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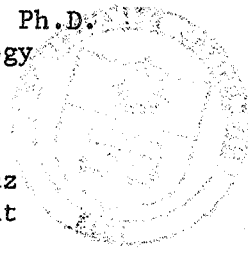
Annual Pittman-Robertson Report

to

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reticulatum, and its relation to cyclic patterns

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SUMMARY

The marsh crab, Sesarma reticulatum (Say), feeds primarily upon the cordgrass, Spartina alterniflora, during the summer months in Canary Creek Marsh (Lewes, Delaware). In so doing, Sesarma is a part of the second, or herbivore, trophic level in the marsh.

A study was undertaken to determine the energy utilized by Sesarma in feeding upon Spartina over lunar-monthly periods. Amounts of Spartina ingested and assimilated, in terms of grams dry weight, were found for three groups of crabs. These studies indicate a possible relationship between the quantity (i.e. grams dry weight) and/or quality (i.e. associated with maturity) of Spartina available to the crabs and the amounts ingested and assimilated. These data, in addition to data from respiration measurements, were combined with information from the literature to construct energy budgets, in terms of caloric values, for the three groups.

Efficiencies of energy utilization were calculated and compared with known values for other invertebrates. Comparison of consumption and assimilation efficiencies implies a decrease in the amount assimilated with an increase in amount ingested.

Amounts ingested and assimilated daily were examined over time to discern patterns of food utilization by Sesarma. A possible pattern of ingestion and assimilation, with peaks occurring between the first quarter and full moon lunar phases, was found. However, the test procedures used make it difficult to discount a pattern

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initiated by test procedures rather than a naturally-occurring pattern. An apparent pattern of food utilization in relation to molting was found. Amounts ingested and assimilated show a gradual increase and peak, followed by a decline and subsequent cessation of feeding as the day of molting approaches.

INTRODUCTION

The marsh crab, Sesarma reticulatum (Say), is a Grapsid crab found in coastal areas from Woods Hole, Massachusetts, to Calhoun County, Texas (Williams, 1965). It is a semiterrestrial animal, living in the intertidal areas of salt marshes dominated by the cordgrass, Spartina alterniflora. Sesarma burrows into the muddy substrate of what Teal (1958) calls the tall Spartina edge marsh (near creek banks), the medium Spartina levee marsh (on the top and far side of natural creek embankments), and the short Spartina low marsh (in low areas between creeks). Teal's sampling of crab populations in a Georgia salt marsh indicates the greatest concentration of adult S. reticulatum in the tall Spartina edge marsh (30 crabs/m^2), with a somewhat lower concentration in the medium Spartina levee marsh ($21/\text{m}^2$), and a low concentration in the short Spartina low marsh ($2\text{-}3/\text{m}^2$) and on the creek bank ($1/\text{m}^2$). Field observations in part of Canary Creek Marsh, Lewes, Delaware, indicate a similar general distribution. Crichton (1965) estimates the density of Sesarma in this marsh as 13.8 crabs/m^2 along Canary Creek and $10.5/\text{m}^2$ along the drainage ditches. Assuming distribution of Sesarma in 2-m wide strips along either side of the creek (3200 m in length) and in 1-m wide strips along the drainage ditches (7500 m in total length), Crichton estimates total population size of Sesarma in Canary Creek Marsh as 3.3×10^5 crabs.

In constructing an energy flow diagram for a Georgia salt marsh, Teal (1962) classified both Sesarma and Uca (fiddler crab)

as detritus and algae feeders. However, Teal and Teal (1969) describe Sesarma feeding upon the outer leaves of Spartina. Investigation of stomach contents and fecal pellets, together with field observations of feeding habits, suggest that in Canary Creek Marsh a major portion of Sesarma's diet is composed of Spartina (Crichton, 1960; Daiber and Crichton, 1967). Spartina stands are sometimes grazed to such an extent that only stubble is left. Sesarma will occasionally prey upon Uca, which is often found in the same area of the marsh (Crichton, 1960).

A caloric study of the energy transferred daily to Sesarma feeding upon Spartina was conducted by Daiber and Crichton (1967) over a 9-day period. Biological efficiency (BE) was determined on a daily basis as follows:

$$\begin{aligned} \text{BE} &= \frac{\text{energy offered} - \text{energy unconsumed} - \text{fecal energy}}{\text{energy offered}} \times 100\% \\ &= \frac{\text{energy utilized}}{\text{energy offered}} \times 100\% \end{aligned}$$

A comparison of BE versus time in days showed fluctuations which suggested a possible cyclic pattern of energy utilization.

The possible existence of feeding rhythms has been investigated for few intertidal organisms. Many species display feeding activity at a particular tidal stage and/or time of day. In addition to these feeding patterns, tidal and/or diurnal rhythms of locomotor activity and oxygen consumption often occur. Cardium edule, a filter-feeding bivalve mollusk, exhibits a tidal rhythm of adductor movement coupled with tidal rhythms of water filtration and, consequently, feeding and digestion (Morton, 1970). Another filter-

feeder, the mole crab Emerita asiatica (Chandrashekar, 1965), and the isopod Naesa bidentata (Wieser, 1962) feed during flooding or high tide, when they also display the greatest locomotor activity and oxygen consumption. Uca spp. inhabiting areas with semi-diurnal tides feed during a daytime low tide, but Uca spp. from areas with diurnal tides feed during either daytime or nighttime low tides (Fingerman, 1957). Teal (1958) observed adult U. pugnax feeding on the marsh surface during a flooding tide, while U. pugilator was seen feeding at low tide. Two Grapsid crabs -- an omnivore (Pachygrapsus crassipes -- Bovbjerg, 1960) and a scavenger (Hemigrapsus oregonensis -- Symons, 1964) -- are apparently nocturnal feeders. Paine (1965) states that Navanax inermis, a carnivorous gastropod, appears to have no tidal or diurnal rhythms of feeding rate. Navanax, which shows tidal movement in its habitat, was shown to be capable of capturing and eating prey during both day and night. Since Navanax is predacious, Paine has assumed that its feeding would be dependent upon prey availability rather than any tidal or diurnal periodicity.

