
26. Calculation of population oxygen consumption for the 1955 year class of <u>Littorina</u> in February, 1957.....	106
27. Calculation of correction factors for oxygen consumption of <u>Littorina</u> at mean monthly temperatures.....	107
28. Population oxygen consumption of the 1955 year class of <u>Littorina</u>	108
29. Population oxygen consumption of adult <u>Littorina</u> and small <u>Littorina</u> of undetermined age.....	109
30. Population oxygen consumption for 1956 and 1957 year classes of <u>Littorina</u>	110
31. Data for calculation of production in <u>Orchelimum</u>	113
32. Data for calculation of production of <u>Orchelimum</u> for each sampling interval.....	115

33. Production of <u>Orchelimum</u> for each sampling interval.....	116
34. Weights and rates of oxygen consumption for different size classes of <u>Orchelimum</u>	117
35. Population oxygen consumption in <u>Orchelimum</u>	118
36. Temperature corrections for <u>Orchelimum</u> respiration.....	120
37. Production and respiratory energy use in <u>Orchelimum</u>	121
38. Data for calculation of ingestion rates of <u>Orchelimum</u>	123

LIST OF FIGURES

FIGURE	PAGE
1. Sapelo Island and the surrounding waters.....	12
2. Relationship between height of <u>Spartina alterniflora</u> and marsh altitude.....	13
3. The principle physiographic units of the salt marsh ecosystem.....	15
4. Drainage pattern and marsh types of a high marsh area.....	16
5. Transect of an area of middle marsh.....	18
6. Drainage pattern of a middle marsh area.....	19
7. The standing crop of <u>Spartina</u> on the high marsh.....	22
8. The standing crop of <u>Spartina</u> on the streamside-levee marsh.....	23
9. Size distribution of a <u>Littorina</u> population over a 21 month period.....	36
10. Size difference between <u>Littorina</u> from two sections along a sampling transect.....	43
11. Survivorship curve of the 1955 year class of <u>Littorina</u>	45
12. Survivorship curve of adult <u>Littorina</u>	47
13. Relationship between body weight and total shell length of <u>Littorina</u>	48
14. Oxygen consumption of different sizes of <u>Littorina</u>	52

15. Survivorship curve of <u>Orchelimum</u> during the summer of 1957..	61
16. Oxygen consumption of different sizes of <u>Orchelimum</u>	64
17. Numbers, biomass and population respiration at 30 degrees Centigrade of <u>Littorina</u>	69
18. Population density, standing crop and assimilation of <u>Orchelimum</u>	71
19. Comparison of seasonal net production of <u>Spartina</u> , and assimilation in <u>Littorina</u> and <u>Orchelimum</u>	72
20. Rankits for a high marsh sample of living <u>Spartina</u>	88
21. Rankits for a high marsh sample of dead <u>Spartina</u>	89
22. Relation of respiration to temperature in <u>Littorina</u>	125
23. Relation of respiration to temperature in <u>Orchelimum</u>	126

INTRODUCTION

Investigators have usually combined two methods when undertaking functional analyses of ecosystems; (1) whole-system measurements, particularly applicable where water flows over a biotic environment (H. T. Odum, 1956) and (2) measurements of components of the systems (H. T. and E. P. Odum, 1955; H. T. Odum, 1956; Teal, 1956). In these studies, ecosystems are described in terms of their energy content and in terms of the rate of energy transfer into the system and through its biotic components.

Studies of entire natural systems have emphasized the need to achieve a better understanding of the energetics of species populations. In the tidal marshes of the Georgia coast, there are relatively few species of important macroscopic invertebrates. Work can be logically confined to the extensive areas where Spartina alterniflora is the only higher plant and the major primary producer, simplifying the estimation of production and trophic structure of the biotic components of the system.

In the present study, two animal populations of the tidal marsh ecosystem are given special attention with the purpose of describing them from a functional viewpoint and relating them to measurements of net production of Spartina.

The components which have been studied are the marsh grass, Spartina alterniflora Loisel, the salt marsh periwinkle, Littorina irrorata Say, and the long-horned grasshopper, Orchelimum fidicinum Rehn and Hebard.

Littorina and Orchelimum were chosen because (1) they are easily studied in the field and laboratory, (2) on preliminary examination, they seemed to have a population structure amenable to analysis and (3) they are abundant and conspicuous components of the marsh.

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to Dr. E. P. Odum, who has been most generous with his advice and help throughout the course of this study. Financial support was made possible by a National Science Foundation grant to Dr. Odum. The staff of the Marine Institute of the University of Georgia, Drs. R. A. Ragotzkie, L. R. Pomeroy and J. M. Tesl, extended help in many ways. I am also indebted to J. B. Gentry and Smith Kimball for help in field and laboratory. Since the salt marsh has been studied by various people at the Marine Institute, unpublished data from sources other than my own research is occasionally used, and noted in the appropriate place. Marsh insects were identified by Dr. W. H. Cross (Orthoptera), Dr. R. H. Foote (Diptera) and J. P. Kramer (Homoptera). Clyde E. Connell helped with calorimetry; Wallace A. Tarpley helped with various insect problems.

METHODS

Measurement of Production

Production is the amount of organic matter or protoplasm incorporated into a population per unit time. Production in this study is expressed as kilogram calories per square meter per year. Gross Primary Production is the rate of synthesis of organic matter by photosynthetic organisms. Net Primary Production is the organic matter remaining after respiratory needs of a photosynthetic organism are satisfied by the primary photosynthate.

Net production of Spartina was measured by periodically harvesting the standing crop of the grass. High marsh Spartina was sampled each month at ten stations ten meters apart in a straight line across an area which was considered typical of the high marsh. The grass was clipped at the level of the mud from a 0.1 square meter area at each station. In the laboratory, the dead grass was separated from the living grass; both were then dried at a temperature of 100 degrees Centigrade, and weighed. Normally, production is then calculated by adding the increases in biomass during each sampling period (Penfound, 1956). However, if some of the grass dies, is consumed, or is otherwise removed from the area between samples, the net production is underestimated. In determining Spartina production of the high marsh, both living and dead standing crops were measured and the results for the high marsh calculated as follows:

(1) If there was both an increase in the standing crop of living Spartina and an increase in the standing crop of dead Spartina, then net production was the sum of the increases.

(2) If both living and dead standing crop decreased, then production was zero. Since production is defined as synthesis of organic matter, it cannot be negative, and decreases must be accounted for in terms of consumption, sedimentation, or loss from the system.

(3) If the standing crop of living Spartina increased and the standing crop of dead Spartina decreased, production was equal to the increase in the living Spartina. Any decrease in dead Spartina is assumed to be due to loss to the tidal waters, but an increase in living Spartina can only be due to net production.

(4) If the amount of dead Spartina increased and the amount of living decreased, they were added algebraically; if the result was negative, production was zero; if the result was positive, the resulting figure was equal to production.

The standing crop of grass on streamside and levee marshes was measured by R. A. Ragotzkie, who kindly made available his unpublished data. These were also clip samples, but of three 40 square meter quadrats. The different quadrat size was used because the taller grass of the streamside marshes is discontinuous due to washouts, minor drainages and constant slumping of the bank, while the high marsh is relatively uniform. Production was determined by finding the increase of the living grass, since the dead grass does not accumulate in the streamside-levee marsh.

Animal production was also determined from periodic censusing of the population. If there is no recruitment, animal production is the sum of two parameters; (1) the amount of biomass accumulated during the study period by the surviving animals, and (2) the amount of biomass accumulated by animals lost to the population by mortality, from the beginning of the study period to the time of their death.

The caloric content of Orchelimum, Littorina and Spartina was determined in a Parr Adiabatic Bomb Calorimeter and the resulting conversion factors used to express production in Calories. One precaution in interpreting the results of bomb calorimetry deserves mention. The values obtained are the total potential energy resulting from complete oxidation of the sample, not the energy which is available to the organisms which eat this material. The amount of energy actually utilized is a function of the ability of an organism to assimilate and oxidize a nutritive source. It may be assumed, however, that eventually all the energy which is stored in the tissues of the plant or animal being considered is expended in the form of heat or lost to the biotic system through advection or sedimentation.

Measurement of Respiration

The energy required for the various life processes of an animal, such as food-getting, reproduction, locomotion, etc., is obtained by oxidation of foodstuffs ingested and absorbed by the animal. The oxygen consumption of different sizes of Orchelimum and Littorina was determined in order to obtain the amount of energy use. Respiration

was measured by a variable volume respirometer consisting of a pipette inserted into a vial. The animals were placed in the vial along with a CO₂ absorbent and the apparatus immersed in a constant temperature water bath. The progress of the water into the free end of the pipette measured the amount of oxygen used by the animals. Provision was made for re-injecting air into the system at intervals. Results were reduced to standard temperature but not standard pressure. Failure to correct for pressure may have resulted in maximum errors of plus or minus 3 percent.

Oxygen consumption rates were expressed as dry weight of individual animals against milliliters of oxygen consumed per hour. The regression of weight against oxygen consumption is given according to the equation

$$Y = aX^b$$

where a and b are constants, as suggested by Brody (1945) and Bertalanffy (1957). The expected linear relationship between the logarithm of weight and the logarithm of oxygen consumption was obtained. Respiratory rates for animals whose weights were obtained from population samples were then calculated from the regression equation.

To achieve the uniformity of units previously mentioned, it is necessary to convert oxygen consumption to calories. This can be done best if the fat, carbohydrate, and protein content of the material being oxidized is known. With information of the composition of food, conversion to calories can be accomplished with well established coefficients. But the exact nature of the material assimilated, much less oxidized, is seldom known. Ivlev (1934) attacked the problem by

finding (either from the literature or independently) (1) the amount of oxygen necessary to completely oxidize fat, protein and carbohydrate and (2) the caloric value of each material. He then calculated the calories/gram oxygen for each component, which he called the oxycaloric coefficient. Then, by determining the composition of a number of organisms which constituted potential fish food, he was able to calculate a coefficient for each organism. The resulting coefficients of energy conversion were quite constant for the various species, and their mean was called the "universal" oxycaloric coefficient. The universal oxycaloric coefficient is 4.83 calories per milliliter of oxygen. Of course, the values found by Ivlev refer to the caloric value of the organisms which are likely to be ingested, not the assimilated portion; the resulting errors are probably small in terms of the use to which the coefficient will be put here. Ivlev's oxycaloric coefficient is used to convert oxygen consumption of Littorina to caloric values.

Since an analysis of Spartina is available (Burkholder, 1956), an opportunity arose to use a more accurate conversion factor for respiration of Orchelimum. Two refinements were possible:

(1) Burkholder gives a separate analysis for leaves only; field observations show that Orchelimum feeds only on the leaves of Spartina, so stem and whole plant analyses can be omitted.

(2) Crude fiber is not available to the vast majority of insects (Trager, 1953) and thus this fraction of Spartina was not considered.

The relevant analyses from Burkholder (1956) are given in Table 1, along with Ivlev's coefficients for the appropriate fractions. The

Table 1. Analysis of the fraction of mature Spartina leaves which are available to Orchelimum, and its oxycaloric coefficient. After Burkholder (1936), and Ivlev (1934).

	% dry weight (mean of 3 samples)	Yield in cal/ mgm. O ₂
Fat	4.25	3.280
Protein	13.41	3.305
N-free extract	82.34	3.529

Mean caloric yield from Spartina leaves exclusive of crude fiber--
3.45 calories per milligram of oxygen or 4.93 calories per milliliter of oxygen.

resulting oxycaloric coefficient for Spartina which is available to Orchelimum is 4.93 calories per milliliter of oxygen.

Measurement of Ingestion

Ingestion is considered to be the sum of assimilation and the feces deposited by an animal, with losses from secretions unaccounted for. Grasshoppers were kept in a container with Spartina leaves for short periods (between two and three hours) immediately after being collected from the marsh. The feces and grasshoppers were weighed, and the respiration of grasshoppers of the appropriate weight at the experimental temperature calculated from previous experiments. By applying the production/assimilation ratio obtained for the entire population, production could be added for the experimental animals and an assimilation/ingestion ratio calculated.

MARSH MORPHOLOGY AND ITS RELATION TO VEGETATION

The tidal marshes of the Georgia coast lie either (1) between the coastal islands ("Sea Islands") and the mainland, or (2) between the islands and their barrier beaches. The research reported here was concentrated on the "inner" marshes west of Sapelo Island (Figure 1). The substrate of these extensive marshes consists almost entirely of a muddy mixture of silt and clay, with sand present in but small amounts. There is an underlying sand layer, sometimes at depths of ten meters or more.

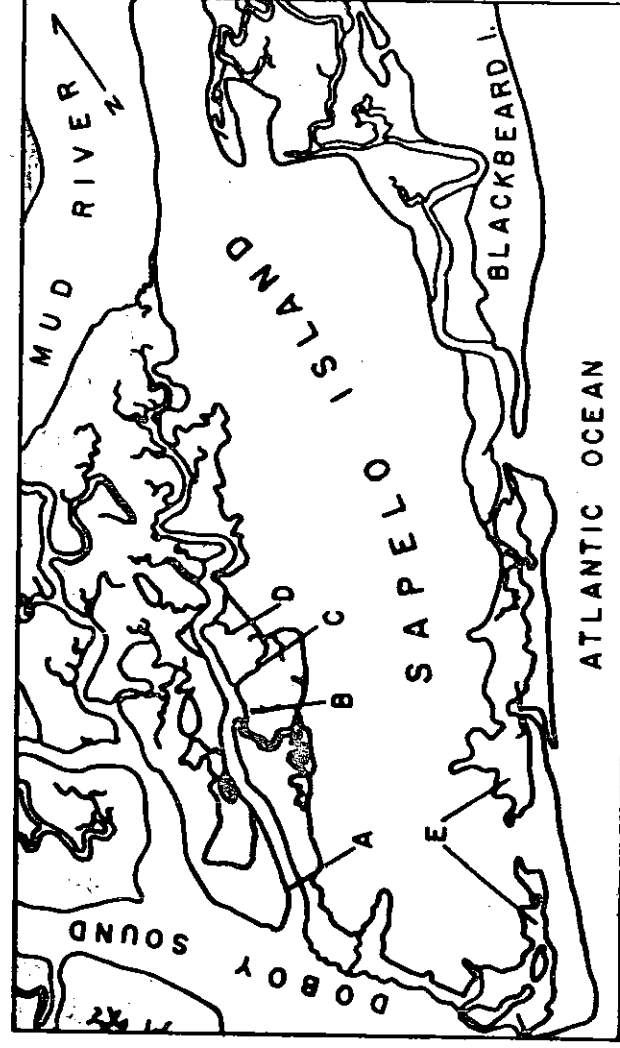
The marsh is a complex of tidal streams, mud flats which typically border the streams at low tide, and extensive areas of marsh grass. Unless otherwise specified, all of the present research was concentrated on the Spartina marsh.

All streams mentioned here are tidal in nature. The hydrography of the Duplin River, the main stream in the area studied ("A" in Figure 1), has been described by Ragotzkie and Bryson (1956).

Marsh types are classified according to the following criteria:

- (1) altitude
- (2) drainage pattern
- (3) nature of Spartina
- (4) substrate

The marsh types and their relation to Spartina height are shown in Figure 2, and may be briefly described as follows:



SCALE 1:80,000

Figure 1. Sapelo Island and the surrounding marshes. A--Duplin River; B--High marsh study area for *Spartina* and *Littorina*; C--location of Figure 4; D--*Orchelinum* study area and location of Figure 6; E--marshes between Sapelo Island and its barrier beach. Salt marsh is shaded green.

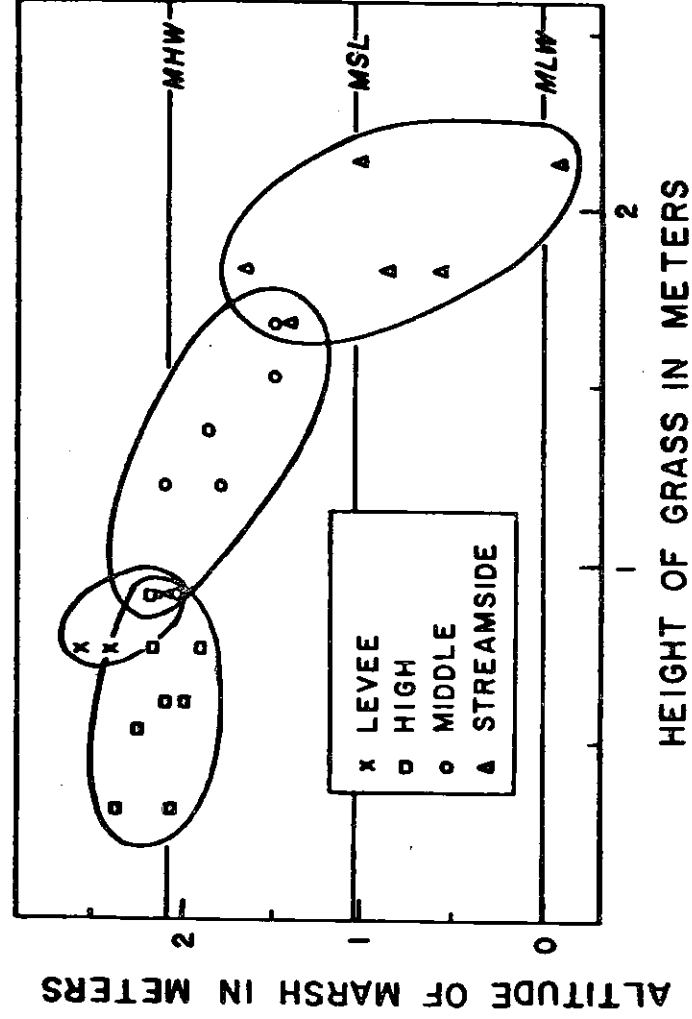


Figure 2. Relationship between height of Spartina and marsh altitude. The points upon which the boundaries of the marsh types are based represent actual measurements in the marsh. Some of the levee and high marsh points are from transects run by L. R. Pomeroy.

Streamside. Occurs along the edge of all but the smallest streams, gradually disappearing and merging with the middle marsh toward the headwaters of a drainage system. The grass is very tall (two meters or more), and the substrate very soft and difficult to cross on foot.

Levee. Occurs along all of the larger streams. The substrate is soft, although the highest levees sometimes become dry and quite hard during periods of neap tides. The Spartina is usually of moderate height, and is dense and lush, except in very high areas along large rivers and sounds, where the levees are so high that they are seldom inundated. Here the grass is sparse or absent altogether.