In showing a tidal rhythm for the rate of water propulsion in the mussels Mytilus californianus and M. edulis, Rao (1954) suggests that a greater "amplitude of the environmental rhythm" may lead to a more "marked and measurable ... intrinsic rhythm of the organism". Although a direct relationship may exist between tidal amplitude and respiratory or locomotor rhythm amplitudes, no conclusive decisions have been made (e.g. Chandrashekar, 1965). Damping or fading of these rhythms over time (in constant conditions)

have been found in many crustaceans tested (e.g. Emerita -- Chandrashekaran, 1965; Naesa -- Wieser, 1962; Carcinus maenas -- Arudpragasam and Naylor, 1964). Species which have both diurnal and tidal rhythms (e.g. Carcinus -- Naylor, 1958; Uca spp. -- Brown, et al., 1954; Bennett, et al., 1957) generally show an increased amplitude when the diurnal and tidal maxima occur simultaneously. This, in turn, results in a semilunar rhythm since about twice a month, a tide occurs at approximately the same time of day. However, since two semi-lunar rhythms occur at different times of the lunar month, a lunar-monthly rhythm may also result. Some species exhibit possible seasonal variations in rhythms of oxygen consumption (e.g. Hemigrapsus nudus and H. oregonensis -- Dehnel, 1958; Uca pugnax -- Webb and Brown, 1961) and locomotor activity (e.g. Hemigrapsus edwardsi -- Williams, 1969).

Sesarma reticulatum exhibits both tidal and diurnal rhythms of locomotor activity, with most activity occurring between 1800-0400 h (greatest activity from 1800-2400 h) and at high tide (Palmer, 1967). Amplitude of the tidal rhythm is about half that of the diurnal rhythm; it is not always evident in individual crabs. Simultaneous occurrence of tidal and diurnal peaks (e.g. at new and full moon lunar phases) results in increased amplitude of the single peak but does not increase or decrease total activity per day. Crabs were seen outside their burrows during the night, regardless of tidal stage, never being seen out of their burrows during a daytime low tide. (J. D. Palmer, personal communication).

According to Teal (1959), S. reticulatum is active at high tide or on cloudy days; at low tide Sesarma is found in its burrow, usually near the entrance, where it can be in either air or water. The present investigator has also noted the latter phenomenon in the field. Teal and Teal (1969) state that in the marsh, S. reticulatum remains in its burrow at high and low tides, coming out to feed on Spartina at mid-tide.

In view of the demonstration of oxygen consumption rhythms in several crustaceans, especially in the marsh-dwelling Uca species, it is probable that Sesarma exhibits a rhythm of oxygen consumption. The relation between rhythms of oxygen consumption and of locomotor activity seen in other crustaceans suggests that Sesarma may show peaks of oxygen consumption near the times of greatest locomotor activity (i.e. at night and at high tide).

Three major environmental cycles may affect Sesarma in the marsh. The intensity of illumination varies between day and night, and seasonal variations occur in length of the photoperiod. Temperature varies diurnally and seasonally with solar radiation, but it can be affected by such factors as cloud cover and wind. Tidal inundation is a third factor, with Canary Creek having two complete tidal cycles per day and the marsh characteristically flooded only on monthly spring tides.

Since Sesarma is mainly herbivorous, its obtainment of food would not be dependent upon a movable prey. However, environmental conditions of light, temperature, and the presence or absence of water with varying salinities might restrict Sesarma's feeding

activity to a certain time period. If the time of occurrence and actual duration of feeding are restricted to one part of the diurnal and/or tidal cycles (e.g. possibly at night or near high tide, as indicated by Sesarma's locomotor activity -- Palmer, 1967), a corresponding pattern of food ingestion and assimilation might occur. In view of the cyclic energy demands of such biological rhythms as oxygen consumption and locomotor activity, it may be that a corresponding depletion of the body's energy stores is coupled with a cyclic replenishing.

The main objectives of the present study are:

- 1) To determine energy utilization (in terms of ingestion, assimilation, and respiration) of the marsh crab, Sesarma reticulatum, feeding upon the cordgrass, Spartina alterniflora, over a lunar-monthly period.
- 2) To determine whether ingestion and assimilation follow a cyclic pattern.
- 3) To construct an energy budget for S. reticulatum.

MATERIALS AND METHODS

I. FEEDING

A. Collection

Collections were made in Canary Creek Marsh, an intertidal salt marsh located near the mouth of Delaware Bay. Man-made drainage ditches, somewhat perpendicular to the creek, occur throughout the marsh. Spartina distribution along and between the ditches is similar to that along the creeks described by Teal (1958).

Adult male Sesarma were dug from their burrows along a drainage ditch in the lower reaches of the marsh. Group I (7 crabs) was collected on June 18, 1971, Group II (15 crabs) on July 23, and Group III (14 crabs) on September 20; all collections occurred in the afternoon near the time of low tide. A plastic tub containing shallow seawater was used to transport the crabs to the Bayside Laboratory.

In all three groups, the crabs were rinsed with seawater to remove adhering mud, blotted with a paper towel, then weighed on a triple-beam balance. A few crabs were minus a walking appendage; the number and position of each missing limb were recorded.