High. The substrate is quite firm, making it easy to traverse on foot. The drainage pattern is either dendritic, sub-dendritic, or modified pinnate (nomenclature after Zernitz, 1932), and the Spartina is short, seldom exceeding one meter. The marsh is devoid of well-marked drainage channels and is poorly flushed by the tide. High marsh forms a continuum with the transition marsh of Juncus, Distichlis, Salicornia, etc., which borders the terrestrial vegetation. Although of great interest floristically, the transition marsh is not considered here.

A diagrammatic cross-section of marsh is shown in Figure 3. The water, mud flat, streamside marsh, levee marsh, high marsh sequence is illustrated. Areas such as those shown in Figure 3 are customarily encountered when entering the marsh from a boat. Figure 4 is a map drawn from an aerial Kodachrome taken by R. A. Ragotzkie, and illustrates a marsh dominated by the streamside-levee-high marsh sequence.

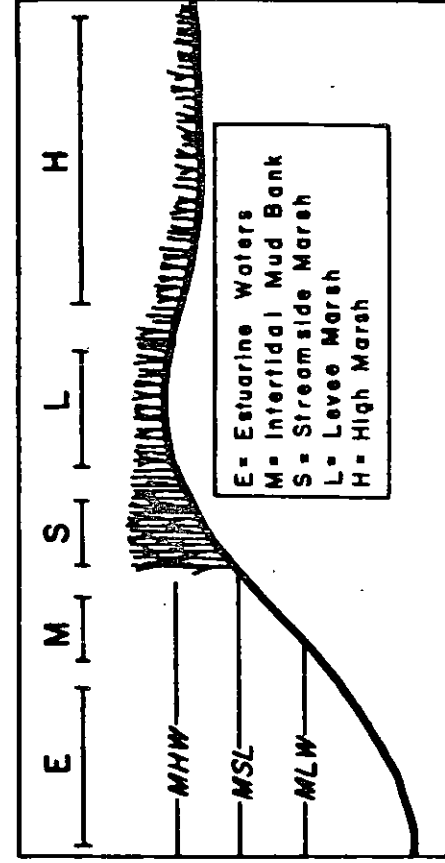


Figure 3. Diagram of the principle physiographic units of the salt marsh ecosystem. MHW--mean high water; MSL--mean sea level; MLW--mean low water.

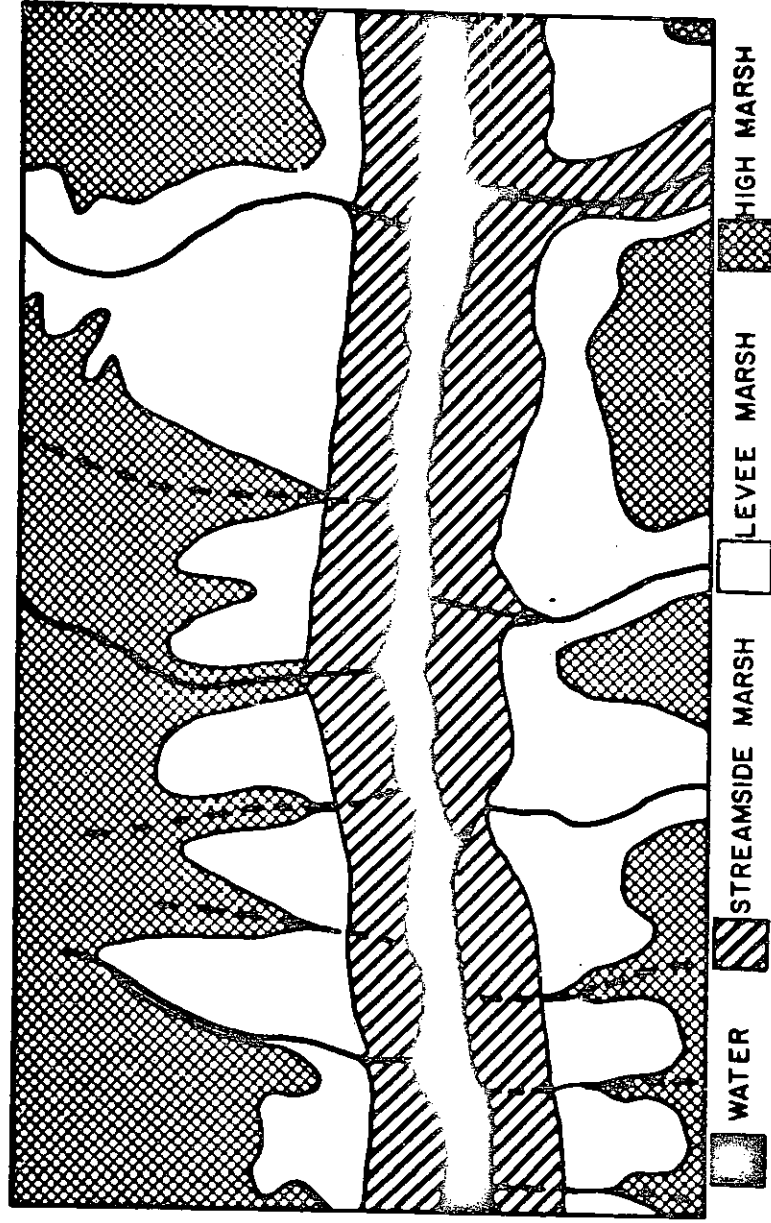


Figure 4. Drainage pattern and marsh types of a high marsh area, drawn from an aerial Kodachrome. Exposed mud banks are narrow or absent along this section of tidal creek. Scale, approximately 1:1100.

Figure 4 is at "C" in Figure 1. Notice the modified pinnate drainage in which the small streams meet the larger stream at nearly right angles. Several small tributary streams are large enough to develop levees, but only one has a streamside marsh. Most of the small creeks are short and do not penetrate far into the high marsh. Creeks in high marsh areas are widely spaced and do not anastomose.

Middle. Middle marsh forms a continuum between the high marsh and streamside marsh. Compared with the high marsh, the middle marsh is lower in altitude, the substrate is not as firm, and the grass, while taller, usually grows in a sparser stand than in the other marsh types. The drainage is of an anastomosing type. During low tide there are usually at least a few millimeters of water standing on the middle marsh, while all of the water drains from the surface of the levee.

Since the middle marsh is a more subjective category than the other marsh types, a section of an actual transect, chosen to illustrate features of the middle marsh, is shown in Figure 5. The grass is distinctly taller than the high marsh grass, but not as tall as streamside marsh grass. The altitude is lower than either levee marsh or high marsh. Grass may grow in the lowest areas, but these shallow drainage channels may eventually become creeks, in which case the middle marsh would then be replaced by streamside marsh.

Figure 6 is drawn from an aerial Kodachrome of an area with an anastomosing creek pattern (located at "D" in figure 1). Many of the numerous creeks have well developed levees, so the levee marsh forms a large proportion of the total area shown. Even where creeks are not

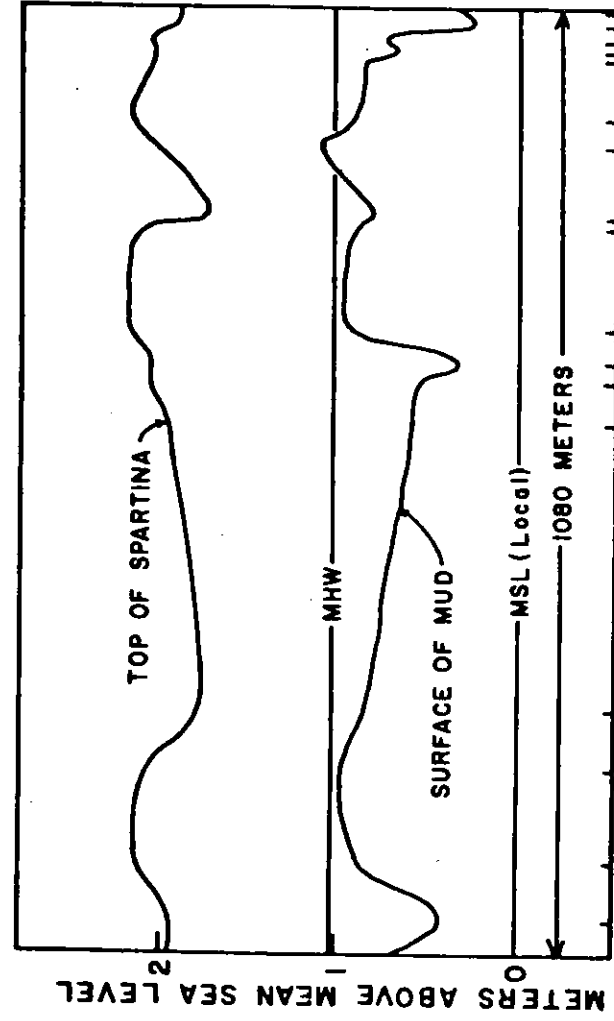
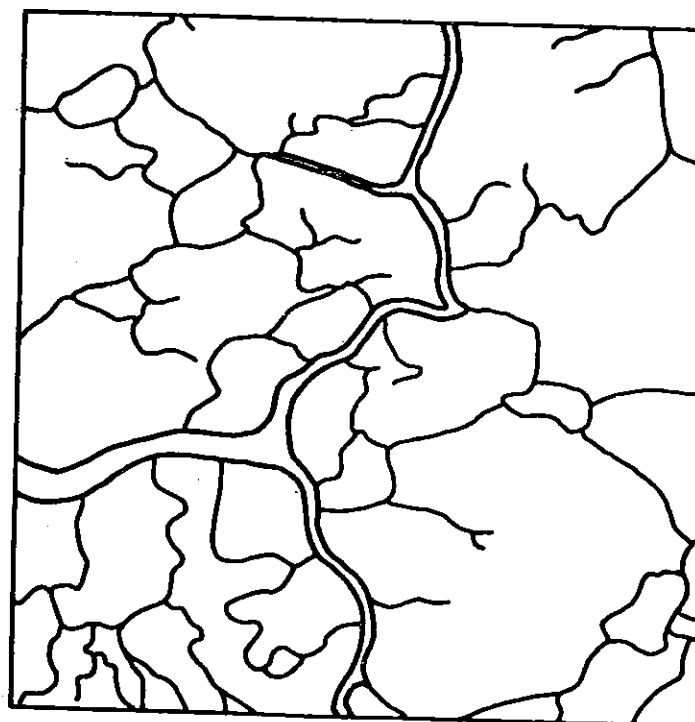


Figure 3. Transect of an area of middle marsh between "Boy's Camp" and Duplin River. August, 1956. The marks along the baseline are points at which altitude was determined.



SCALE 1:1525

Figure 6. Drainage pattern of a middle marsh area, drawn from an aerial Kodachrome.

actually shown in Figure 6, there are numerous smaller drainage channels, usually supporting Spartina of medium height and constituting middle marsh.

There is a tendency for extensive high marshes to occur at the seaward end of major drainages such as the Duplin River. The regions at the heads of creeks tend to be characterized by anastomosing drainages dominated by levee and middle marsh types.

Littorina is primarily an inhabitant of the high marsh, although young individuals may be found in the other marsh types. Orchelimum lives in the taller grass of the middle, levee and streamside marshes and is found but sparingly in the short grass of the high marsh.

THE NET PRODUCTION AND SEASONAL GROWTH CYCLE

OF SPARTINA ALTERNIFLORA

Seasonal curves for the standing crop of Spartina are shown in Figure 7 for the high marsh and Figure 8 for the streamside-levee marsh. Tables 2 and 3 give the Spartina standing crop, the biomass changes between samples, and the net production of high and streamside-levee marsh respectively. The first two and last two samples shown in Figure 7 are not included in Table 2 because the time interval between samples was too great for the calculation of net production.

Since the coefficient of variation is based on a normal distribution, it is desirable to demonstrate normality in the samples. By using "rankits" (Bliss and Calhoun, 1954), it is possible to test for normality in small samples, particularly where a series of comparable samples are available, as in the present case. Some typical rankits for the high marsh transect samples are shown in Figures 20 and 21, Appendix 1.

In the salt marsh tidal action tends to remove leaves and stems as they die or break off, especially in the streamside marsh. In the high marsh where grass is not removed rapidly, measurements of dead standing grass can be used to improve estimates of production when grass is growing and dying during the sample interval. The per cent underestimate in high marsh annual production which would have resulted if dead grass had not been considered, proved to be 26.6%, which

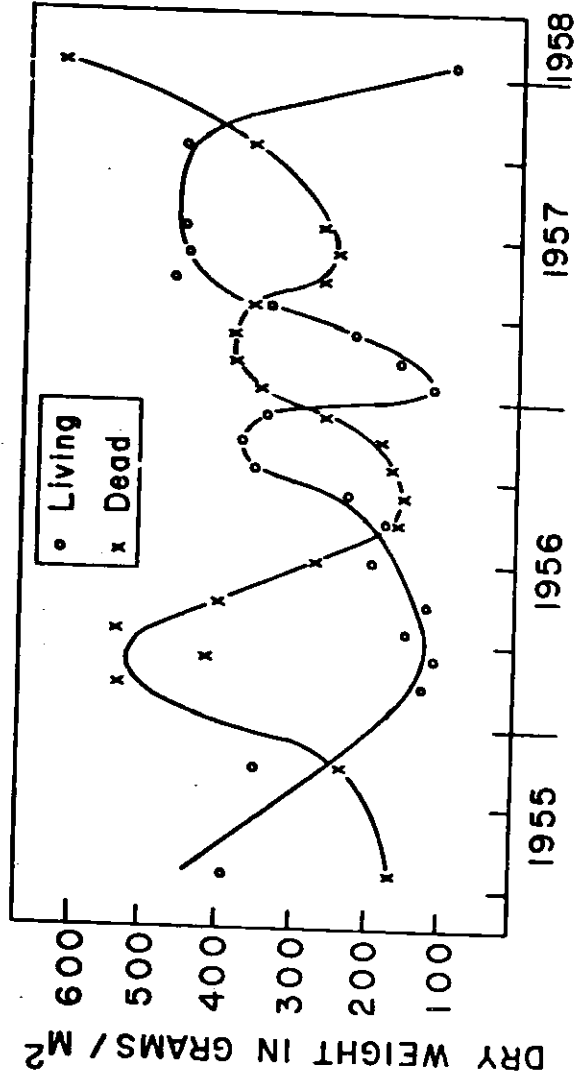


Figure 7. The standing crop of *Spartina* on the high marsh.

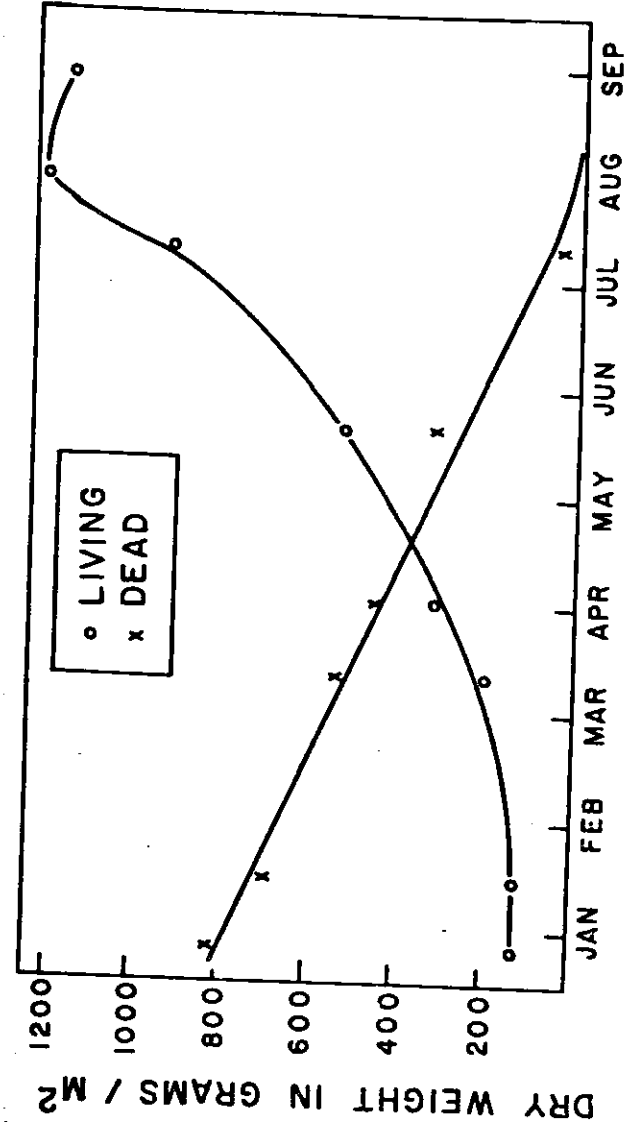


Figure 8. The standing crop of Spartina on the streamside-levee marsh in 1957.

Table 2. Net production of Spartina on the high marsh in grams dry weight per square meter. V is the coefficient of variation.

Sample Date	Standing Crop Living	Standing Crop V	Standing Crop Dead	Change V Living	Change Dead	Net Production	Net Production/Day
II:11:56	131.0	20	546.0	24			
III:14:56	118.9	34	427.5	32	-12.1	0.0	0.0
IV:17:56	153.2	74	545.6	44	34.3	152.4	4.5
V:14:56	125.9	70	404.0	44	27.3	27.3	1.0
VII:3:56	203.6	43	278.2	39	77.7	77.7	1.6
VII:9:56	183.5	44	166.9	39	-20.1	0.0	0.0
IX:11:56	236.7	43	159.5	36	53.2	53.2	1.6
X:14:56	363.0	42	176.1	42	126.3	142.9	4.3
XI:10:56	377.8	23	195.2	23	14.8	33.9	1.3
XII:18:56	342.3	27	269.1	34	-35.5	38.4	1.0
I:24:57	120.5	42	354.0	40	-221.8	84.9	0.0
II:23:57	165.1	39	386.1	44	44.6	76.7	2.6
III:14:57	227.0	50	390.3	29	61.9	66.1	3.5
IV:23-24:57	342.6	25	366.7	27	115.6	115.6	2.9
V:20:57	472.1	41	275.1	25	129.5	129.5	4.9
VI:17:57	456.7	24	252.4	28	-15.4	0.0	0.0
VII:18:57	462.3	32	274.5	44	5.6	27.7	0.89

Mean annual net production for the period II:11:56 to VII:18:57 643.2

Table 3. Net production of Spartina on the streamside-levee marsh in grams dry weight per square meter.