The carapace width of each of 23 male Sesarma was measured as the distance between the lateral points on the outer edges of the eyestalk sockets. Carapace width versus wet weight was plotted and a least-squares regression (Steel and Torrie, 1960) was calculated to cover only the range measured.

Sample size of Group I was chosen arbitrarily. To determine sample size needed for subsequent groups, biological efficiencies (based upon feeding data for 7 crabs on each of 7 days, converted to caloric values) were subjected to an analysis of variance (Snedecor and Cochran, 1967). Based upon this, it was ascertained that a minimum sample size of 14 crabs would be adequate.

Group III crabs, placed in individual containers of seawater, were transported to Newark, Delaware, along with medium-tall Spartina alterniflora plants with their root masses. These crabs were not fed in the laboratory on the day of collection. The following day, fecal pellets produced in the containers were examined for general comparison with those obtained during the feeding experiment.

B. Experimental Conditions

The crabs were placed in individual clear plastic boxes (4 x 5 x 7 in.) containing coarsely-filtered seawater (Groups I and II) or artificial seawater (Group III) to a depth of about 1.5 cm (not quite covering the carapace). Each crab was assigned a number.

To check for the presence of possible feeding rhythms, without entrainment to an artificial lighting cycle, the crabs were maintained in darkness. Preliminary observations indicated that Sesarma could eat Spartina in darkness. For Groups I and II, the containers were placed on shelves on a light-tight laboratory bench made by draping black plastic sheeting from the top of the shelves. Entrance to the "dark-room" was obtained by crawling

under the sheeting. Two 25 W red light bulbs were used for illumination when working within the "dark-room". Group III crabs were retained for three days in a basement room in which there was no definite light/dark cycle. They were then transferred to a darkroom four stories above. Again, two 25 W red light bulbs were used for illumination only when working with the crabs; otherwise, the room was in constant darkness.

C. Measurement of Energy Pathway Components

The outer blades of Spartina alterniflora were collected daily for Groups I and II from the marsh adjacent to Bayside Laboratory. Blades for Group III were obtained daily from the Spartina supply maintained in plastic buckets. The leaves were wiped with a paper towel to remove adhering dirt particles and salt crystals. They were then cut into pieces 4 cm long; only the mid-blade section, not the tip or the lower end, was used. Three pieces of Spartina were weighed (wet weight) together on an analytical balance and offered daily to each crab.

Three additional aliquots, each containing three 4-cm pieces of Spartina cut at the same time as those fed to the crabs, were weighed. The aliquots were dried in pre-weighed aluminum pans in an oven at 100° C for about one-half hour for Group I; aliquots for the remaining groups were dried for several hours, to constant weight, at 100° C (Group II) and 54° C (Group III). They were then allowed to cool for about one minute and weighed again; weight differences were recorded as dry weight of Spartina. Percent dry weight was determined by averaging the three results. Daily

percentages were then used to calculate an average percent dry weight for each group's test period.

Seawater was collected daily from the Broadkill River at the same time as the Spartina for Groups I and II. The water was filtered through coarse filter paper (Fisher, # 09-795) to remove large particles. Artificial seawater (Instant Oceans sea salts) was stored in a 30-gallon plastic container for Group III.

Daily each crab was removed from its container. The uningested Spartina fragments were removed using forceps and transferred to numbered plastic vials. The seawater, which contained fecal material and minute uningested Spartina fibers, was poured into a numbered 125-ml Erlenmeyer flask. The box was rinsed with tapwater once again and the water discarded. Freshly-filtered seawater was poured into the container to a depth of about 1.5 cm. The crab was replaced, along with its allotment of Spartina, and the lid closed.

The uningested Spartina fragments were removed from each vial, rinsed in tapwater to remove excess salt, then blotted on a paper towel. Water samples containing fecal material were filtered separately using coarse filter paper. Uningested Spartina and feces were subjected to the same drying and weighing procedures used for the fresh Spartina. Occasional small fragments of uningested Spartina were found with the filtered feces; these were transferred to the appropriate pan of uningested Spartina. Dry weight of uningested Spartina and of unassimilated Spartina (feces) was recorded.

Dry weight of the Spartina offered was calculated as follows:

$$(1) \text{ Dry weight} = \text{wet weight} \times \% \text{ dry weight}$$

where % dry weight is the average value for that group. Dry weights were used to compute the following:

$$(2) \text{ Amount ingested} = (\text{amount offered}) - (\text{amount uningested})$$

$$(3) \text{ Amount assimilated} = (\text{amount ingested}) - (\text{amount unassimilated})$$

Daily records were kept for time of water change and time of feeding. Air temperature near the crab containers was recorded once daily (at the time of water change) using a mercury thermometer; temperature was recorded soon after the red lights were turned on, since heat from the lights caused a slight increase in temperature. For Groups II and III, salinity of the seawater used in changing the container water was also measured, using a refractometer (Group II) or a hydrometer (Group III).

It was assumed that unassimilated Spartina was egested as feces during the same 24-hour period in which the Spartina was offered to the crabs. To check this assumption, a time study of fecal production was conducted. Since the Spartina supply had been depleted, lettuce was used in lieu of Spartina to give a general indication of fecal production rates. Seventeen adult male Sesarma (most of which had been used in the feeding study) were starved for one day. Seawater (about 30 ‰) in the individual crab containers was changed at 1900h. The crabs were fed unmeasured but excess amounts of lettuce at 1920h and the lights were turned off. The next day, the containers were checked at 1140,

1400, 1600, and 1620h. At these times, the presence of feces was recorded and all feces were removed.

II. RESPIRATION

Prior to the experiments, the crabs were kept on an LD 12:12 cycle, with lights on at 0800h and lights off at 2000h (EST). They were maintained on a Spartina (Part A) or a lettuce (Part B) diet except for a 24-hour starvation period before the experiments.

A. Water

Respiration in water was determined using a standing-water method. Artificial seawater was bubbled with air for approximately 15 minutes to increase the oxygen concentration to near-saturation. The oxygen content was ascertained by pouring water into a 500-ml glass jar and siphoning it from this closed vessel into numbered 150-ml flasks. The samples were immediately fixed with Winkler reagents (Welsh et al., 1968) and stoppered for later oxygen analysis. The oxygenated water from the reservoir vessel was poured into both control (artificial seawater) and experimental (artificial seawater and a crab) jars, which were stoppered, placed in a stirred water bath for one hour, and then removed. Two 150-ml water samples were siphoned from each jar, care being taken to allow the water to overflow the flask to displace water previously in air contact. The samples were fixed and stoppered, and recorded oxygen values were averaged.

A total of 23 crabs was used, with the wet weight of each crab determined at the end of a trial. Crab volume was found by water displacement in a graduated cylinder. Experiments were

conducted between 1100 and 1700h to lessen effects of possible diurnal rhythms of oxygen consumption. Additional records were kept for time of runs, barometric pressure, air temperature, water bath temperature, and salinity of the experimental water. Stopped flask volumes and jar volumes were determined using water and a graduated cylinder.

Respiration of the crabs was calculated as follows:

$$(4) \text{ Respiration of crab and material in water} = \frac{(I_i - R_f) \text{ jar vol. of } R_f - \text{vol. of crab}}{1000 \text{ ml}}$$

where $I_i = O_2$ concentration of initial seawater

and $R_f = O_2$ concentration of water in jar containing crab (i.e. respiration jar) at end of 1 hour.

$$(5) \text{ Respiration of material in water} = \frac{(I_i - H_f) \text{ jar vol. of } R_f - \text{vol. of crab}}{1000 \text{ ml}}$$

where $H_f = O_2$ concentration of water in control jar at end of 1 hour. Subtracting equation 5 from equation 4, the respiration of the crab is found as follows:

$$(6) \text{ Respiration} = \text{ml } O_2/\text{hr.} = \frac{(H_f - R_f) \text{ jar vol. of } R_f - \text{vol. of crab}}{1000 \text{ ml}}$$

Weight-specific values of oxygen consumption were then calculated as follows:

$$(7) R = \text{ml } O_2/\text{g per hr.} = \frac{\text{ml } O_2}{\text{hr}} \times \frac{1}{\text{g wet weight of crab}}$$

B. Air

Respiration in air was determined using a Scholander manometric apparatus (patterned after that of Welsh et al., 1968) with Brodie's solution as the manometric fluid. The animal chamber

contained a wire mesh stage on which the crab rested. Below this stage was placed a well with fluted filter paper and about 2-4 ml of 10% KOH solution to absorb CO_2 . The compensation chamber contained two rubber stoppers to approximate and compensate for the volume of the crab; however, it was later found that use of the stoppers was unnecessary to maintain equilibrium. Both chambers were moistened with artificial seawater of approximately 30 ‰ and a crab was placed in the animal chamber prior to closing the system. All open joints -- stopper hole, syringe hole, and chamber circumferences -- were sealed with Lubriseal. The closed system was allowed to equilibrate in a water bath for one-half hour. Readings were then taken at three half-hourly intervals. The manometer fluid was adjusted to a marked level position by slowly injecting air from the syringe into the system. Milliliters of oxygen consumed were read from the syringe barrel. After readings were taken, the system was removed from the water bath. The crab was removed from the chamber and weighed on a triple-beam balance.

Respiration trials were conducted between 0900 and 1600h. Additional records were kept for time of measurements, barometric pressure, air temperature, and water bath temperature.

Oxygen consumption per hour was calculated by averaging three half-hourly readings and multiplying by two. Weight-specific oxygen consumption was calculated.