Sample Date	Standing Crop Living	Standing Crop Dead	Change Living	Change Dead	Net Production	Net Production/Day
I:9:57	132	830				
I:29:57	134	696	2	-134	2	0.1
III:26:57	219	549	85	-147	85	1.5
IV:16:57	328	461	109	-88	109	5.2
VI:4:57	537	332	209	-129	209	4.3
VII:23:57	947	61	410	-271	410	8.4
VIII:13:57	1230	0	283	-61	283	13.5
IX:11:57	1180	0	-30	0	0	0.0
Total Net Production from I:9:57 to IX:11:57						1091

is, of course, a minimum value. Because of the more rapid removal of dead grass from the streamside-levee marsh, production rates shown in Table 3 are underestimates. Since the pattern of growth and death of leaves and stems is similar throughout the marsh, the same correction (26.6%) is applied to the streamside-levee marsh as had been found necessary in the high marsh, in order to account for grass which died during the sample periods. It is also necessary to estimate growth during the fall when no measurements were made. In the high marsh approximately one-third of the growth occurred during the fall months, and we may assume that a similar percentage of growth occurred in the other marshes. The corrected net production for the streamside-levee marsh is thus approximately 2240 grams/square meter/year.

Table 4 shows results of experiments in which quadrats of medium height *Spartina* were clipped and checked for re-growth approximately one month later. Re-growth was greater during spring and early fall than during the mid-summer. A mid-summer depression in growth was also evident in the high marsh (Fig. 7, Table 2) but not in the streamside marsh.

The results of measurements of caloric content of *Spartina* are shown in Table 5.

Table 4. Spartina production (grams dry weight per square meter) in an area of Levee Marsh. On each of five dates (first column), a square meter of undisturbed Spartina was clipped and regrowth measured approximately one month later.

Date Clipped	Date Reclipped	Days Elapsed	Yield	Net Production/ Day
April 5	May 9	34	91.0	2.7
May 9	June 6	28	31.6	1.1
June 6	July 12	36	28.0	0.78
July 12	August 7	26	7.1	0.27
August 6	September 14	39	35.3	0.91

Table 5. Caloric content of Spartina alterniflora.

Date Collected	Plant Part	Test Number	Gram-calories per gram
VIII:27:55	Stems (Dead)	1	3765
		2	3789
IV:27:55	Entire Plant	1	4078
		2	4075
VIII:22:56	Leaves Only	1	4091
		2	4101
		3	4180
VIII:14:55	Leaves Only	1	4016
		2	4178
VIII:20:55	Entire Plant	1	3968
		2	4021
		3	3996
Mean (Living only)			4070
Mean (Total)			4022

THE ENERGY FLOW OF TWO INVERTEBRATE COMPONENTS
OF THE SALT MARSH ECOSYSTEM

LITTORINA IRRORATA: AN AUFWUCHS-DETRITUS FEEDER

Methods of Determining Population Density

A transect was established on a section of marsh where the Spartina was short and the marsh altitude high (about seven feet above Mean Low Water). Ten poles were placed ten meters apart in a straight line. Subsequent experience proved that the transect was representative of the high marsh. Spartina and Littorina were sampled from the same quadrats.

Each month all the snails were removed from a quadrat 0.10 square meters in the vicinity of each pole. Care was taken not to locate the quadrat in an area which had been trampled during the previous sampling period. To minimize bias on the part of the investigator, the quadrat was always located at the same place relative to the marker for a given sample.

The large snails were removed to containers in the field; the grass was then clipped and taken to the laboratory where the small snails were carefully separated from the marsh grass. The first samples obtained had to be discarded, since it takes some experience to separate effectively the very small snails, but with experience, it is believed that few, if any, snails were missed. The maximum shell

length of each snail was then measured with vernier calipers.

The class intervals used in measuring snails were 0.5-1.49 mm.; 1.5-2.49 mm.; etc.

Life History and Behavior

General distribution: Littorina irrorata Say is the common salt marsh periwinkle of the South Atlantic and Gulf coasts of the United States. The genus Littorina is world-wide in distribution, and so far as is known to the writer, all the species in the genus are intertidal forms.

In the marshes of the Georgia coast, Littorina is restricted to areas covered with Spartina or Juncus roemerianus Scheele. Littorina is never found on the mud border at the edge of creeks and only a few small individuals are found in the dense stands of tall Spartina which characterize the streamside marsh (Figure 4). Snails are most common on the marshes of high altitude where there may be large areas of short Spartina which are not adjacent to creeks (Figures 3 and 4).

Behavior: Littorina shows marked differences in behavior which coincide with tidal cycles. During periods of spring tides, when the high marsh is flooded twice each day, the snails are active; almost all of them will have their foot out of the shell. During prolonged neap tides, when the marsh is relatively dry (or perhaps one should say "less wet"), most of the snails will withdraw their foot and remain attached to the Spartina by a few weak strands of dry mucus. On one occasion, on a marsh which is slightly over two meters above Mean

Low Water, dormancy was observed to persist for eight days. In the sense of Allee, et al. (1949), dormancy during a dry season is called aestivation; neap tide dormancy of Littorina meets this definition except for the relatively short time period involved. Numerous observations show that snails remain active above about 10 degrees Centigrade if the marsh is flushed daily by the tides. The mean monthly temperature during the study period never dropped below 10 degrees (Table 27, Appendix 4).

A seasonal periodicity in behavior has also been observed. During the summer, the snails crawl up on the Spartina, and are one of the conspicuous features of the marsh. During cold weather, they descend to the floor of the marsh, usually remaining clumped about the base of the grass stems when they are not feeding.

Reproduction: The sexes are separate in Littorina irrorata. The anatomy of the reproductive system is similar to that of Littorina littorea L. (Linke, 1933).

The first indication of the breeding season during 1957 was noted on April 24 when a change in color of the prostate gland from a chocolate brown to a bright pink was observed in a male. On May 13, a female with a swollen albumen gland was examined. Subsequently the ovaries of the female and the seminal vesicle of the male became swollen and conspicuous. The penis enlarges, although unlike many prosobranchs, it is present throughout the year in Littorina irrorata. The period of gradually increasing glandular activity is quite long. Snails were first observed copulating, in the marsh, on June 12. The first eggs seen were spawned on July 8 by snails in the laboratory.

Thus 26 days elapsed between observations of copulating and spawning.

The eggs and larvae of Littorina irrorata are planktonic. The eggs are perfectly spherical, and thus differ from the helmet-shaped eggs of L. littorea. The veliger larvae are similar to those of L. littorea but lack pigment on the velar lobes.

Larvae of Littorina were identified (1) by comparing larvae in the plankton with those which developed in the laboratory (none was reared to maturity) and (2) by comparing larvae with figures of the larvae of Littorina littorea. Littorina irrorata is the only littorinid snail occurring in the Sapelo Island region; no other species of snail larvae were observed in the summer plankton of tidal creeks.

Larvae could be found in the plankton from a tidal creek from July 8 until the end of August. The writer was absent from the laboratory for a three week period in September and by the end of September the larvae had disappeared from the plankton.

Early life in the marsh: The young snails enter the marsh from the plankton from July to October. They possess from $3\frac{1}{2}$ to 4 nuclear whorls. The smallest Littorina observed on the marsh were in the size range of 0.8 to 1.0 mm. Small Littorina have never been found on the surface of the mud. They spend the early part of their lives exclusively within the curled-up leaves of Spartina plants, or between the leaves and stem. It is not known whether they settle directly on the Spartina plants or on the mud, later crawling up the plants. In either event, they probably remain on the first plant encountered, at least for the first nine to twelve weeks of their

life. It has been repeatedly observed that large, vigorous young plants will harbor few young snails, while dead standing grass from the previous year may contain numerous small snails. Snails are usually four to five millimeters long before they are found on the outside surface of the grass or on the surface of the mud.

Distribution in different marsh types: Table 6 shows the distribution of different sized snails in two marsh types. In the high marsh, there is a peak in the frequency distribution at both the 0-5 millimeter size and the 15-21 millimeter size. On the other hand, the large snails are almost completely absent in the middle marsh. Apparently recruitment is similar in both marsh types, but snails fail to survive in the levee-middle marsh. In the high marsh, survival is sufficient to maintain a dense population of large snails.

Two interesting characteristics of snail distribution as shown by Table 6 are (1) snails are generally absent near creeks, so the areas of anastomosing drainage, where any location in the marsh is close to one or more creeks, are areas of low snail population density and (2) the small snails disappear as soon as they are large enough to leave the protective cover of the Spartina. Although no direct evidence is available, the above observations suggest that predation by animals which enter the marsh during high tide may influence the distribution of snails.

Table 6. Size distribution of Littorina in two marsh types, (1) high marsh, poorly flushed (Barn Creek), (2) levee-middle marsh, well flushed (Jack Creek). Figures are numbers of individuals/meter square.

Locality	Date	Total shell length in millimeters			
		0-5	6-10	11-15	16-21
Barn Creek	May 14, 1955	507	17	33	182
Jack Creek	May 22, 1955	388	5	2	2

Population Density

The results of the monthly samples on the High Marsh study area for a 21 month period from February, 1956 to October, 1957 are shown in Table 19, Appendix 2. Samples were not obtained in June and July, 1956, nor in August and September, 1957. To illustrate trends in population density and snail growth, frequency distributions for four samples distributed over the study period are shown in Figure 9.

In every sample, there is a peak in the frequency distribution caused by the presence of a group of large snails. The population has been divided, somewhat arbitrarily, at 13.5 millimeters, and the two resulting groups referred to as "small" snails and "adult" snails. The adult snail population is characterized by low mortality and the mean size does not change with time, remaining constant at 17.71 ± 0.28 millimeters. The snails are probably growing, but growth is slow, and during the study period recruitment was low, as can be seen from the very low frequency of 12-14 millimeter snails (Table 19, Appendix 2); it is entirely reasonable that any mortality of large snails which did occur was balanced by a low rate of recruitment. The clear division of the population into small and adult snails suggests that the two population segments can best be treated separately, and this course is followed.

Turning now to the small snails in February, 1956, it can be seen from Figure 9 that there is a marked peak in numbers at the two millimeter size class. Since small snails also appeared on the marsh in October, 1956 and October, 1957 (Table 19, Appendix 2), the time of

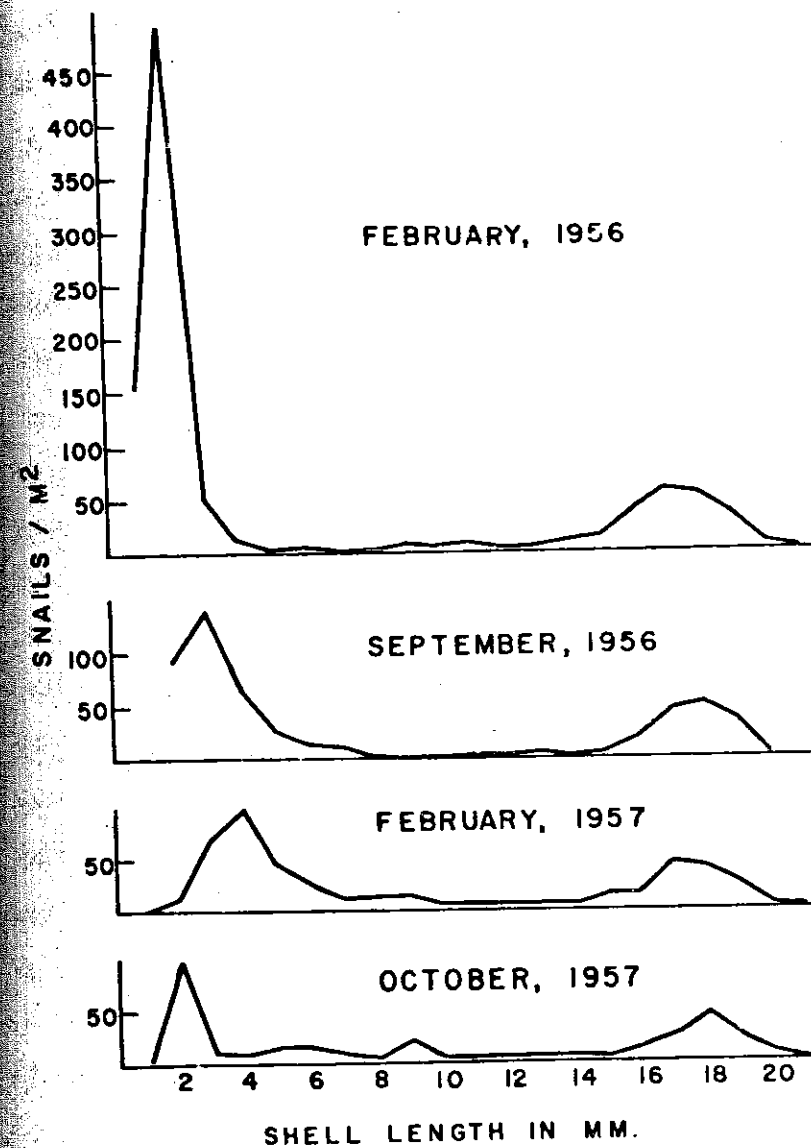


Figure 9. Size distribution of a *Littorina* population over a 21 month period.

recruitment can be set in October. The peak of small snails in February, 1956 may then be attributed to recruitment in October, 1955. The large numbers of two millimeter snails in February, 1956 are thus assigned to the 1955 year class.

From these data it is also possible to infer that recruitment into the marsh from the plankton in 1954 was very poor, assuming no catastrophic mortality. In September of 1956, the peak of the 1955 year class is at 3 millimeters, with a strong "tail" extending to about seven millimeters. The curve for February, 1956, drops quite abruptly from the two millimeter peak. The absence of the three millimeter peak indicates a dearth of snails from the 1954 year class. As can be seen from the curve for February, 1957, it is likely that recruitment in 1954 was of the same order as recruitment in 1956. With these facts in mind, the peak in numbers of small snails in February, 1956 may be assigned entirely to the 1955 year class with the possibility of only small errors, and it becomes practical to follow the growth and mortality of the 1955 year class by inspection of the frequency distribution.

The advent of the 1956 year class in October of that year increased the difficulty of distinguishing the limits of the 1955 year class. The snails were accordingly measured to the nearest 0.10 millimeter instead of the nearest 1.0 millimeter. The results of the October, 1956 sample (Table 7) shows the ease with which the two year classes can be separated when one of them is newly recruited. By the following July (1957), the year classes have become more difficult to separate (Table 8). However, if the population is followed month by

Table 7. Size distribution of small Littorina irrorata from high, short-Spartina marsh. October, 1956.

Length in millimeters	Quadrat									
	1	2	3	4	5	6	7	8	9	10
1.0										
1.1							1			
1.2		2								1
1.3		1								
1.4		1			1					
1.5		1						1		
1.6	1	1				1				
1.7						1				
1.8						1				
1.9										
2.0										
2.1										
2.2										
2.3				2				1		
2.4		1		1	4	1			1	1
2.5				1		1		2		2
2.6			1	3	3	2			1	1
2.7	1			2	3	2	1		1	1
2.8		1		1	3	3	2	1	1	2
2.9	1	1	3	2	2	1	1	2	2	
3.0	1	1	1	2	2	5	1		1	3
3.1			1	1	5				1	
3.2	1	1	1	5	3	3			3	1
3.3						3	2	1	1	
3.4	2	2				2			1	

Table 8. Size distribution of small Littorina irrorata from high, short-Spartina marsh. July 18, 1957.

Length in millimeters	Quadrat									
	1	2	3	4	5	6	7	8	9	10
2.2										
2.3				1	2					
2.4					2					
2.5										
2.6					1	1				
2.7				1	1			1		
2.8				2	1					
2.9	2		1			1				
3.0		1	1		2					
3.1	1	1		1	1	1				
3.2		1		2	1					1
3.3				1		1		1		
3.4				2	1					
3.5			1	2	4					1
3.6			1							
3.7				1						
3.8			2	2	1		1			1
3.9		2			1			1		
4.0			1		1			1		
4.1										
4.2				1	1		1			
4.3										1
4.4			1					1		
4.5				1	2			1		
4.6						1			1	1
4.7	1				2			1		
4.8					4				1	
4.9				5	1	1			2	1
5.0					1	1		1		
5.1										
5.2	1		1			1				1
5.3	1				1					
5.4				1						
5.5	1	1		1	1	1		1	1	
5.6	1		2	2	1			1		
5.7					2	2	1			
5.8		1	1		3	1				
5.9	1				2	2		1		1

month and if the samples are carefully compared with other years, quadrat by quadrat analysis can extend the period of year class recognition. Increasing size variation with increasing age eventually forces abandonment of the frequency distribution inspection method of separating year classes. A similar method of analysis was used by Moore (1937) for Littorina littorea.

Population Density and the Growth Rate of Snails

The population density of the 1955 year class was consistently greater in the middle of the transect than at either end. Associated with population density differences was a difference in the mean size of individuals. To illustrate these phenomena, population density and mean size are broken down into three groups along the sampling transect, as shown in Tables 9 and 10. The mean size of the first two groups, which differed most, are plotted against time in Figure 10. For the sake of clarity of illustration, Quadrats 7-10 are omitted from Figure 10; however, from Table 9, it can be seen that the mean sizes for Quadrats 7-10 would, with one exception, fall between the two curves in Figure 10, after May, 1956. It is readily seen that the quadrats with the higher population density (4-6), had a lower growth rate than the low density quadrats (1-3). The difference between the mean size was more than twice the standard error of the difference for both October, 1956 and July, 1957.

The relation between size and population density was tested further by calculating a correlation coefficient between mean snail

Table 9. Mean size in millimeters of the 1955 year class of Littorina in three sections along the sampling transect, from February, 1956 to October, 1957.

Sampling Period		Quadrats			Total
		1-3	4-6	7-10	
1956	F	1.87	1.88	1.92	1.89
	M	2.00	2.11	2.13	2.09
	A	2.02	2.18	2.33	2.17
	M	2.24	2.39	2.28	2.34
	J	-	-	-	-
	J	-	-	-	-
	A	3.44	2.61	2.98	2.95
	S	3.71	3.16	3.72	3.44
	O	4.53	3.91	4.00	4.11
	N	5.11	4.62	4.84	4.78
	D	5.23	3.92	4.55	4.38
	J	5.16	4.32	4.72	4.58
1957	F	5.55	4.76	4.83	4.92
	M	5.74	4.78	5.22	5.16
	A	5.63	5.10	5.22	5.33
	M	6.95	5.83	6.78	6.38
	J	7.67	6.23	6.41	6.57
	J	7.50	5.92	6.80	6.51
	A	-	-	-	-
	S	-	-	-	-
	O	8.65	7.16	8.49	8.06

Table 10. Population density of 1955 year class of Littorina divided into three sections along the sampling transect. The numbers for quadrats 7-10 are adjusted to the same area as the other two sections, or 0.3 square meter (numbers in parentheses).

Sampling Period	Quadrats			Total
	1-3	4-6	7-10	
1956 F	138	356	219(164)	713
M	134	275	191(143)	600
A	163	233	145(109)	541
M	131	256	120 (90)	507
J	-	-	-	-
J	-	-	-	-
A	81	169	123 (92)	373
S	77	177	107 (80)	361
O	81	162	113 (85)	356
N	94	160	90 (68)	344
D	69	180	152(114)	401
1957 J	44	145	97 (73)	286
F	53	137	107 (80)	297
M	69	141	85 (64)	295
A	57	104	34 (70)	255
M	62	124	107 (80)	293
J	51	132	63 (47)	246
J	51	115	59 (44)	225
A	-	-	-	-
S	-	-	-	-
O	31	37	35 (26)	103

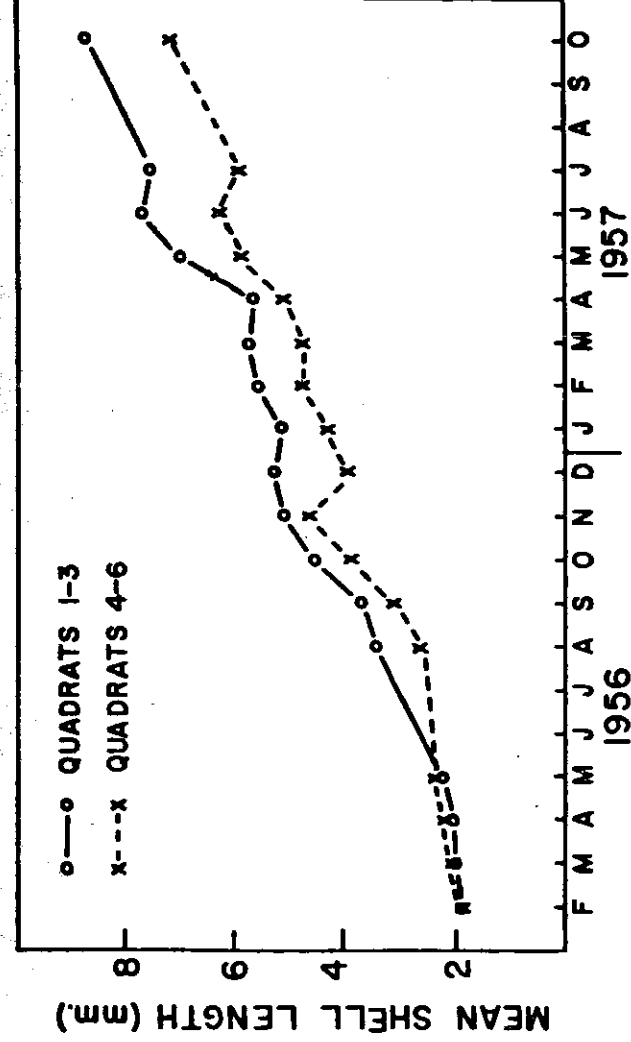


Figure 10. Size differences between Littorina of the 1955 year class from two sections along a sampling transect.

size and population density for 180 quadrat samples, representing all of the samples taken over the two year study period. Only the adult snails were considered, in order to minimize the effects of growth and mortality. The resulting coefficient was -0.27 , which is significant at the 0.1% level by "Students" t -test, and demonstrates an inverse relationship between individual size and population density.

The foregoing observations, together with the likelihood, already discussed, that small snails stay in the same place during the early part of their lives, show that factors important in "setting" will, in part, influence both the population density and individual size of Littorina. If few snails settle, they grow rapidly; if many settle, growth per snail is slower.

Mortality

Figure 11 shows that a straight line regression of the population estimates for the 1955 year class gives a reasonable picture of mortality between February, 1956 and October, 1957. A linear relationship between survivors and time is not typical of animal populations (Deevey, 1947), but it must be remembered that the data in Figure 11 are from a segment of a much longer life span, with neither the very young nor the very old individuals represented.

The mortality rate for the period studied, calculated from the regression equation, was 23.94 snails per square meter per month. The regression was calculated from total survivors, which requires the assumption that mortality was evenly distributed among the various

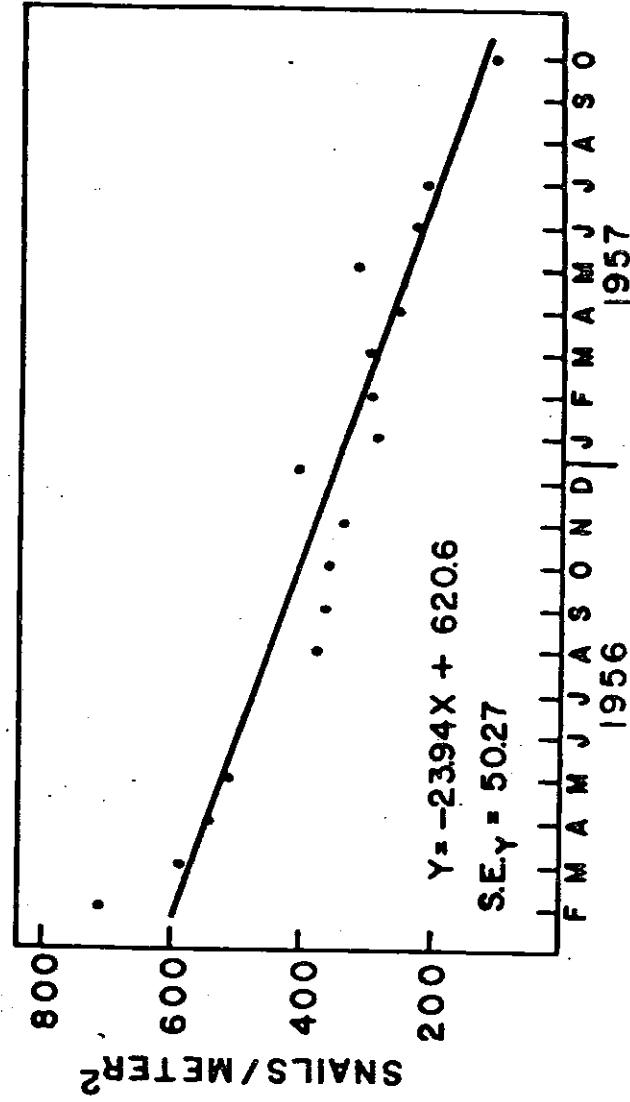


Figure 11. Survivorship curve of the 1955 year class of Littorina.

size classes of snails in the 1953 year class.

A similar survivorship curve was fitted to the population density of the adult snails (Figure 12). Here the fit is not so satisfactory, but nevertheless the use of a regression seems the best way of obtaining an average, integrated rate, since it is apparent that very few snails were entering the adult class during the period studied.

Mortality rate of adult snails, calculated in this manner, was 2.8 per square meter per month.

Production

The cube root of the dry body weight of Littorina is directly proportional to the total shell length (Figure 13). The regression equation of Figure 13 was used to convert census data to body weight of the snails. The weight in turn was converted to calories on the basis of the caloric content of Littorina which is given in Table 11. A mean of the calorimetric determinations was used since there is no evidence that the caloric content of Littorina varies with age. By means of these conversions, the production of Littorina can be given directly in calories.

Table 12 shows the results of production calculations. The growth of surviving snails is the difference in caloric content of the survivors of the 1953 year class from the beginning to the end of the study period. Mortality is the sum of the caloric content of the snails which died in each sampling period, less their caloric content at the beginning of the study period. A more detailed account of

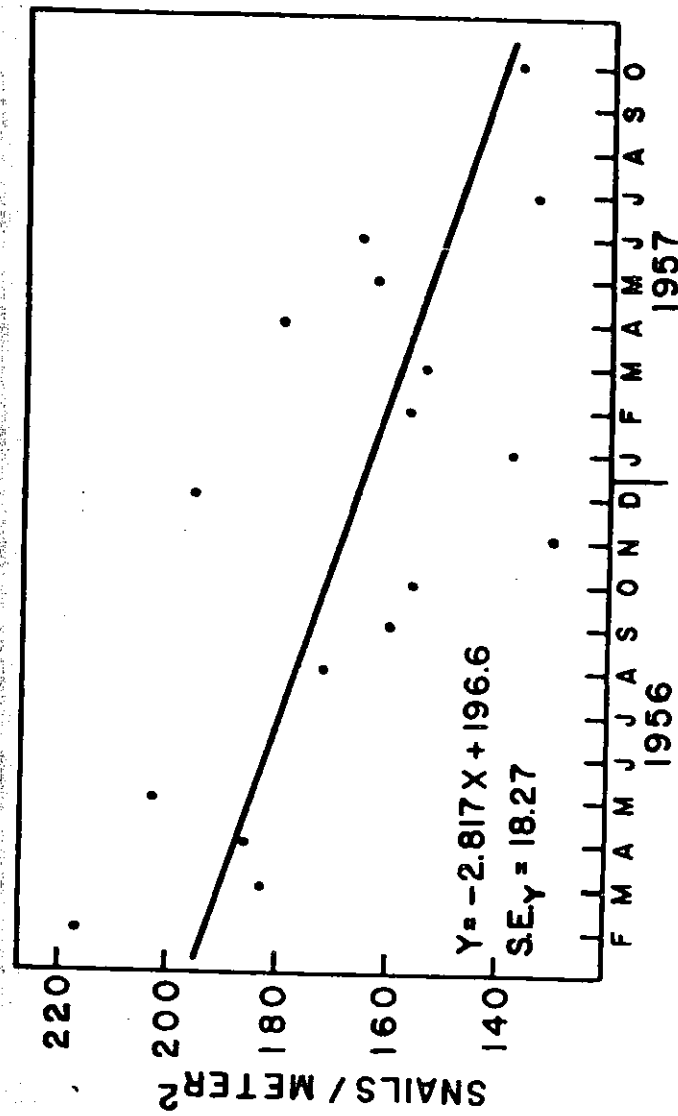


Figure 12. Survivorship curve of adult Littorina.

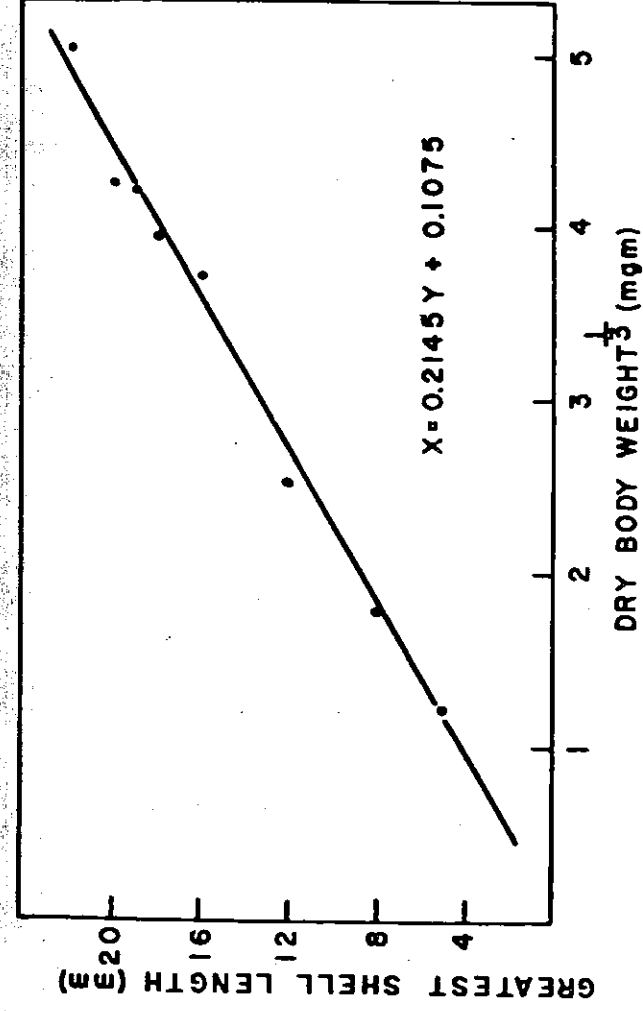


Figure 13. Relationship between body weight and total shell length of Littorina. Each point is the mean of ten or more determinations.

Table 11. Caloric content of Littorina.

Mean length of snails (mm)	N	Total dry weight (gms)	Gram cal/gm
11.9	11	0.2089	4390
11.9	11	0.2183	3972
11.9	11	0.1984	4219
15.1	6	0.2188	4301
14.9	6	0.2467	4062
14.9	9	0.3215	4205
17.0	3	0.1232	4153
18.0	3	0.1411	3828
18.0	3	0.1492	3359
21.4	3	0.2363	4156
21.2	3	0.2480	4065
21.9	3	0.2747	4205
Total.....72			Mean.....4076

Table 12. Energy flow in a population of Littorina from February, 1956 to October, 1957, in kilogram-calories per square meter per year.

		1955 year class	1956 & 1957 year class and small snails of undetermined age	Adults
A. Production				
1.	Growth of Surviving snails	1.50		
2.	Mortality	1.97		
	Total Production	3.47	2.09	
B.	Respiratory Energy Loss	21.9	7.48	253
C.	Assimilation	25.4	9.57	
D.	Respiration/Assimilation x 100	86.2%	86.2% (1)	

(1) Respiration/Assimilation assumed to be the same as 1955 year class and the production calculated from known respiratory rates and this ratio.

calculations may be found in Appendix 4.

There was no discernible growth in the adult snails, and recruitment, as previously noted, was either zero or was too small to balance the mortality which is shown in Figure 12. Therefore production of this group of Littorina was considered to be essentially zero during the study period.

Calculation of production in the remaining groups of snails ("1956 & 1957 year class and small snails of undetermined age" in Table 12) must await further analysis of the 1955 year class.

Energy Utilization

The rates of oxygen consumption for different sizes of snails is shown in Figure 14. The oxygen consumption values for each millimeter size class of snails were multiplied by the number of snails of that size class in each monthly sample. The resulting rates of oxygen consumption for the individual size classes were added and converted:

- (1) to a monthly basis.
- (2) to the mean monthly temperature from the nearest U. S. Weather Bureau station, according to a regression of temperature against respiratory rate (Figure 22).
- (3) to calories by Ivlev's oxycaloric coefficient. The sum of the oxygen consumption rates obtained were converted to a yearly basis and are given in Table 12. The energy utilization figures in Table 12 are somewhat high, since, in converting to an annual basis, respiratory rates at summer temperatures are given more weight than winter

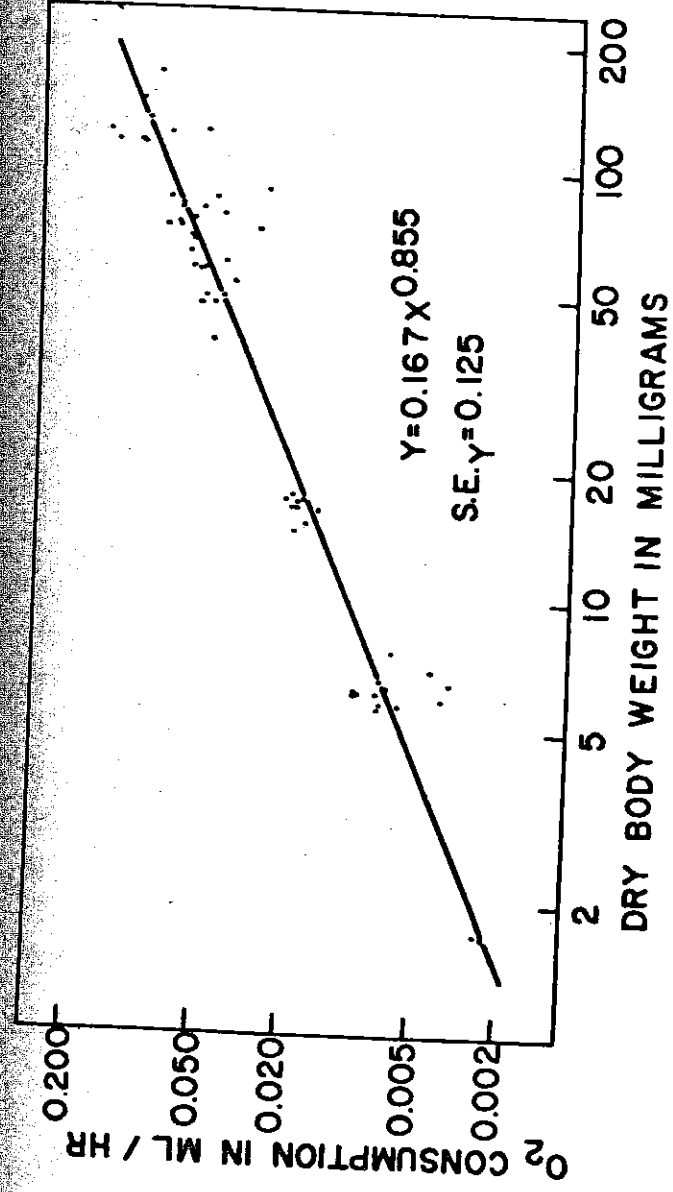


Figure 14. Oxygen consumption of different sizes of *Littorina* at 30 degrees centigrade.

respiratory rates, since part of one winter is not included in the 21 month study period.

These calculations are given in detail in Appendix 4.

To find production in 1956, 1957 and undetermined year classes, a Respiration/Assimilation ratio of 86.2% was calculated for the 1955 year class (Table 12). Assuming that this ratio was the same for all the small snails, the production was calculated from the energy utilization figures for the small snails.

Ingestion

Rates of ingestion or defecation were not determined directly for Littorina. However, North (1954) gives a (production/organic matter defecation) ratio of 11% for Littorina planaxis Philippi. Returning to Table 12 and considering only the 1955 year class, an 11% production/defecation ratio would result in an estimate of 31.5 kilocalories/year organic matter passing through the gut. Assimilation plus defecation would yield an estimate of 56.9 kilocalories/year/square meter, which is approximately equal to ingestion. The growth efficiency (E_g or production/assimilation) would then be 13.7%. The assimilation efficiency (E_a or assimilation/ingestion) would be 44.6%.

ORCHELIMUM FIDICINIUM: A PRIMARY CONSUMER

Certain insects appear to be the only primary consumers which feed directly on the living marsh grass. During the summer, Orchelimum is the most conspicuous of the herbivorous insects, and the only abundant Orthoptera of the marsh. Orphulella sp. occurs near the border of the marsh and the terrestrial vegetation. During the winter months the herbivorous leafhoppers, Prokelesia marginata Van Duzee and Liburnia detecta Van Duzee (Homoptera:Fulgoridae) are abundant, persisting as adults in smaller numbers through the summer. Also suspected as Spartina consumers are a somewhat less abundant beetle of the family Mordellidae (absent in winter) and the larvae of two flies, Chaetopsis aenea (Wied.) and C. apicalis Johns. (Diptera: Otitidae) (present throughout the year). Adult Diptera of the family Ephydriidae are common in the marsh, and are said to feed on algae; the larvae may be herbivorous (Wirth and Stone, 1956).