RESULTS

I. FEEDING

A. Weight and Size of Crabs

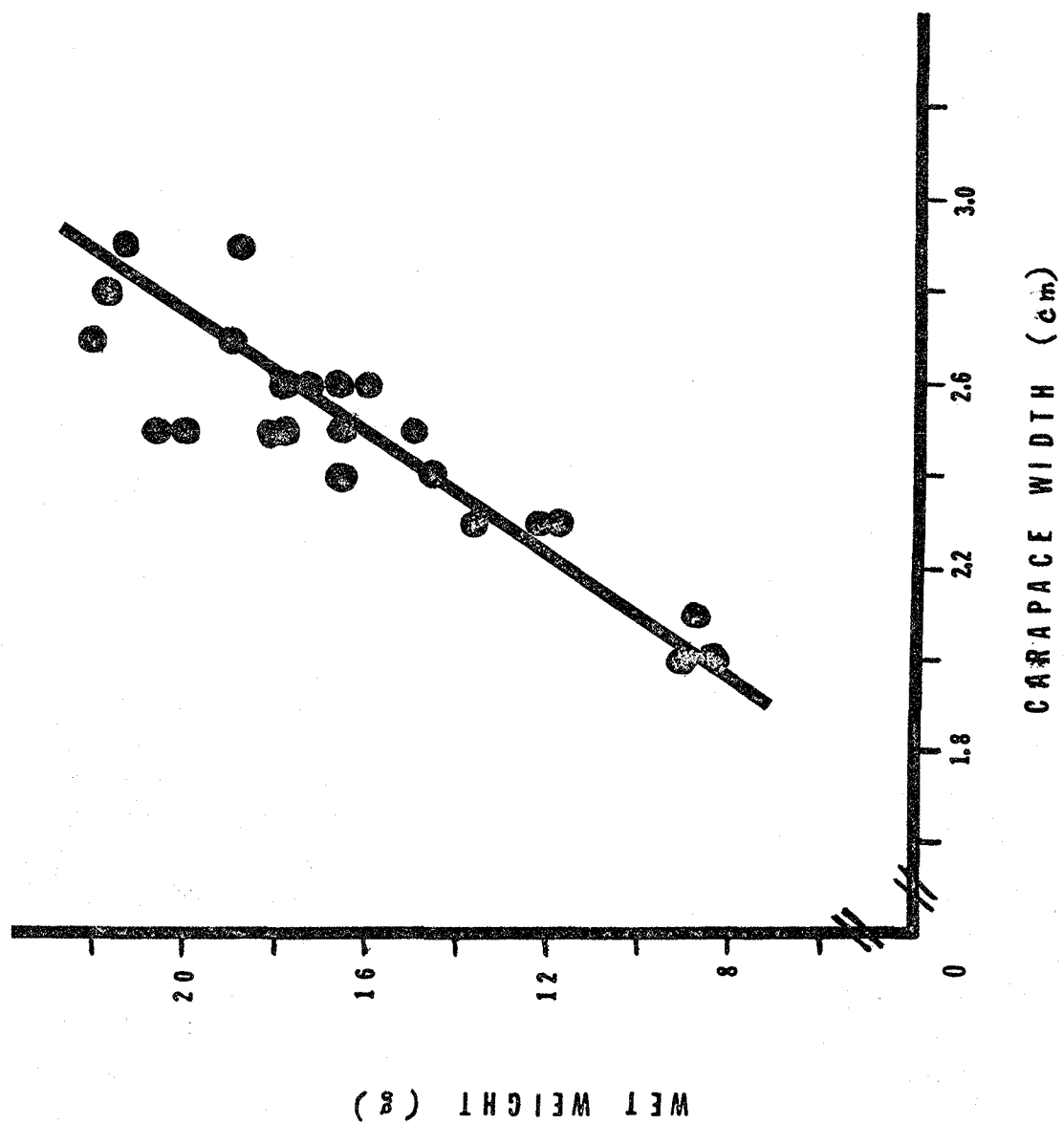
Initial wet weight of crabs used in the feeding experiments is shown in Table 1. The second set of initial weights and the final weights (i.e. at end of feeding experiment) for Groups II and III are for those individuals with complete weight records. (Weight records are incomplete for Group II individuals which molted and for one Group III individual which was used in a separate experiment prior to weighing.) Weight range and mean weight are greatest for Group II, with Group I having the smallest range and mean. The data from Table 1 indicate weight gains for Groups I and III, while all crabs in Group II which survived molting or did not molt appeared to decrease in weight. It is not known to what extent weight was affected by water present in the gill chamber.

The wet body weight (W) - carapace width (C) relationship for 23 adult male Sesarma was calculated as $W = -20.46 + 14.71C$; the regression line and actual data are shown in Figure 1. The standard error of estimate (S_E) is 2.55. Standard error of the regression coefficient (S_b) is 2.21; a t-test indicates that the slope is significantly greater than zero at the 0.05 confidence level. It should be noted that this regression is valid only for the range of carapace values from 2.0-2.9cm.

Table 1. Wet weight of Sesarma reticulatum (in grams) collected from Canary Creek Marsh during the summer of 1971.

GROUP	DATE	N	RANGE	TOTAL	\bar{X}	S
I	6/19/71	7	11.1-17.7	99.9	14.3	2.5
	7/24/71	7	11.3-19.2	103.4	14.8	2.9
II	7/24/71	13	11.6-23.6	242.8	18.7	7.6
	7/24/71	8	11.6-23.3	150.9	18.9	4.2
	9/19/71	8	11.3-22.3	133.6	16.7	4.0
III	9/21/71	14	11.7-20.9	238.8	17.1	2.5
	9/21/71	13	11.7-20.9	218.0	16.8	2.4
	12/13-12/18/71	13	11.8-21.0	219.9	16.9	2.4

Figure 1. Carapace width - wet body weight relationship
for male Sesarma reticulatum collected from
Canary Creek Marsh during the 1971 summer.



B. Energy Pathway Components

Fecal pellets were produced by 11 of the 14 freshly-collected crabs. Of these, feces from nine contained plant material similar to that in feces produced by crabs fed Spartina in the laboratory. Fecal pellets from one crab contained some plant fibers, what appeared to be brown diatoms, and unidentified particles. Another crab's fecal pellets contained some plant fibers, small chitinous plates and crustacean appendages with spines, a few small sand grains, and unidentified particles. Thirteen of these crabs ate Spartina in the laboratory the first day it was offered; by the third day, all 14 crabs were eating the grass.

Unassimilated food was egested fairly rapidly. In the study of fecal production rates, 11 of the 17 crabs tested produced fecal pellets within 16-1/3 hours. Six produced no fecal pellets within 21 hours. It is not known whether these crabs actually ingested lettuce.

During the feeding experiments, the crabs were exposed to ambient room temperatures (i.e. 24-26°C for Groups I and II, 20-26°C for Group III). Salinities of seawater used in Groups I and II varied with tidal stage at time of collection (e.g. average of 27 ± 3.5 ‰ for Group II); Group III salinities were kept fairly constant (i.e. average of 30 ± 1.1 ‰).