Orchelimum fidicinium first appears on the marsh in late April and largely disappears by mid-August, although scattered individuals persist into September. Although generally widespread over the marsh, the populations of the high marsh are of low density.

Population Density

During the summer of 1957, sweep samples were taken at regular intervals in an area of Middle Marsh and Levee Marsh on Sawmill

Creek (Figure 6).

Usually five samples of 25 sweeps each were taken at intervals of from four to six days. Successive samples were not taken in the same place, because of the possibility of depleting the population. So far as was possible, similar areas were chosen on the basis of marsh altitude and Spartina height and density, but the sampling was not random. Since no systematic relationship between the appearance of the marsh and the density of the Orchelimum population could be discerned, this procedure had an element of randomness, as long as efforts were confined to the middle-levee marsh types.

The samples were taken to the laboratory, the grasshoppers killed and counted, and the total length of individuals and the dry weight of each size class recorded. The results of these samples are shown in Table 22, Appendix 3. The use of five millimeter intervals is arbitrary, and does not bear a known relationship to size at various instars. The sample dates are the midpoints of the sampling intervals. When more than five samples were taken, the results were adjusted to five samples. Small numbers of grasshoppers are usually seen in late August and early September, but they are too few to appear in routine sweep samples.

To convert the results of sweep samples to numbers per unit area, a modification of the method used by Beall (1935) and Cross (1957) was adopted. A cage, one meter square and 30 inches high, covered on the top and sides with fine mesh copper screening, was constructed. The cage was held between two men, who then ran over the marsh, and at a signal, placed the cage sharply down on the ground. The grasshoppers

were picked out and counted. They were immediately released, to minimize disturbance of the population. The cage samples were then compared with sweep samples taken on the following day. The results are shown in Table 13. The cage and sweep samples were combined, resulting in conversion factors of 0.78 and 1.66 square meters/sweep sample for nymphs and adults respectively.

There is probably a behavioral difference between nymphs and adults which results in the sweep sample being more efficient for adults. The winged adults tend to be herded in front of the person taking the sample, thereby becoming concentrated, whereas the nymphs tend to evade the oncoming net by hopping down into the thick growth of Spartina, where the most vigorous efforts of the sweeper fail to reach them. The difference between nymphs and adults found for Orchelimum in salt marshes are exactly opposite to those found by Cross (1956) for Melanoplus spp. in old fields. In spite of the high standard errors of the samples (Table 13), the nymph-adult difference is quite consistent and can be accepted with confidence.

The population density for each sampling interval was then found by applying the conversion factors in Table 13 to the sweep samples, and the results appear in Table 14.

Mortality and Production

The total population density, as shown in Table 14, decreases abruptly between May 18 and 22, and June 19 and 25. The percent of the different size classes was computed (Table 15), but there are no

Table 13. Estimates with a portable cage of the number of grasshoppers per unit area captured with a sweep net. Each cage sample with N of 12; each sweep sample with N of 10.

<u>Date</u>	<u>Grasshoppers/sample</u>				<u>Square meters/sweep sample</u>	
	<u>12 cage samples</u> (1 square meter each)		<u>10 sweep samples</u>		<u>Nymph</u>	<u>Adult</u>
	<u>Nymph</u>	<u>Adult</u>	<u>Nymph</u>	<u>Adult</u>		
July 22-23, 1957	2.00	3.17	2.20	12.80	1.10	4.04
Aug. 11-12, 1957	0.50	1.50	0.60	2.90	1.20	1.93
July 1-2, 1958	8.50	4.50	6.60	5.10	0.78	1.13
July 8-9, 1958	3.75	3.83	2.30	3.00	0.61	0.78
July 10-11, 1958, "A"	1.67	2.92	1.10	5.80	0.66	1.92
July 10-11, 1958, "B"	2.50	4.50	2.20	4.50	0.88	1.00
Totals	3.15±1.44	3.40±1.38	2.50±1.20	5.65±2.42	0.79	1.66

Table 14. Population density, in numbers per square meter, of Orchelimum in 1957.

Date	Size Class					Total	Standing crop in K-cal/M ²
	0-5	5-10	10-15	15-20	Adult		
May 13	37.4	17.4	-	-	-	54.8	1.94
18	28.2	36.9	0.3	-	-	65.4	3.09
22	5.1	17.7	0.3	-	-	23.1	1.34
27	3.8	23.6	1.3	-	-	28.7	1.90
Jun 3	1.8	7.9	10.3	1.3	-	21.3	3.25
7	0.5	9.2	15.1	3.1	-	27.9	4.81
11	0.3	7.2	9.7	5.1	0.5	22.8	4.61
15	1.0	9.0	10.3	3.6	1.0	25.4	4.69
19	-	9.2	12.1	8.2	1.7	31.2	7.04
19	-	7.2	8.7	6.7	1.8	24.4	5.72
25	-	1.8	4.6	2.8	1.1	10.3	2.70
Jul 1	-	0.8	3.6	1.5	1.2	7.1	2.01
5	-	0.3	3.1	1.5	3.1	8.0	2.94
9	-	0.8	2.6	3.8	5.9	13.1	5.29
16	-	-	3.3	1.0	9.6	13.9	6.41
23	-	-	1.5	1.3	7.7	10.5	5.10
30	-	-	4.6	0.5	7.0	12.1	5.03
Aug 12	-	-	0.5	0.3	1.8	2.6	1.22

Table 15. The percent of different size classes in an Orchelimum population throughout the life cycle.

Date	Size Class				
	0-5	5-10	10-15	15-20	Adult
May 13	68	32			
18	43	56	1		
22	22	77	1		
27	13	82	5		
Jun 3	9	37	48	6	
7	2	33	54	11	
11	1	31	43	23	2
15	4	35	43	14	4
19		30	39	26	5
19		30	36	27	7
25		17	45	27	11
Jul 1		11	50	22	17
5		3	39	19	39
9		6	20	29	45
16			24	7	69
23			15	12	73
30			38	4	58
Aug 12			20	10	70

consistent changes which show a correlation with the periods of high mortality. Thus, mortality associated with moults cannot be demonstrated; nevertheless, this does not provide conclusive evidence, since the size classes are arbitrary and do not necessarily correspond with instars. Since high tides might contribute to mortality by making the grasshoppers more vulnerable to predators, the Marine Institute's tidal records for the study period were examined, but again without disclosing any significant pattern. The irregularities in mortality rate, on the basis of incomplete evidence, are ascribed either to sampling variations or to recruitment which, as shown in Figure 19, may continue through May.

The seasonal distribution of different sizes of grasshoppers as shown in Figure 19 demonstrates that recruitment virtually ceases about the end of May, and probably before. Taking advantage of this distribution, and of the roughly concave form of the curve in Figure 19, the data were plotted as time against the logarithm of the population density (Figure 15). Although the regression of survivors is used here, as with *Littorina*, mainly for convenience in calculating production, a straight line with a logarithmic ordinate has ecological significance, since it implies that the mortality factor or factors are operating in a density-proportional manner (E. P. Odum, 1954).

Using the regression of Figure 15, mortality for each sampling period was computed. The mortality figures for each sampling period were then multiplied by the corresponding mean weight of the grasshoppers, which gave the weight of the grasshoppers dying in the

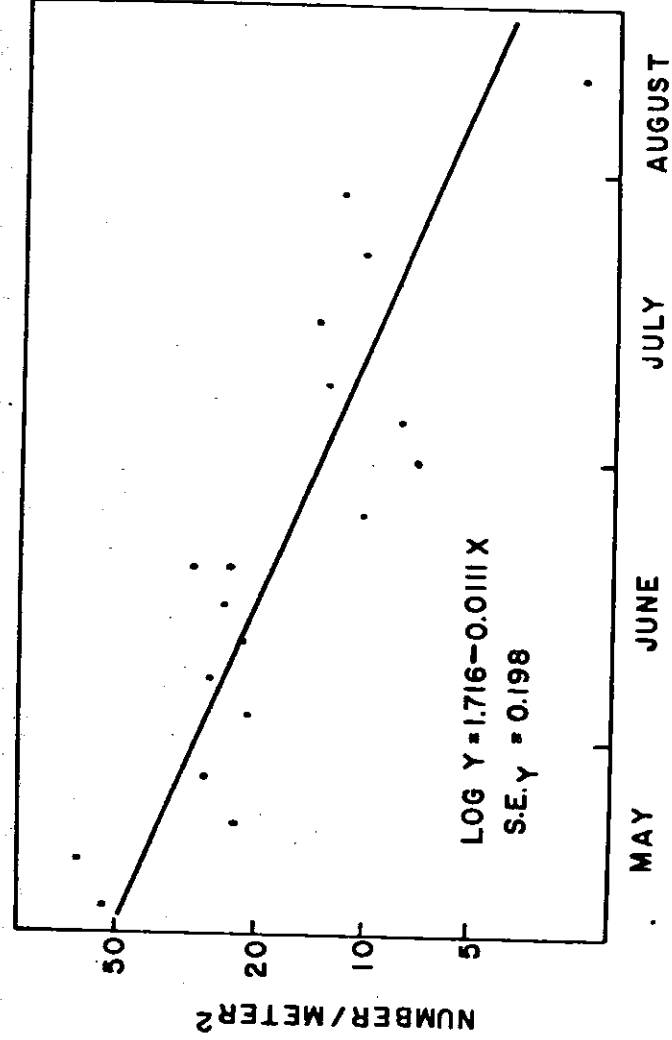


Figure 15. Survivorship curve of Orchelimum during the summer of 1957.

sampling period. Weight was converted to calories by means of the values in Table 16, which shows the caloric content of Orchelimum and of Orchelimum feces. The mean of these values was used, omitting the last figure because of the inefficiency of combustion associated with a small sample. There is no obvious relationship between grasshopper size and caloric content. The sum of the mortality figures expressed in calories per meter square is equivalent to yearly production, since all the grasshoppers die during a given annual cycle, and their caloric content at death equals the total organic matter added to the herbivore trophic level by their growth. The production of Orchelimum is thus 10.82 kilogram calories per square meter per year. The calculations are shown in greater detail in Appendix 3.

Referring again to the constants used to convert samples to an area basis, it may be seen by examination of the survivorship curve (Figure 19) that use of the same calibration figure for both nymphs and adults would have led to an unreasonably high late summer population of adult grasshoppers.

Energy Utilization

The energy used in the life processes of the grasshoppers and dissipated as heat was calculated from the population density (Table 14) and the oxygen consumption of different sized grasshoppers (Figure 16). No attempt was made to smooth the survivorship curve, as was done for computing mortality, since energy utilization may be

Table 16. Caloric content of Orchelimum and Orchelimum feces.

Size Class	N	Dry Weight (grams)	Gram-calories/ gram
Adult	3	0.4010	5682
Adult	3	0.4180	5717
Adult	3	0.3200	5527
Adult	3	0.3226	5432
15-20	4	0.2541	5773
15-20	4	0.2936	5822
10-15	3	0.0959	5302
5-10	20	0.2199	5033
0-5	20	0.0413	3802
Mean (last value omitted because of small sample).....			5536
Feces			3463
			3580
Mean.....			3522

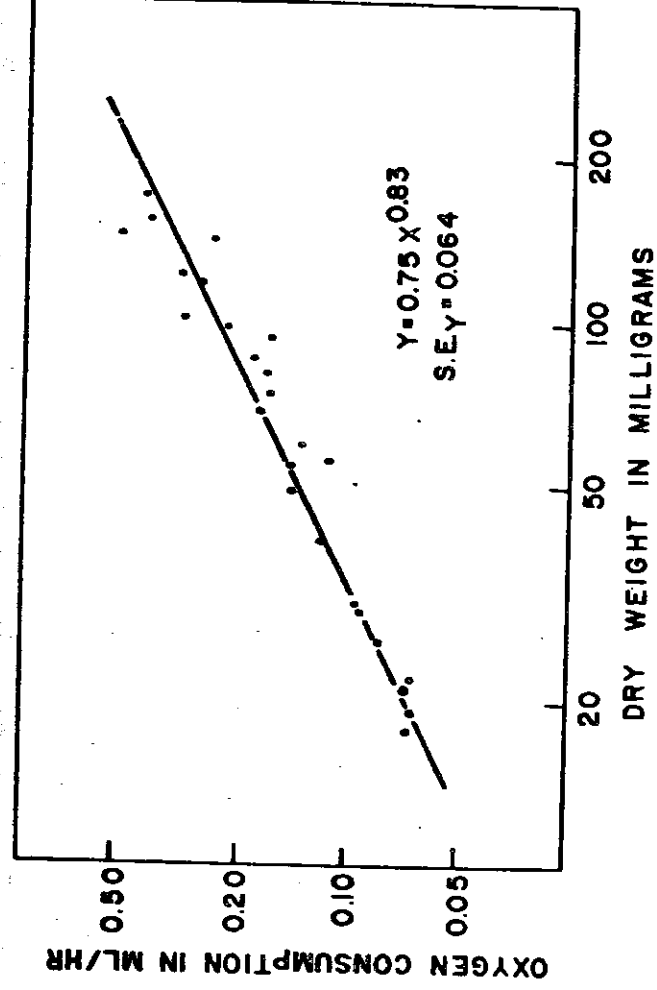


Figure 16. Oxygen consumption of different sizes of *Orchelimum* at 30 degrees Centigrade.

conveniently found from the raw data. The mean weights for the grasshoppers in each size class were found from the data in Table 22, Appendix 3. Respiratory rates were determined for grasshoppers of different sizes (Figure 16). The respiratory rate for each mean weight of the size classes was then found from the regression of weight against oxygen consumption, giving the mean oxygen consumption for a grasshopper in each of the size classes. These figures could then be multiplied by the number of grasshoppers in each size class on a given sampling date, as found in Table 14. The result for each sample was multiplied by the number of hours in the sampling period and corrected for temperature. The sum of these figures yields the total oxygen consumption during the life cycle of one generation of Orchelimum. Oxygen consumption was converted to calories by means of the appropriate oxycaloric coefficient (Table 1) to give a total energy utilization of 18.6 kilogram calories/square meter/year. When this figure is added to the annual production of 10.8 kilogram calories/square meter/year, an estimate of assimilation of 29.4 kilogram calories/square meter/year is obtained. A detailed account of the calculations may be found in Appendix 5.

Ingestion

The results of ingestion experiments with Orchelimum are shown in Table 17, with the data upon which they were based in Table 38, Appendix 5. The pooled assimilation efficiency was found to be 27.4%.

Table 17. Ingestion rates of Orchelimum, from ten experiments.

N subjects		Temp. corrected O ₂ consumption cal/hr/hopper	Assimilation cal/hr/ N hoppers (1)	Defecation cal/hr/ N hoppers (2)	Ingestion cal/hr/ N hoppers (2)	Assimilation Efficiency (%)
Nymphs	Adults					
	2	0.9342	2.95	7.04	9.99	29.5
14		0.7025	15.54	46.14	61.68	25.2
18		0.8223	23.38	71.14	94.52	24.7
11	10	1.266	20.00	65.16	85.16	23.5
	11	0.8401	14.60	30.29	44.89	32.5
8		1.300	22.59	36.98	59.57	37.9
		0.8218	10.38	18.95	29.33	35.4
	10	1.191	18.82	71.50	90.32	20.8
	13	1.304	26.78	68.68	95.46	28.0
	11	1.297	22.54	55.30	77.84	29.0
Total						
Total organic			177.58	471.18	648.76	27.4
(1) Assuming a production/respiration ratio of 58%, and adding production.				416.99	594.57	29.9
(2) Assimilation plus defecation.						

Using this efficiency, the total ingestion of grass for the population studied was 107 kilogram calories/square meter/year.

DISCUSSIONS AND CONCLUSIONS

Population Phenomena and Energy Flow

In Figure 17, population density, population oxygen consumption, weight/animal and population weight of four categories of the Littorina population are compared. The difference between the population density and the weight of individual snails reflects the large weight differences among the age classes. On the other hand, differences in population oxygen consumption and population weight correspond closely from one age class to another.

It is becoming commonplace to point out that a poor picture of the biotic components of an ecosystem is presented by merely comparing biomass of organisms, since the weight-based metabolic rate of very small organisms, such as bacteria or nematodes, is high compared with snails or grasshoppers (see, for example, H. T. Odum, 1956, and MacFadyen, 1957). But the range of weights and metabolism involved in very diverse organisms may be quite large; Zeuthen (1953) needed 18 orders of magnitude to encompass the weight range of bacteria and large mammals. Approximately the same range of magnitude is needed to show oxygen uptake for the same organisms. Since oxygen uptake per unit weight decreases over this range, the net result is a very significant difference in metabolic activity between large and small organisms.

The weight and metabolism of Littorina varies over only three

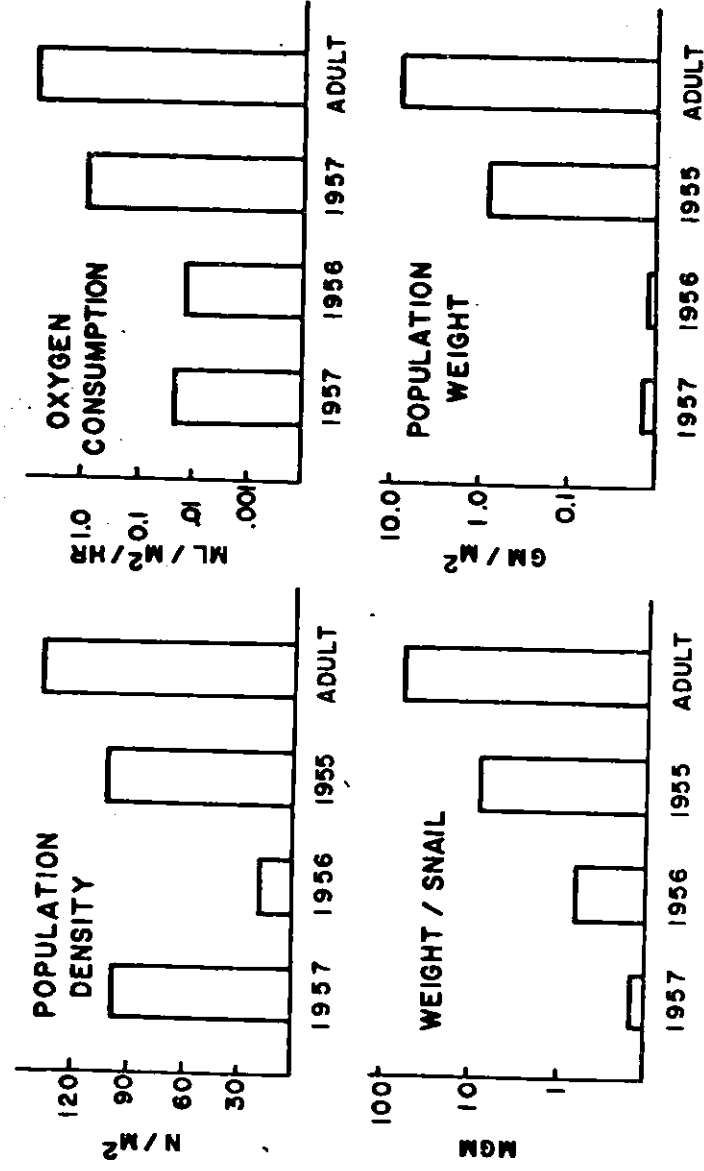


Figure 17. Numbers, weights of individual animals, population biomass and population respiration (at 30 degrees Centigrade) of four age classes of a population of *Littorina*.

orders of magnitude (Figure 17), so that the adult snails, with their relatively great biomass, are of more importance than the small snails, in spite of the large numbers and higher metabolic rate of the latter.

Figure 18 compares population density, standing crop and assimilation for the Orchelimum population over one life cycle. Numbers vary over only one order of magnitude; assimilation over two orders of magnitude. Here again, the biomass tends to determine the activity of the population, regardless of the size of the animals, which are, of course, much smaller near the beginning of the life cycle. There is present in the Orchelimum population a definite tendency for the higher metabolic rate of the small grasshoppers to balance the higher biomass of the large animals so that the rate of assimilation tends to remain more constant than the standing crop.

Seasonal Activity of Littorina and Orchelimum and Spartina Production

A comparison of the annual cycle of net primary production of Spartina and assimilation of Littorina and Orchelimum is shown in Figure 19. The Spartina curve is a composite, combining high marsh and streamside-levee marsh estimates and including corrections for autumn production of the latter. When data for Littorina assimilation were available for the same month in 1956 and 1957, a mean value was used.

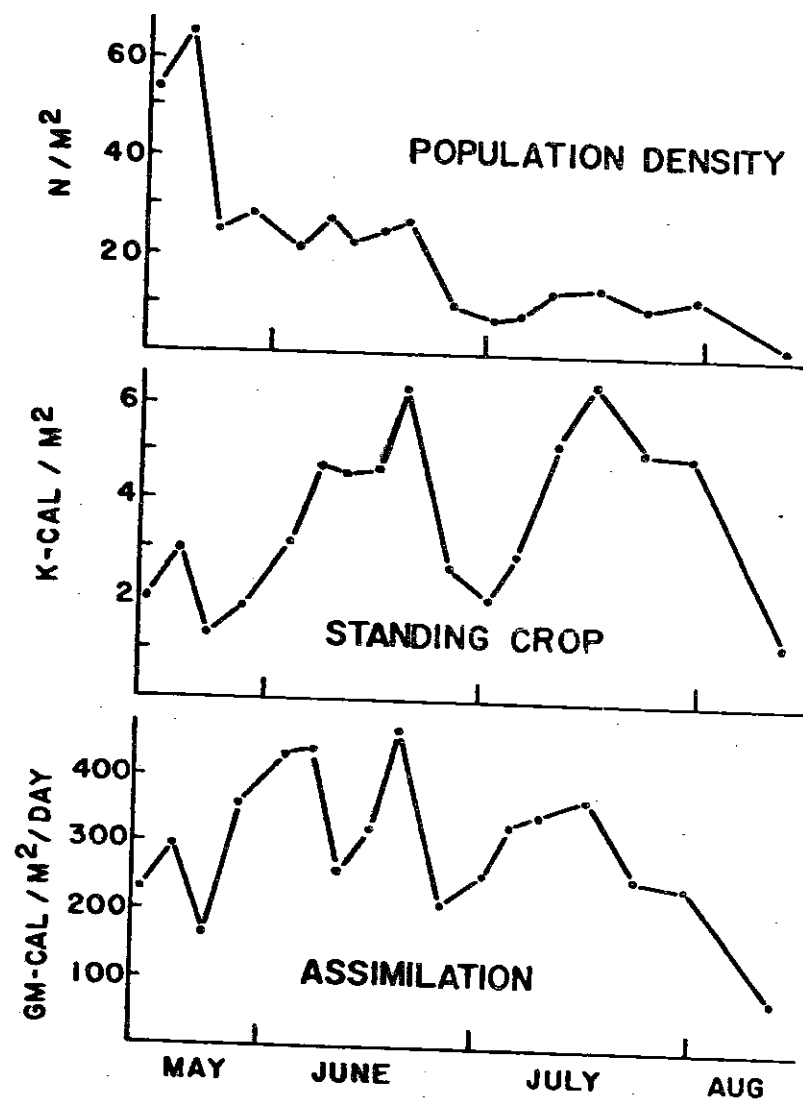


Figure 18. Population density, standing crop and assimilation of an Orchelimum population in the summer of 1957.

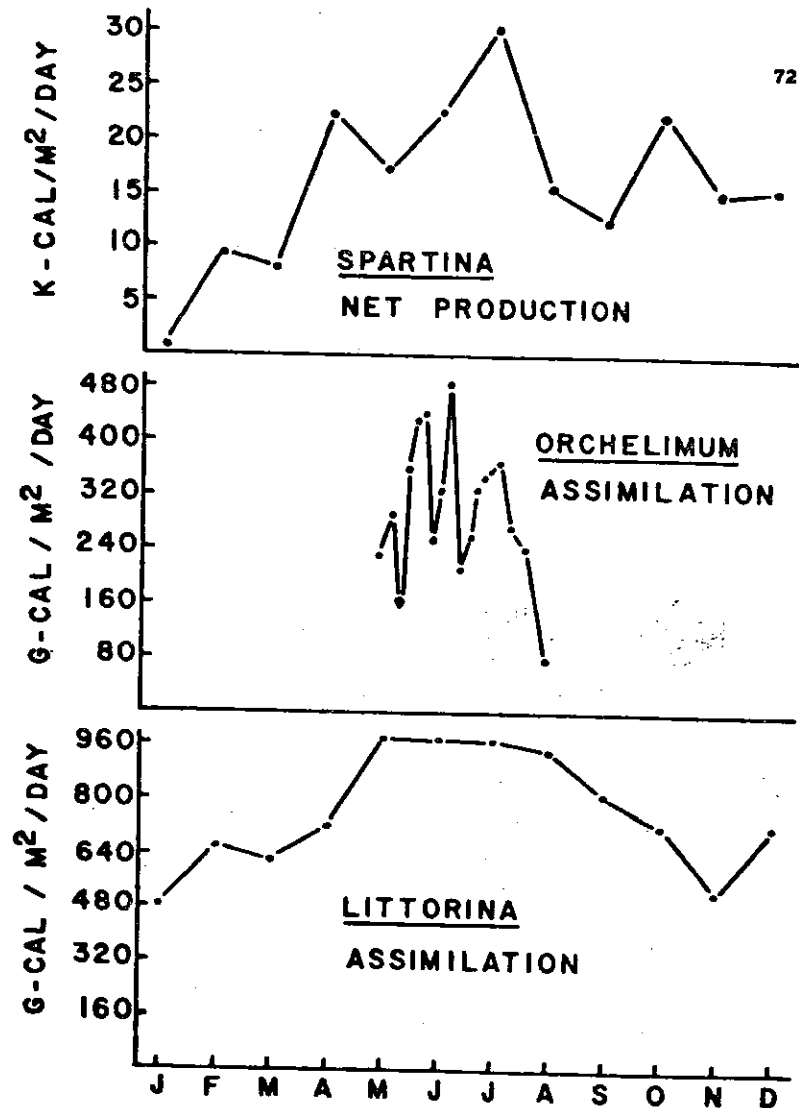


Figure 19. Seasonal fluctuations in Spartina net production, and Orchelimum and Littorina assimilation.

The seasonal cycle of activity of the Littorina population is quite constant. The summer high cannot be attributed to population characteristics, but is caused by the increased respiratory rate associated with the high summer temperature. On the other hand, the Orchelimum activity is restricted to a four month period in late spring and summer.

When the food source of the two animals is considered, it is seen that the period of grasshopper activity corresponds with the major production pulse of Spartina, its only food source. The Littorina population, however, can draw its food from several sources--detritus resulting from Spartina decomposition, mud surface algae and planktonic algae, as well as the microscopic consumers of the mud surface and Spartina aufwuchs. Figures 7 and 8 show that the washing out of Spartina into the water and subsequent decomposition occurs over a period of time, and therefore tends to damp the seasonal oscillation of production.

The seasonal activity of each animal is correlated with its food source--the grasshoppers with an annual grass which shows a strong pulse of production in spring and summer, and the snails with a variety of food sources whose supply is relatively constant.

There are data available from several sources which demonstrate the tendency of population energy flow to remain more constant than the numbers of animals in the population. The inverse correlation between snail size and population density acts as such a control. The Littorina population is stable over long periods of time (Figure 19), the long-lived adult population more than compensating for the

irregular recruitment of small snails. The assimilation rate of grasshoppers remains more constant than the population density (Figure 18), even though assimilation is determined by a number of complex factors, such as body weight, population density, respiratory rate and temperature.

The data presented here lead to the conclusion that energy flow, which is the best available measure of a population's activity, tends to remain more constant than population density.

Efficiency of Energy Utilization in Orchelimum and Littorina

H. T. Odum (1957) gives an interesting summary of ratios or "ecological efficiencies" which may be used to describe energy transfer, utilization and loss between entire trophic levels. In this paper, similar ratios have been adapted for use for species populations.

The growth and assimilation efficiencies are defined on page 77. The "assimilation utilization efficiency" (E_{ua}) is the ratio of the assimilation of one trophic level (or population) to the production of the next lower trophic level. The "ingestion utilization efficiency" (E_{ui}) is the ratio of the ingestion of one trophic level (or population) to the production of the next lower trophic level.

Odum (1957) uses ingestion of the food source as a measure of utilization, but when speaking strictly of energy flow, it is necessary to relate assimilation to P_{n-1} , since the material ingested

and not assimilated does not change trophic levels. However, the importance of the material ingested and not assimilated cannot be ignored, since it may be altered physically and chemically and moved to a different locality by the consumer, resulting in significant changes in trophic structure. Consequently, two utilization efficiencies are used.

Although there may be seasonal differences in efficiencies, it is more accurate, with the data at hand, to restrict discussion of efficiencies to annual totals. Ingestion, assimilation and production of Orchelimum and the 1955 year class of Littorina are compared in Table 18. The net organic production of 5200 kilogram calories per square meter/year shown for Spartina is a mean of the high marsh and corrected streamside-levee marsh production estimates. Since Orchelimum populations were sampled in areas of levee and middle marsh this mean Spartina production figure closely approximates the production of typical Orchelimum habitat.

Utilization efficiencies for Littorina cannot be calculated from these data, since (1) Littorina food may come from any of the several primary producer components of the marsh-estuarine ecosystem, and (2) as with any detritus feeder, Littorina may draw its nutritive source from more than one trophic level.

The utilization efficiencies in Table 18 show that Orchelimum utilizes a very small amount of Spartina and has little effect on annual net production. All of the grasshopper utilization falls within a short period of time, a circumstance which lowers the efficiency. Table 18 shows two types of utilization efficiency. The

Table 18. Some efficiencies of Littorina (1955 year class only) and Orchelimum. Ingestion, assimilation and production rates are in kilogram calories/square meter/year.

	Ingestion	Assimilation	Production	E _a	Efficiencies		
					E _g	E _{ua}	E _{ul}
<u>Spartina</u>			5200 (net)				
<u>Orchelimum</u>	107	29.4	10.3	36.4%	36.7%	0.57%	2.1%
<u>Littorina</u>	56.9	23.4	3.5	45.0%	14.0%		

grasshoppers had actually available for their growth and maintenance, only 0.57% of the Spartina crop, or the amount which they assimilated. However, they removed over 2% of the Spartina, which is then deposited on the floor of the marsh or into the water, where it becomes available for use by other consumers. The measure of this difference is the assimilation efficiency.

The growth efficiencies of the Littorina and Orchelimum population show differences which logically follow from their population characteristics. The slow-growing, long-lived snails use a relatively small amount of the assimilated matter for growth, whereas the grasshoppers, which emerge, grow and die within the space of a summer, convert almost half of the assimilated material into protoplasm. Since comparative data on other invertebrates is not yet available, it is difficult to generalize on the relations between population growth and longevity and efficiency, but it is suggested that the relationship between growth rate, longevity and growth efficiency demonstrated by Littorina and Orchelimum may have wide application.

The assimilation efficiencies show just the reverse of the growth efficiencies; that of Littorina is higher than Orchelimum. Thus, Littorina is more efficient than Orchelimum in assimilating the organic matter passing through its gut, but markedly less efficient in transforming it into protoplasm. Following an idea presented by Odum and Pinkerton (1955), it is suggested that the grasshoppers sacrifice efficiency of food concentration for a higher production rate. The coincidence of Orchelimum and Spartina production (Figure

19) and the low utilization efficiency confirm the abundance of a food source, and the adaptation of the life cycle of the grasshopper to take advantage of it. The food available to Littorina was not measured, but during the summer, the period of highest assimilation (Figure 19), the snails spend virtually all their time on Spartina stems in the high marsh (possibly an escape mechanism to avoid predators in the tidal waters), where the available aufwuchs certainly appears to be in poor supply. The snails, then, appear to sacrifice production for high food concentrating efficiency. The long-lived, low production snail population can well "afford" to "spend" some productive capacity in order to take advantage of an environment characterized by a poor food supply, a problem which does not confront Orchelimum.

Energy Flow as an Index to Animal Activity

Some of the limitations of energy flow measurements, and some of the possibilities for refinement of techniques will be discussed briefly.

The assimilation chamber used in measuring respiration is a highly artificial environment. In the case of the active grasshoppers, the respiration in the vial probably represents a basal metabolic rate, which is, of course, undesirable when attempting to measure energy utilization of a free-living population.

Measurement of respiration rates in dormant Littorina was attempted, but met with little success. The assimilation chamber is

moist and a dry environment is apparently a prerequisite for dormancy. On the other hand, the snails do not move around much in the vials and thus do not duplicate natural behavior in the marsh. Using animals fresh from the field, or maintaining good culture conditions in the laboratory is of advantage in metabolic measurements.

Temperatures for correction of respiration data to the environmental rates were obtained from mean monthly temperatures at local U. S. Weather Bureau stations. It would be desirable to know the temperatures of the actual microenvironment of the animals in the marsh.

Knowledge of the food which is actually assimilated by an animal is most useful. Fortunately this information could be estimated for Orchelimum, but is completely unknown for Littorina. Many animals fall into the category of "detritus feeders", and the nature of their nutritive source is seldom known and difficult to determine.

To summarize, energy utilization data can be refined by seeking more complete information on:

- (1) Activity of animals and its relation to oxygen consumption.
- (2) Microenvironmental temperatures.
- (3) Composition of nutritive sources.

The lack of these data is not too discouraging, since even with the simplified techniques used in this study, energy flow remains a much superior approximation of an organism's significance in the ecosystem than can be obtained from counting animals.

It is obvious that the conclusions reached on the relative efficiencies of grasshoppers and snails could not have been reached

with population or biomass data alone. In addition, Figure 19 is a comparison of rates, and the significance of the seasonal activities of the three components would be lost if standing crops were the only source of data. A direct comparison of grasshoppers with their food source was made possible by equating the two components with units of energy. It is evident that a clearer understanding of ecosystem function will result from consideration of energy flow of populations.

SUMMARY

1. Energy relationships of three components of a salt marsh were studied; the marsh grass, Spartina alterniflora, the only higher plant on the areas studied, a snail, Littorina irrorata, and a grasshopper, Orchelimum fidicinum.
2. Net production of Spartina was measured by periodic harvesting, and calculation of the between-harvest increase of living grass.
3. Animal production was found by periodic harvesting, and calculation of population biomass accumulation plus biomass lost through mortality.
4. Caloric contents of the three components were determined in a bomb calorimeter.
5. Respiratory rates of the two animal components were determined and converted to calories by means of Ivlev's oxycaloric coefficient or a modification thereof.
6. Ingestion in grasshoppers was determined by weighing feces collected under controlled conditions and adding production and respiration. Ingestion for Littorina was found with the aid of a production/defecation ratio for Littorina obtained from the literature.
7. From the results of observations and measurements of altitude, the marsh was divided into four types; (1) streamside marsh, (2) levee marsh, (3) high marsh, and (4) middle marsh.
8. Seasonal curves and standing crop estimates for the high and streamside-levee marsh are presented; the net production for the high

marsh was estimated at 643.2 grams dry weight/square meter/year. After appropriate corrections, the net production of the streamside-levee marsh was estimated at 2243 grams/square meter/year.

9. Littorina are found only in marshes where Spartina or Juncus roemerianus grows; they are most active during spring tidal cycles, and spend the warm months of the year on the Spartina plants.

10. The eggs and larvae of Littorina are planktonic; the reproductive cycle and planktonic life of the young snails extended, in 1957, from April 24 to October.

11. Young Littorina enter the marsh from the plankton from July to October and probably spend the early part of their life on the same Spartina plant.

12. Littorina is most abundant on the high marsh and is rare or absent along tidal streams; there is some indication of predator control of distribution.

13. Snails recruited into the marsh grow and die at rates which can be determined by separating year classes on the basis of total shell length. A population of large snails exists which is constant in size and decreased very slowly during the study period; production in the "adult" snails could not be measured with the techniques used.

14. An inverse relationship was found between population density and growth rate of snails.

15. Production of the 1955 year class of snails was found to be 3.47 kilogram calories/square meter/year.

16. Energy utilization, as found by oxygen consumption, and after correction for environmental temperatures, was 21.9 kilogram

calories/square meter/year for the 1955 year class of Littorina, and 253 kilogram calories/square meter/year for adult snails. By applying the respiration/assimilation ratio of the 1955 year class (86.2%), to the respiration in other age classes of small snails, production of the 1956 and 1957 year class and small snails of undetermined age could be estimated at 2.09 kilogram calories/square meter/year.

17. Ingestion of the 1955 year class of Littorina, assuming a production/defecation ratio of 11%, was 56.9 kilogram calories/square meter/year.

18. Orchelimum populations were censused by sweeping; the sweep samples were calibrated by comparing them with grasshopper counts made with an open-bottomed wire cage dropped over the marsh.

19. Grasshoppers appear on the marsh in early May and disappear in September; recruitment probably ceases before the end of May.

20. Production of the Orchelimum population was calculated by measuring mortality of the grasshoppers, and was found to be 10.82 kilogram calories/square meter/year.