Results of the feeding experiment are seen in Table 2. Length of the experiment was 25 days for Group I, 42 days for Group II, and 38 days for Group III. To keep a constant time factor, totals for Groups II and III were calculated using values for one lunar

Table 2. Total amounts of Spartina alterniflora offered to and processed by the three Sesarma reticulatum groups during one lunar period. Values given as total grams dry weight and grams dry weight of grass/grams wet weight of crab.

Group	<u>Spartina</u> <u>Offered</u>	<u>Uningested</u> <u>Spartina</u>	<u>Ingested</u> <u>Spartina</u>	<u>Unassimilated</u> <u>Spartina</u>	<u>Assimilated</u> <u>Spartina</u>
I	35.642 g 0.36 g/g crab	21.496 0.22	14.146 0.14	6.873 0.07	7.273 0.07
II	88.703 g 0.37 g/g crab	74.411 0.31	14.292 0.06	4.717 0.02	9.575 0.04
III	71.177 g 0.30 g/g crab	21.603 0.09	49.574 0.21	28.285 0.12	21.289 0.09

month (i.e. 30 days), beginning with the first quarter lunar phase. Since Group I was not studied for an entire lunar period, values for one semi-lunar period (i.e. 15 days), beginning with the first quarter phase, were summed and then doubled to approximate a lunar period. Sample size of Group II was reduced from 15 to 13, since one crab died and another crab molted prior to the end of the 30 days.

Average percent dry weight of Spartina was $28.4 \pm 1.74\%$ for Group I, $28.4 \pm 2.12\%$ for Group II, and $33.7 \pm 2.04\%$ for Group III.

The lunar-monthly totals of the three groups cannot be compared, since the groups included different numbers and weights of crabs. For a more valid comparison, on a crab weight basis, feeding data were divided by the total wet weight of crabs in each group. As seen in Table 2, the amounts of Spartina ingested/g crab and assimilated/g crab are highest for Group III and lowest for Group II.

Of the 14 crabs in Group II which survived during the feeding experiment, 12 molted; half of these died during or shortly after molting. One individual molted at the new moon lunar phase (August 20, 1971); the others molted within a 5-day period between the first quarter (August 29) and full moon (September 5) phases. Three crabs retained from Group I molted at the same time as those of Group II. No crabs from Group III molted. In all cases where a walking appendage had been missing, a new appendage (though pale in color) was present after molting.

The possibility of molting occurring during the feeding

experiment had not been considered; consequently, precautions had not been taken to insure proper conditions for ecdysis. When the first crabs molted, seawater was added to all containers to a level covering the carapace. The crabs were retained in the "dark-room" laboratory bench and the daily feeding procedure was continued. One crab was seen holding a piece of Spartina with its chelipeds the day after it molted; however, it did not appear to eat any of the grass.

To check for possible cycles over a lunar-monthly period, daily individual crab values for Spartina ingested and assimilated were summed for each group and plotted versus time. Lunar phases (first quarter, full moon, last quarter, new moon) were included as reference points. Since sample size of the three groups differed, the exact values of the data represented on these graphs cannot be compared but the form of the graphs can be. Similar graphs, with decreased amplitudes, result when these values are plotted on a per-gram-crab basis.

Total amount ingested is greater than total amount assimilated in all groups. Group I (Figure 2) shows peaks of ingestion and assimilation near days 6 and 20, with a low point occurring about day 13. Fluctuation is more pronounced in amount ingested than in amount assimilated. Group II (Figure 3) shows an apparent pattern of food utilization in relation to molting. The amounts ingested and assimilated show a fairly rapid increase from day 4 to about day 12. A gradual decline follows, reaching zero at the time of molting. Amounts ingested and assimilated in Group III

Figure 2. Total g dry weight of Spartina ingested (●) and assimilated (○) daily by all Sesarma in Group I (N = 7).

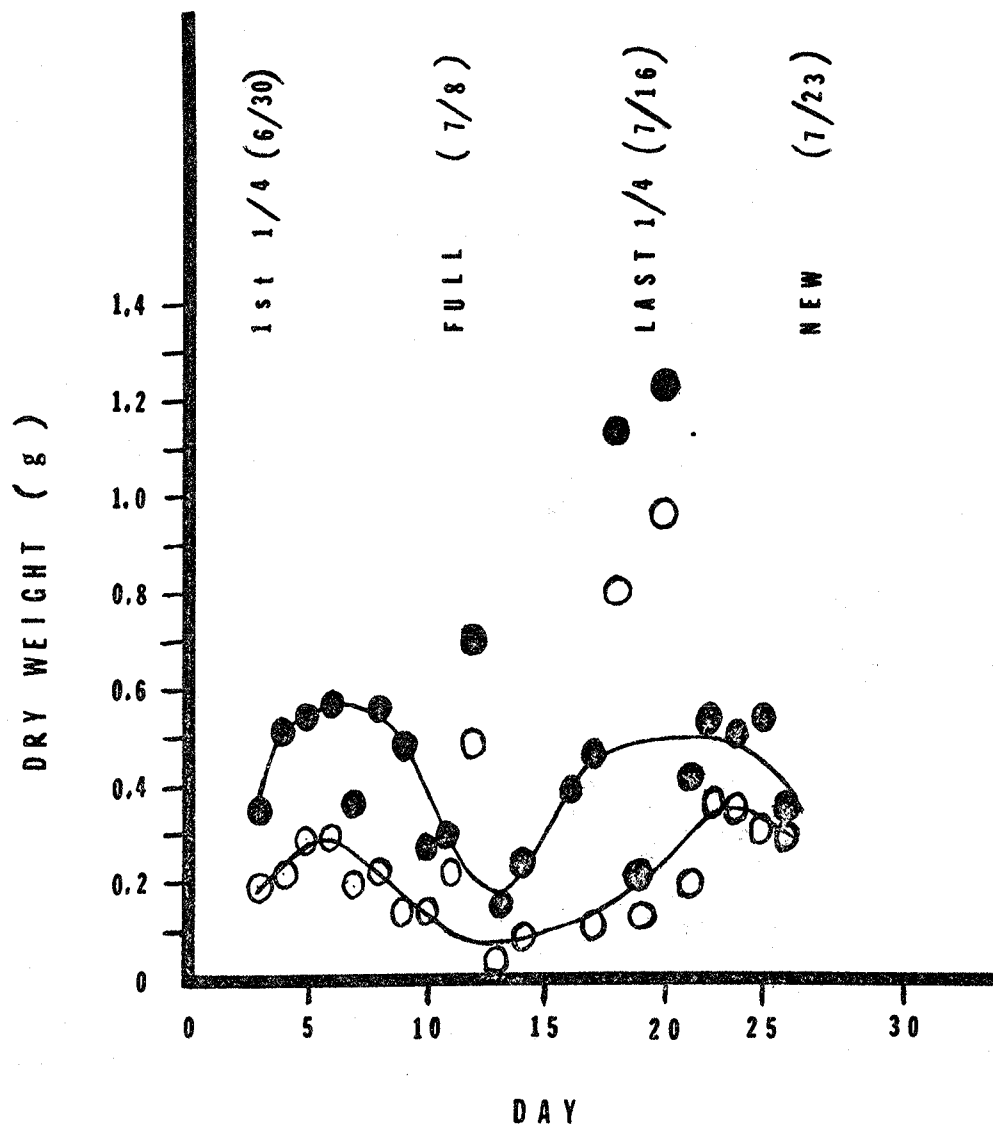
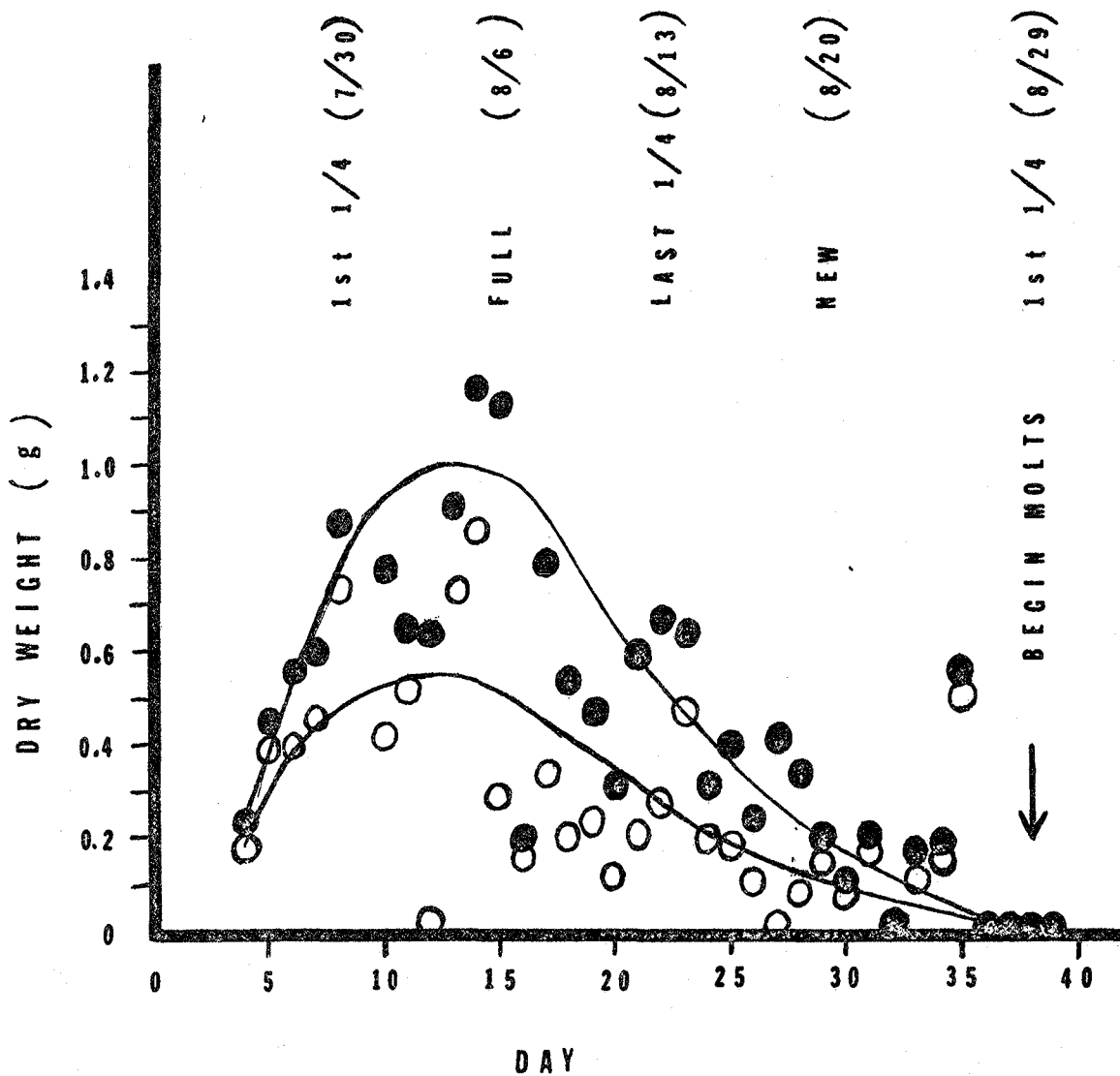


Figure 3. Total g dry weight of Spartina ingested (●) and assimilated (○) daily by all Sesarma in Group II (N = 13).