21. Respiratory energy loss by grasshoppers was 18.6 kilogram calories/square meter/year.

22. Ingestion experiments yielded an estimate of 98.3 kilogram calories/square meter/year of Spartina organic matter eaten by the grasshopper population.

23. Because of the relatively small range of weights of individual Littorina and Orchelimum encountered in the marsh, the increase of weight-based respiratory rates were not as important in determining energy flow differences between population components as

were differences in biomass.

24. The grasshoppers are short lived and fast growing; the snails long-lived and slow growing. Because of these population characteristics, the grasshoppers' greatest period of activity coincides with the annual production pulse of Spartina, while the Littorina population, which draws its food from several sources, maintains a relatively steady level of activity throughout the year.

25. Energy flow of snails and grasshoppers tends to remain more steady seasonally than does population density.

26. Orchelimum, with an abundant food supply, has a lower assimilation efficiency and a higher growth efficiency than Littorina, which has a sparse food supply and apparently sacrifices efficiency of growth for a greater efficiency in assimilating its food.

27. Some of the limitations for energy flow measurements are discussed, and it is concluded that in spite of these limitations, energy flow measurements are the best available index to an animal's significance in the ecosystem.

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Appendix 1. Rankits for Spartina clip samples.

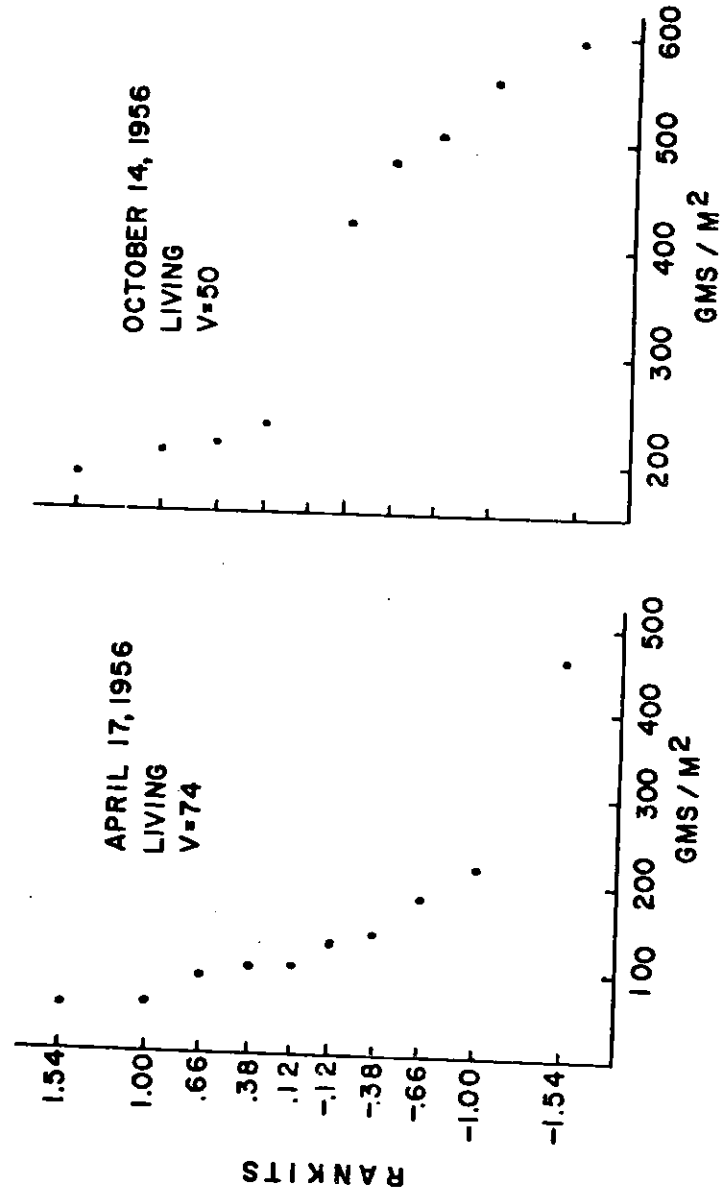


Figure 20. Rankits for two high marsh samples of living Spartina.

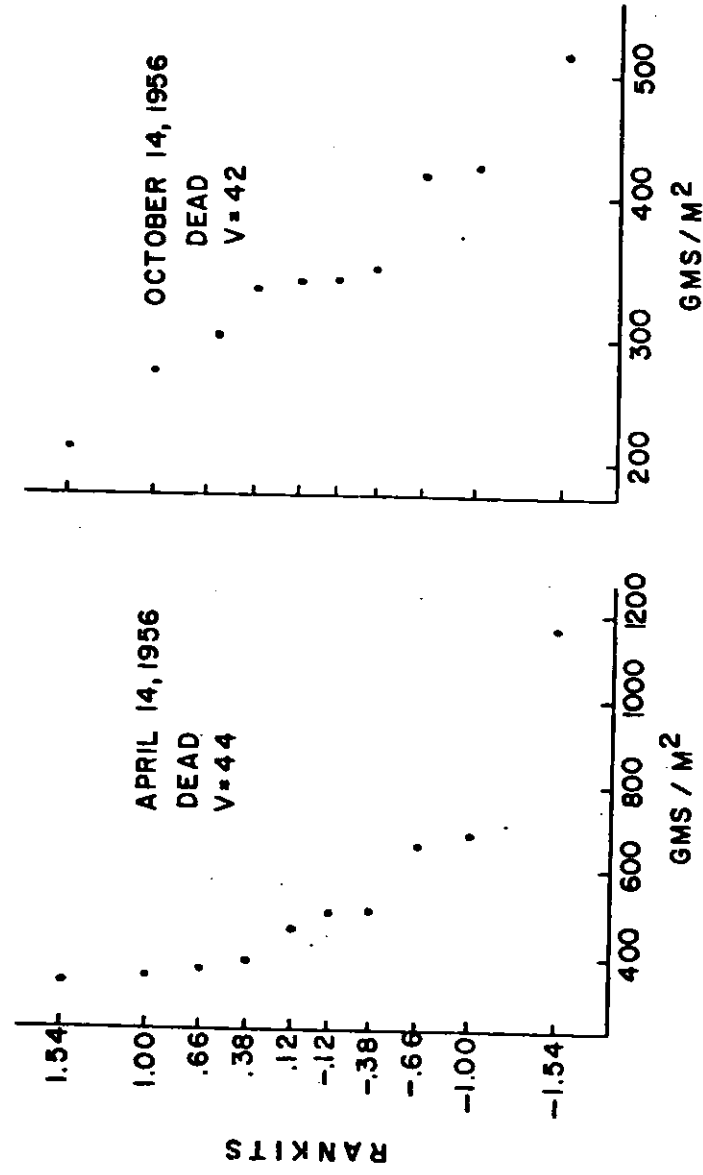


Figure 21. Rankits for two high marsh samples of dead Spartina.

Appendix 2. Population estimates of Littorina.

Table 19. Population density in numbers per square meter, and size distribution of the 1955 year class of Littorina.

Length in mm.	1956											
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1	154	81	54	10			167	91	13	2	14	
2	494	413	379	355			124	139	125	66	90	
3	53	83	81	108			47	67	125	113	164	
4	12	16	15	25			15	29	47	71	69	
5		7	12	9			11	17	17	39	22	
6							7	14	15	18	20	
7							2	4	7	18	12	
8									7	7	10	
9										5		
10												
11												
12												
13												
Total	713	600	541	507			373	361	356	339	401	

Table 19. (cont.)

Length in mm.	1957									
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
1										
2	4	2		2						
3	73	69	70	27	14	2	14			4
4	108	98	86	72	42	26	21			16
5	42	48	49	63	60	56	36			17
6	19	27	27	34	63	52	47			11
7	16	12	14	22	47	38	43			7
8	6	14	18	14	45	34	28			21
9	12	13	8	9	19	17	17			7
10	6	9	12	5	14	11	11			6
11		5	4	3	11	6	8			8
12			7			4				6
13										
Total	286	297	295	251	315	246	225			103

Table 20. Population density in numbers per square meter, and size distribution of adult Littorina.

Length in mm.	1956											
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
14	10	8	4	8			2	2	4	3	11	
15	15	14	15	13			4	6	13	8	12	
16	39	17	20	29			12	19	16	12	20	
17	59	40	58	34			49	42	33	24	53	
18	53	66	45	52			66	52	40	44	59	
19	34	31	38	51			31	37	39	30	27	
20	6	4	5	14			7	2	8	9	9	
21	1	2	1	2			1		2	2	4	
22											1	
23												
Total	217	183	186	203			172	160	156	130	196	

Table 20. (cont.)

Length in mm.	1957									
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
14	4	6	5	3	6	7	6			8
15	4	14	12	8	8	6	4			7
16	23	16	17	19	21	24	11			14
17	35	44	37	51	46	56	33			28
18	47	42	47	60	60	43	46			45
19	16	27	29	28	20	24	25			24
20	9	5	6	10	2	6	8			9
21		3		1			1			2
22										
23			1							
Total	138	157	154	180	163	166	134			137

Table 21. Population density in numbers per square meter, and size distribution of the 1956 and 1957 year class, and small Littorina of undetermined age.

Length in mm.	1956											
	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
1									8	3	2	
2									6	27	53	
3											10	
4												
5	3											
6	5	5	4	6								
7	2	2	4	5								
8	2	3	3	4								
9	8	6	8									
10	5	7	9	2			1					
11	9	5	4	3			4	2	3	1	4	
12	4	6	4	3			4	3	6	2	7	
13	6	2	1	6			2	4	4	3	3	
							6	4	3	6	11	
Total	44	36	37	29			17	13	30	42	90	

Table 21. (cont.)

Length in mm.	1937									
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct
1		2								
2	23	15	32	14	12		5			4
3	10		5	3	30	31	18			95
4					1	3	9			12
5										6
6										1
7										
8										
9										
10	1									
11	2									
12	5	6		2	3		1			
13	8	8		1	3	1	4			
Total	49	31	37	19	49	35	40			118

Appendix 3. Population estimates of Orchelimum.

Table 22. Numbers (N) and dry weight (W), in grams, of Orchelimum taken in sweep samples of five samples of 25 sweeps each, or adjusted to this sample. Summer, 1937.

	0-5 mm		5-10 mm		10-15 mm		15-20 mm		Adult		Total	
	N	W	N	W	N	W	N	W	N	W	N	W
May 13	146	0.41	68	0.48							214	0.89
May 18	110	0.44	144	1.59							255	2.06
May 22	20	0.08	69	0.88	1	0.03					90	1.03
May 27	15	0.06	92	1.23	5	0.12					112	1.41
Jun 3	7	0.06	31	0.49	40	1.56	5	0.31			83	2.42
Jun 7	2	0.08	36	0.48	59	2.73	12	0.90			109	4.19
Jun 11	1	0.01	28	0.51	38	1.44	20	1.58	4	0.45	91	3.99
Jun 15	4	0.03	35	0.40	42	1.46	14	0.98	8	0.86	103	3.78
Jun 19			36	0.42	47	1.54	32	2.02	14	1.40	129	5.38
Jun 25			28	0.22	34	1.09	26	1.75	15	1.45	103	4.51
Jul 1			7	0.09	18	0.66	11	0.79	9	0.77	45	2.31
Jul 5			3	0.05	14	0.52	6	0.48	10	1.30	33	2.35
Jul 9			1	0.01	12	0.30	6	0.34	26	2.83	45	3.48
Jul 16			3	0.07	10	0.39	15	0.98	49	4.80	77	6.24
Jul 23			13		6	0.36	4	0.22	80	8.81	97	9.39
Jul 30			18		6	0.15	5	0.15	64	6.24	75	6.54
Aug 12			2		18	0.62	2	0.12	58	5.49	78	6.23
			2		2	0.06	1	0.05	14.5	1.15	17.5	1.26
Totals	305	1.17	581	6.92	360	13.10	159	10.67	351.5	35.35		
Mean Weight (mgm)		0.00384		0.01191		0.03639		0.06711				0.10114

Appendix 4. Calculation of production, and respiratory rates in
Littorina.

In the Appendices, calculations are frequently carried out with more figures than are significant.

Littorina Production

The problem is to find the increase in biomass of the snails during the study period, and can be divided into (1) the snails which survived the entire period of study and (2) the snails which gained in weight (the criterion of production used here) during the study period, but died between February 1956 and October 1957. As is evident from previous discussion, only the 1955 year class is considered.

Table 23 shows the mean total shell length of the population for each of the monthly sampling intervals, and the mean weight/snail. Values for months when a sample was not taken are interpolated. The monthly mortality, from the regression in Figure 11, is 23.94 snails. To simplify calculations the weight/snail column in Table 23 can be summed and the result (38.1651) multiplied by 23.94 to give 913.67 mgm. of snails dying during the study period. However, their initial weight was not produced during the study period, so the total mortality, which is equal to the difference between the initial and final population, must be found from Figure 11. The resulting figure, 620.59-117.85, or 502.74, is multiplied by the initial weight of the individual snail, 0.135, to give an initial weight of 67.87 mgm. The difference between this and the weight of the snails which died is 845.8 mgm., or 3.45 kilogram calories/square meter/21 months, or

Table 23. Mean length and weights of snails of the 1955 year class during each sampling interval from February, 1956, to October, 1957. The values for missing months are interpolated.

Month	Mean Length (1)	Weight/Snail (2) (mgm)
Feb	1.89	0.1350
Mar	2.09	0.1719
Apr	2.17	0.1882
May	2.35	0.2289
Jun	2.65	0.3091
Jul	2.65	0.3091
Aug	2.95	0.4060
Sep	2.45	0.6094
Oct	4.11	0.9685
Nov	4.80	1.470
Dec	4.38	1.148
Jan	4.58	1.295
Feb	4.93	1.581
Mar	5.16	1.794
Apr	5.27	1.897
May	6.38	3.214
Jun	6.57	3.491
Jul	6.51	3.402
Aug	7.29	4.674
Sep	7.29	4.674
Oct	8.06	6.199
Total		38.1651

(1) Calculated from Table 21, Appendix 2.

(2) From regression equation, Figure 13.

1.97 kilogram calories/square meter/year.

An error arises from using 0.135 as the initial weight of the individual snails, since 0.135 is the weight calculated from a sample taken mid-way in the first sampling interval; the actual initial weight will be somewhat less. The same underestimate will occur at the end of the study period in calculating production of survivors.

To find production of survivors, the mean size of the snails at the beginning and end of the 21-month study period is found to be 1.89 mm. and 8.06 mm. (from Table 9). The corresponding weights, from Figure 13, are 0.135 mgm. and 6.199 mgm., or a 6.064 mgm. weight gain for each snail. The population at the end of the study period was 105,88 (from Figure 11), giving a weight gain of all surviving snails of 642.056 mgm., or 2.62 kilogram calories/21 months/square meter, or 1.50 kilogram calories/square meter/year.

To find production on a monthly basis, the weight gain for each month is found from Table 9 and Figure 13, and entered into the first column in Table 24. Losses in weight are not counted, since there is no provision for negative production in the definitions upon which these calculations are based. The survivors are found from Figure 11, and production by the survivors is then the product of the number of survivors and the weight gain per snail. Assuming mortality evenly distributed through a sampling interval, production by the snails dying during the study period is half of the mortality times the weight gain. The sum of these two figures yields the total production on a monthly basis (Table 24). The sum of the monthly production will not equal the production calculated previously

Table 24. Monthly production of the 1955 year class of Littorina in milligrams/square meter.

	Weight gain from previous month (mgm)	Survivors	Production by survivors	Production by snails dying in sample period	Total production
1956 Feb					
Mar	0.0369	572.71	21.13	0.441	21.57
Apr	0.0163	548.77	8.94	0.193	9.14
May	0.0407	524.83	21.36	0.487	21.85
Jun	0.0802	500.89	40.17	0.960	41.13
Jul					
Aug	0.0969	453.01	43.90	1.16	45.06
Sep	0.2034	426.07	87.27	2.43	89.70
Oct	0.3591	405.13	145.48	4.30	149.8
Nov	0.5015	381.19	191.17	6.00	197.17
Dec					
1957 Jan					
Feb	0.1110	309.37	34.34	1.33	35.77
Mar	0.2130	285.43	60.80	2.55	63.35
Apr	0.1030	261.49	26.93	1.23	28.16
May	1.317	237.55	31.28	15.8	328.6
Jun	0.2770	213.61	59.17	3.31	62.48
Jul					
Aug	1.183	165.73	196.06	14.2	210.26
Sep					
Oct	1.525	117.85	179.72	18.3	198.02

because population density was not extrapolated to include all of February and October in finding monthly production.

Population Oxygen Consumption in Littorina

The dry body weights and oxygen consumption rates for each millimeter size class of Littorina are found by means of the equations in Figures 13 and 14, respectively, and are shown in Table 25. Next from Tables 19-21, the oxygen consumption rate for each sample is found by cumulatively multiplying the rates in Table 25 times the corresponding number of snails of that size class. Although the operation is carried out on a calculator directly, a sample calculation is given in Table 26. The oxygen consumption rate is corrected for temperature with the coefficients obtained from Table 27. The sum of the products of the temperature corrected oxygen consumption and the hours in the month will yield the total O_2 consumption for the study period, which can then be converted to calories and to an annual basis. The monthly rates of respiratory energy use are shown for the various age categories in Tables 28-30.

Table 25. Calculation of oxygen consumption rates for the various size class of Littorina.

Size class (mm)	Dry body weight (mgm) (1)	Oxygen consumption (mu.l./hr) (2)
1	0.03338	0.08028
2	0.1544	0.2974
3	0.4236	0.7048
4	0.9000	1.342
5	1.643	2.246
6	2.709	3.444
7	4.166	4.976
8	6.068	6.863
9	8.465	9.123
10	11.42	11.78
11	15.01	14.89
12	19.29	18.45
13	24.29	22.47
14	30.08	26.97
15	36.76	32.02
16	44.36	37.60
17	52.91	43.72
18	62.48	50.39
19	73.19	57.69
20	85.07	65.61
21	98.10	74.11
22	112.4	83.26
23	128.1	93.10

(1) From Figure 13.

(2) From Figure 14.

Table 26. Calculation of population oxygen consumption for the 1955 year class in February, 1957.

Size class (mm)	N/M ² (1)	O ₂ consumption (mu.l./hr/snail) (2)	Population O ₂ consumption (mu.l./hr/M ²)
2	2	0.2974	0.5948
3	69	0.7348	48,6312
4	98	1.342	131,516
5	48	2.246	107,808
6	27	3.444	92,988
7	12	4.976	59,712
8	14	6.863	96,082
9	13	9.123	118,599
10	9	11.78	106,02
11	5	14.89	74,45
Total			836,401

(1) From Table 19.

(2) From Table 25.

Table 27. Calculation of correction factors for oxygen consumption of Littorina at mean monthly temperatures.

	Mean monthly temp. in de- grees C.	Weather Station (1)	O ₂ consumption in ml/gm dry weight/hr (2)	% of O ₂ consumption at 30 d. C.
1956 Feb	15.6	B1	0.3414	61.6
Mar	14.8	B1	0.3296	59.4
Apr	18.6	B1	0.3858	69.56
May	23.9	B1	0.4643	83.71
Jun	25.8	B1	0.4925	88.79
Jul	27.5	B1	0.5176	93.32
Aug	27.3	B1	0.5147	92.80
Sep	23.9	SS	0.4643	83.71
Oct	20.5	SS	0.4140	74.64
Nov	14.5	SS	0.3251	58.61
Dec	14.5	B1	0.3251	58.61
1957 Jan	12.4	B1	0.2940	53.01
Feb	15.3	B1	0.3370	60.76
Mar	14.7	B1	0.3281	59.15
Apr	19.7	B1	0.4021	72.49
May	23.3	SI	0.4554	82.10
Jun	26.3	SI	0.4999	90.13
Jul	27.0	SI	0.5102	91.98
Aug	27.3	SI	0.5147	92.80
Sep	26.3	SI	0.4999	90.13
Oct	19.6	SI	0.4006	72.22

(1) B1--Blackbeard Island
 SS--St. Simon's Island
 SI--Sapelo Island

(2) From Figure 22.

Table 28. Population oxygen consumption of the 1955 year class of Littorina.

	Population oxygen consumption ($\text{ml}/\text{m}^2/\text{hr}$)	Temperature corrected O_2 consumption (1)	Hours in month
1956 Feb	212.737	131.046	696
Mar	225.021	133.662	720
Apr	221.221	153.881	720
May	236.262	197.775	744
Jun	278.264	247.071	720
Jul	278.264	259.676	744
Aug	320.267	297.208	744
Sep	435.743	364.760	720
Oct	610.368	455.579	744
Nov	828.403	485.527	720
Dec	791.532	463.917	744
1957 Jan	658.294	348.962	744
Feb	836.401	508.197	672
Mar	964.042	570.231	744
Apr	766.073	555.326	720
May	1462.717	1200.891	744
Jun	1211.407	1091.841	720
Jul	1090.696	1003.222	744
Aug	969.014	899.245	744
Sep	969.014	873.372	720
Oct	847.332	611.943	744

Sum of the products of the temperature corrected respiration and hours in each month.....7941.48 $\text{ml}/\text{m}^2/21$ months.

Caloric equivalent by Ivlev's oxycaloric coefficient.....38357 $\text{cal}/\text{m}^2/21$ months.

Annual energy loss by respiration.....21.9 K-cal/ m^2/year .

(1) From correction factors in Table 27.

Table 29. Population oxygen consumption of adult Littorina and small Littorina of undetermined age.

	Population oxygen consumption ($\mu\text{L}/\text{m}^2/\text{hr}$)		Temperature corrected O_2 consumption	
	<u>Adult</u>	<u>Undetr.</u>	<u>Adult</u>	<u>Undetr.</u>
1956 Feb	9895.78	522.150	6095.80	321.644
Mar	8660.09	415.049	5144.09	245.945
Apr	8737.87	389.103	6081.56	270.816
May	9838.13	331.396	8234.51	277.378
Jun	9130.57	309.460	8107.95	274.800
Jul	9130.57	309.460	8518.82	288.726
Aug	8423.01	287.523	7816.55	266.821
Sep	7682.73	231.910	6430.45	194.109
Oct	7590.37	265.890	5662.42	198.354
Nov	6375.90	231.730	3736.28	135.794
Dec	9250.90	453.870	5421.03	265.968
1957 Jan	6512.82	313.570	3451.79	166.192
Feb	7359.77	290.460	4474.74	176.600
Mar	7304.03		4323.99	
Apr	8650.12	40.920	6271.34	29.667
May	7527.12	122.760	6179.77	100.786
Jun	7676.62	22.470	6916.63	20.245
Jul	6505.44	160.120	5985.00	147.310
Aug	6543.36	80.060	6072.24	74.296
Sep	6543.36	80.060	5895.57	72.134
Oct	6581.28		4751.68	

Sum of the products of the temperature corrected respiration and hours in each month (Table 28).....Adult: 91,768 $\text{mL}/\text{m}^2/21$ months
Undetr: 2572 $\text{mL}/\text{m}^2/21$ months

Caloric equivalent.....Adult: 443 K-cal/ $\text{m}^2/21$ months
Undetr: 12.4 K-cal/ $\text{m}^2/21$ months

Annual energy loss by respiration.....Adult: 253 K-cal/ m^2
Undetr: 7.1 K-cal/ m^2

Table 30. Population oxygen consumption for the 1956 and 1957 year class of Littorina.

	Population oxygen consumption ($\mu\text{l.}/\text{m}^2/\text{hr}$)		Temperature corrected O_2 consumption	
	1956	1957	1956	1957
1956 Oct	2.427		1.8105	
Nov	8.271		4.8468	
Dec	22.971		13.461	
1957 Jan	13.888		7.361	
Feb	4.622		2.8102	
Mar	13.041		7.720	
Apr	6.278		4.552	
May	26.055		21.391	
Jun	25.875		23.313	
Jul	26.251		24.151	
Aug	22.504		20.884	
Sep	22.504		20.276	
Oct	18.756	28.574	13.542	20.630

Sum of the products of the temperature corrected respiration and hours in each month.....1956 yr. class: 122.118 $\text{ml}/\text{m}^2/21$ months
 1957 yr. class: 15.349 $\text{ml}/\text{m}^2/21$ months

Caloric equivalent.....1956 yr. class: 589.9 $\text{cal}/\text{m}^2/21$ months
 1957 yr. class: 74.1 $\text{cal}/\text{m}^2/21$ months

Annual energy loss by respiration..1956 yr. class: 0.34 K-cal/ m^2
 1957 yr. class: 0.042 K-cal/ m^2

Appendix 5. Calculation of production and respiratory rates in
Orchelimum.

Production in Orchelimum

As in Littorina, the problem is to find the increase in biomass during the study period. However, unlike the snails, all of the grasshoppers die by the end of a season, so only the biomass lost by mortality need be considered.

The population at the sampling interval boundaries is found by the equation in Figure 15 and the mortality found by the difference between the population at the beginning and end of each sampling interval. Again assuming mortality evenly divided among the different size grasshoppers, the mean weight in milligrams is found from Table 31 and multiplied by the mortality, giving the mortality in milligrams/square meter (Table 31).

The sum of the mortality column is 1953.88 milligrams, which includes the remaining population at the end of the study period (3.97 grasshoppers). These grasshoppers were assumed to have reached adulthood and converted to weight accordingly, which added 401.63 milligrams to the sum of the mortality column in Table 31. Conversion to calories (Table 16) gives a total production of 10.82 kilogram calories/square meter/year. The column showing mortality in milligrams does not show production for each interval.

To find the production for each sampling interval, it is necessary to add two sources of production, as was done for Littorina: (1) the weight gain by the grasshoppers surviving at the end of each sampling period, and (2) the production by the grasshoppers which

Table 31. Data for calculation of production in Orchelimum.

Mean date of samp- ling in- terval	Population at inter- val bound- aries (1)	Mortality	Mean weight in mgm (2)	Mortality in mgm/m ²
	51.39			
May 13	45.21	6.18	6.405	39.58
18	40.29	4.92	8.527	41.95
22	35.91	4.38	10.392	45.52
27	30.79	5.12	11.919	61.03
Jun 3	26.75	4.04	26.354	106.47
7	24.14	2.61	31.097	81.16
11	21.79	2.35	36.585	85.97
15	19.67	2.12	33.204	70.39
19	17.31	2.36	41.562	98.08
25	14.84	2.47	47.325	116.89
Jul 1	13.06	1.78	51.342	91.39
5	11.79	1.27	66.803	84.84
9	10.24	1.55	73.198	113.46
14	8.560	1.68	83.235	139.83
23	7.155	1.40	87.534	122.55
30	5.539	1.62	75.026	121.54
Aug 12	3.971	1.57	84.525	132.70

(1) From regression in Figure 15.

(2) From Table 22.

died during the sampling period. In Table 32, the weight at the end of each sampling period has been approximated by taking the mean of the weights for the two adjacent periods (which are mean weights at the midpoint of the sampling interval). The weight gain for each interval is then found by difference and entered into the table. The weight gain/grasshopper is then multiplied by the population at the end of the interval (Table 31), giving the production by the surviving grasshoppers for each interval. Assuming that mortality is evenly distributed throughout the sampling period, the total weight gain of the grasshoppers which died during the interval can be approximated by multiplying the number of animals dying (Table 31) times one-half the weight gain, which is entered into Table 33, and can be converted into production/day.

Population Oxygen Consumption in Orchelimum

The procedure is similar to that for Littorina.

1. Respiratory rates for the grasshoppers of each of the size classes used in measuring the grasshopper population are calculated from the weights found from Table 22 and the equation given in Figure 16 (Table 34).

2. The total oxygen consumption for each sampling interval is then found by summing the products of the population densities and the respiratory rates for each size group, resulting in the first column of figures in Table 35.

Table 32. Data for the calculation of production for each sampling interval of Orchelimum.

Mean date of sampling interval	Individual weights between intervals (mgm)	Individual weight gain (mgm)	Survivors weight gain (mgm) (1)
May 13	5.344		
18	7.466	2.122	95.94
22	9.460	1.994	80.34
27	11.155	1.695	60.67
Jun 3	19.136	7.981	245.73
7	28.726	9.590	256.53
11	33.841	5.115	123.48
15	34.894	1.053	22.94
19	37.383	2.489	48.96
23	44.444	7.061	122.23
Jul 1	49.379	4.935	73.24
5	59.072	9.693	126.59
9	70.000	10.928	128.84
16	78.216	8.216	84.13
23	85.385	7.169	61.36
30	81.280	-4.105	
Aug 12	79.776	-1.505	
	89.274	9.498	37.72

(1) Survivors are shown in Table 14.

Table 33. Production of Orchelimum for each sampling interval.

Mean date of sampling interval	Weight gain of 'hoppers dying during interval (mgm)	Production (mgm)	Production/day (mgm)
May 13	6.56	102.50	20.50
18	4.91	85.25	18.95
22	3.71	64.58	14.35
27	20.43	266.16	44.36
Jun 3	19.37	275.90	50.16
7	6.68	130.16	32.54
11	1.24	24.18	6.04
15	2.64	51.60	12.60
19	8.33	130.56	26.11
25	6.10	79.34	13.22
Jul 1	8.63	135.22	27.04
5	6.94	135.78	33.94
9	6.37	90.50	16.45
16	6.02	67.38	9.63
23			
30			
Aug 12	7.46	45.18	3.48

Table 34. Weights and rates of oxygen consumption for different size classes of Orchelimum.

Size class	Mean weight (mgm)	Caloric content (gm-cal)	Respiratory rate (cu.l./hr)
0-5	3.84	21.26	17.18
5-10	11.91	65.93	43.96
10-15	36.39	201.46	109.0
15-20	67.11	371.52	184.4
Adult	101.14	559.91	259.5

Table 35. Population oxygen consumption in Orchelimum.

Mean date of sampling interval	Oxygen consumption in ml/hr/m ²	Temperature corrected O ₂ consump.	Hours in interval
May 13	1.1410	1.00	120
18	2.136	1.61	108
22	0.8941	0.73	108
27	1.243	0.975	144
Jun 3	1.735	1.31	132
7	2.632	2.20	96
11	2.452	1.90	96
15	2.497	2.13	96
19	3.318	2.76	120
25	1.393	1.17	144
Jul 1	1.021	0.92	120
5	1.442	1.21	96
9	2.554	2.18	132
16	3.054	2.67	168
23	2.405	2.17	168
30	2.412	2.07	240
Aug 12	0.558	0.501	312

Total temperature corrected respiration: 3.764 l.O₂.

Respiratory energy use: 18.558 K-cal.

3. The mean temperatures for the sampling intervals, from U. S. Department of Commerce (1956-1957), are then used to find temperature corrections for each sampling period (Table 36). As with Littorina they are expressed as a percent of the oxygen consumption at 30 degrees Centigrade, the temperature at which the rates for the different size grasshoppers were established. The temperature corrected oxygen consumption is then cumulatively multiplied by the hours in the sampling interval, resulting in a total oxygen consumption for the study period of 3.764 liters. Converting by means of the oxygen-caloric coefficient in Table 1, the respiratory energy is seen to be 18.558 kilogram calories/square meter/year.

Table 37 compares production/day, converted into gram calories, from Table 33, and respiration, converted from milliliters/hour/square meter (Table 35) to gram calories/day/square meter.

Table 36. Temperature corrections for Orchelimum respiration.

Mean date of sampling interval	Mean temperature in degrees C.	O ₂ consump- tion (ml/ gm/hr)	% of O ₂ con- sumption at 30 degrees C.
May 13	23.8	2.076	70.9
18	24.8	2.213	75.6
22	26.1	2.392	81.7
27	25.4	2.296	78.4
Jun 3	24.8	2.214	75.6
7	26.5	2.447	83.6
11	25.2	2.268	77.5
15	26.9	2.503	85.5
19	26.4	2.433	83.1
25	26.7	2.474	84.5
Jul 1	27.9	2.639	90.1
5	26.6	2.462	84.1
9	26.9	2.503	85.5
16	27.3	2.557	87.3
23	27.9	2.639	90.1
30	27.0	2.515	85.9
Aug 12	27.8	2.626	89.7

Table 37. Production and respiratory energy use in Orchelimum.

Mean date of sampling interval	Production (gm-cal/day/m ²)	Respiratory energy use (gm-cal/day/m ²)
May 13	113	118
18	105	191
22	79	86
27	246	115
Jun 3	278	155
7	180	259
11	33	225
15	71	252
19	144	326
25	73	138
Jul 1	150	109
5	188	143
9	91	258
16	53	317
23		257
30		245
Aug 12	19	59

Appendix 6. Data for calculation of ingestion rates of Orchelimum.

Table 36. Data for the calculation of ingestion rates of Orchelimum.

Length of experiment (hours)	Temperature (degrees C.)	N subjects		Total weight of grass- hoppers	Weight of feces
		Nymphs	Adults		
2.58	28.6		2	0.1505	0.0052
2.25	26.2	14		0.8514	0.0294
2.17	27.1	18		1.2738	0.0438
2.08	28.2		10	1.1111	0.0384
2.42	27.4	11		0.7844	0.0208
2.25	27.3		11	1.3354	0.0236
2.08	28.5	8		0.5184	0.0112
2.00	27.5		10	1.0780	0.0406
2.67	28.1		13	1.5048	0.0321
2.58	28.0		11	1.2736	0.0406

Appendix 7. The relation of respiration to temperature in Littorina
and Orchelimum.

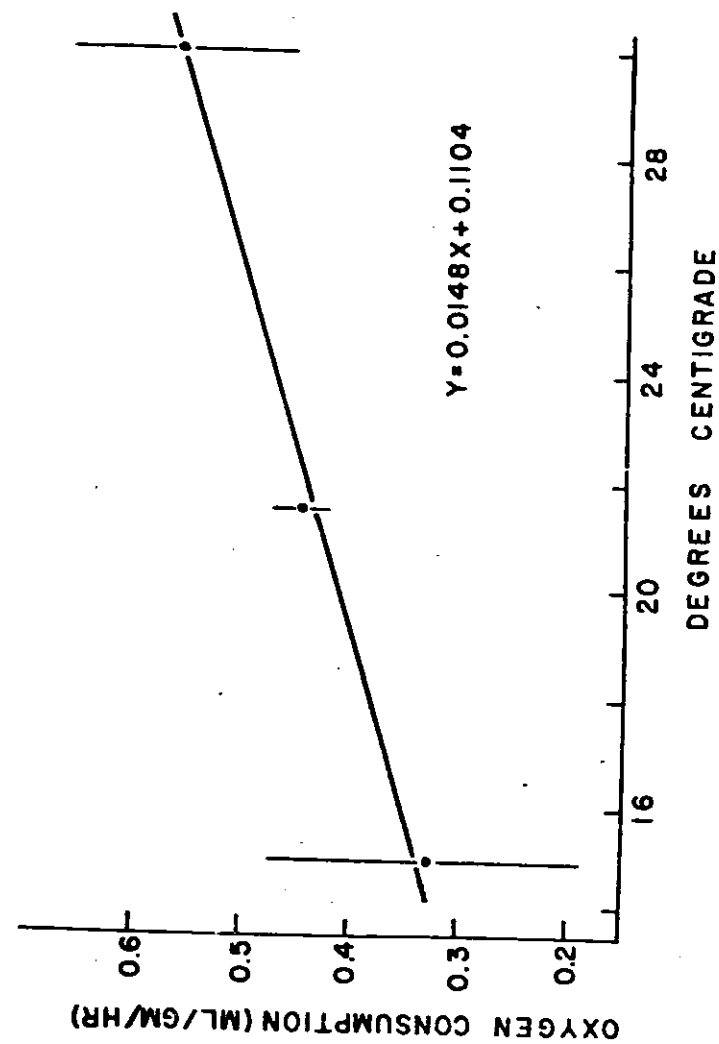


Figure 22. Relationship of respiration to temperature in Littorina. The vertical lines are two standard errors on either side of the mean.

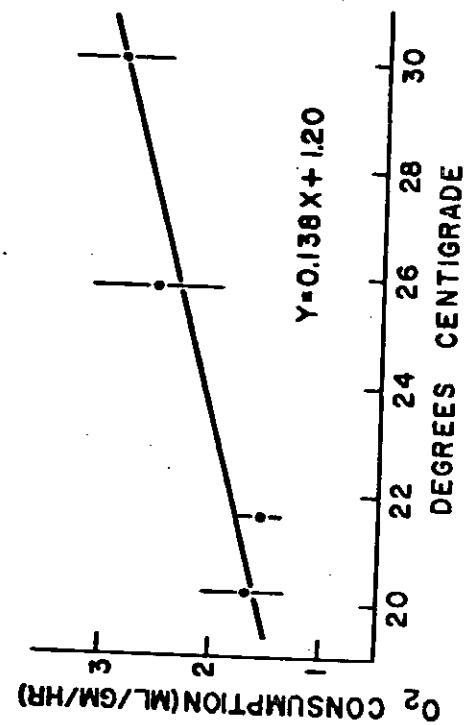


Figure 23. Relationship of respiration to temperature in Orchelimum. The vertical lines are two standard errors on either side of the mean.