(Figure 4) show a large peak near day 8 and a smaller peak on day 20, with low points near days 15 and 23; thereafter, an apparent linear pattern occurs.

Group II was composed of three types of individuals: daily eaters, occasional eaters, and non-eaters. Total amounts ingested and assimilated per day by the daily eaters follow a pattern similar to that of Figure 3. The occasional eaters and non-eaters show an indefinite pattern of ingestion and assimilation.

II. RESPIRATION

A. Water

The weight-specific oxygen consumption (R) versus wet body weight (W) relationship was calculated (after Prosser and Brown, 1966) using the formula

$$(8) R = a W^{(b-1)}$$

The calculated regression is

$$(9) \log R = -0.857 - 0.344 \log W$$

and the initial equation becomes

$$(10) R = 0.139 W^{0.656}$$

The regression line and actual data are seen in Figure 5. S_E was calculated to be 0.087 ml O_2 /g per hour, with $N = 23$. S_b was found to be 0.072. The slope of the regression line is significantly greater than zero at the 0.05 confidence level, since $t = 4.78$ (t for 21 df = 2.08).

Initial oxygen concentration of water used in the experiments averaged 7.5 ppm (about 5.2 ml O_2 /l). Salinity of the water was 29-30 ‰, at an average initial temperature of 22°C. Water

Figure 4. Total g dry weight of Spartina ingested (●) and assimilated (○) daily by all Sesarma in Group III (N = 14).

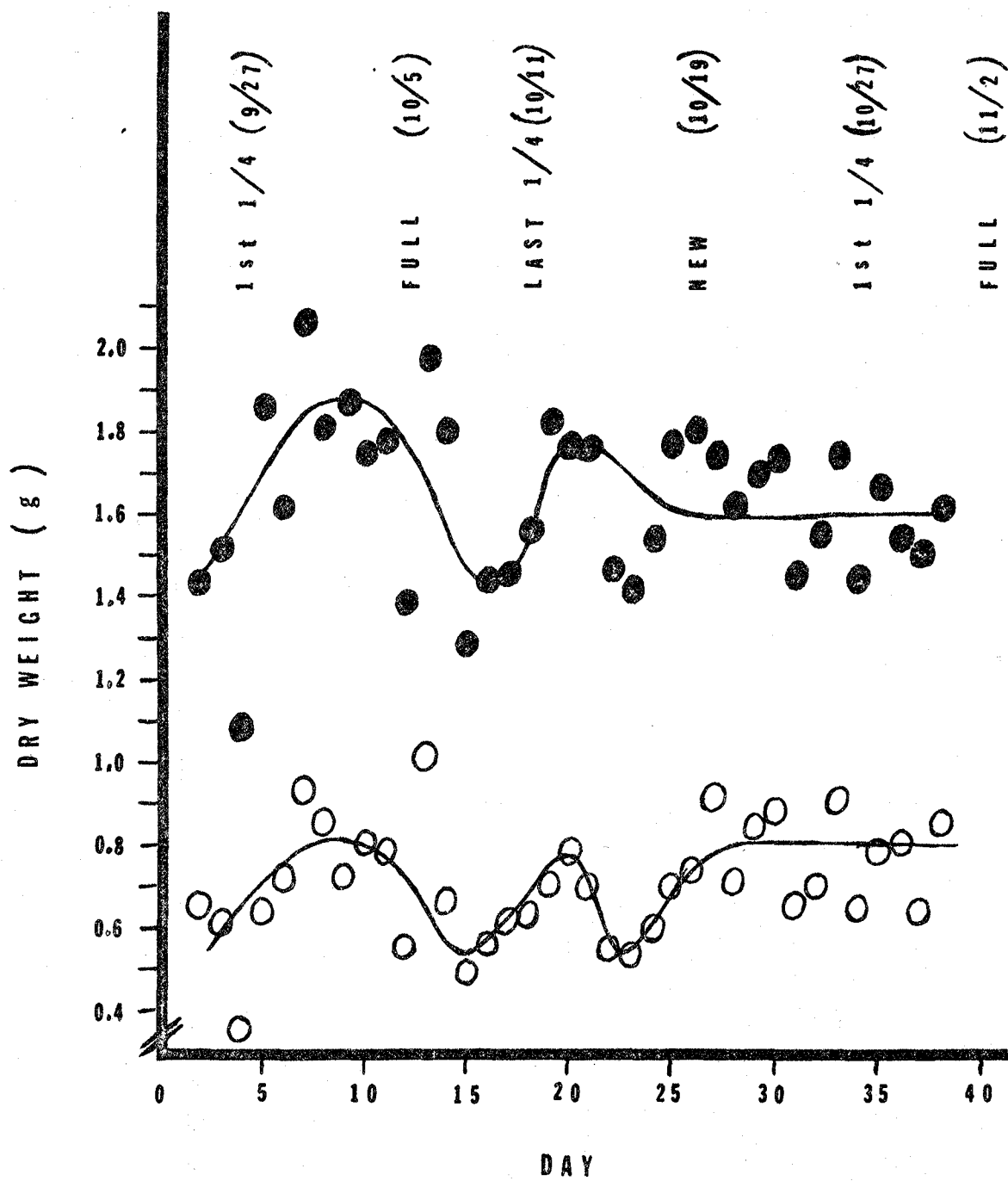
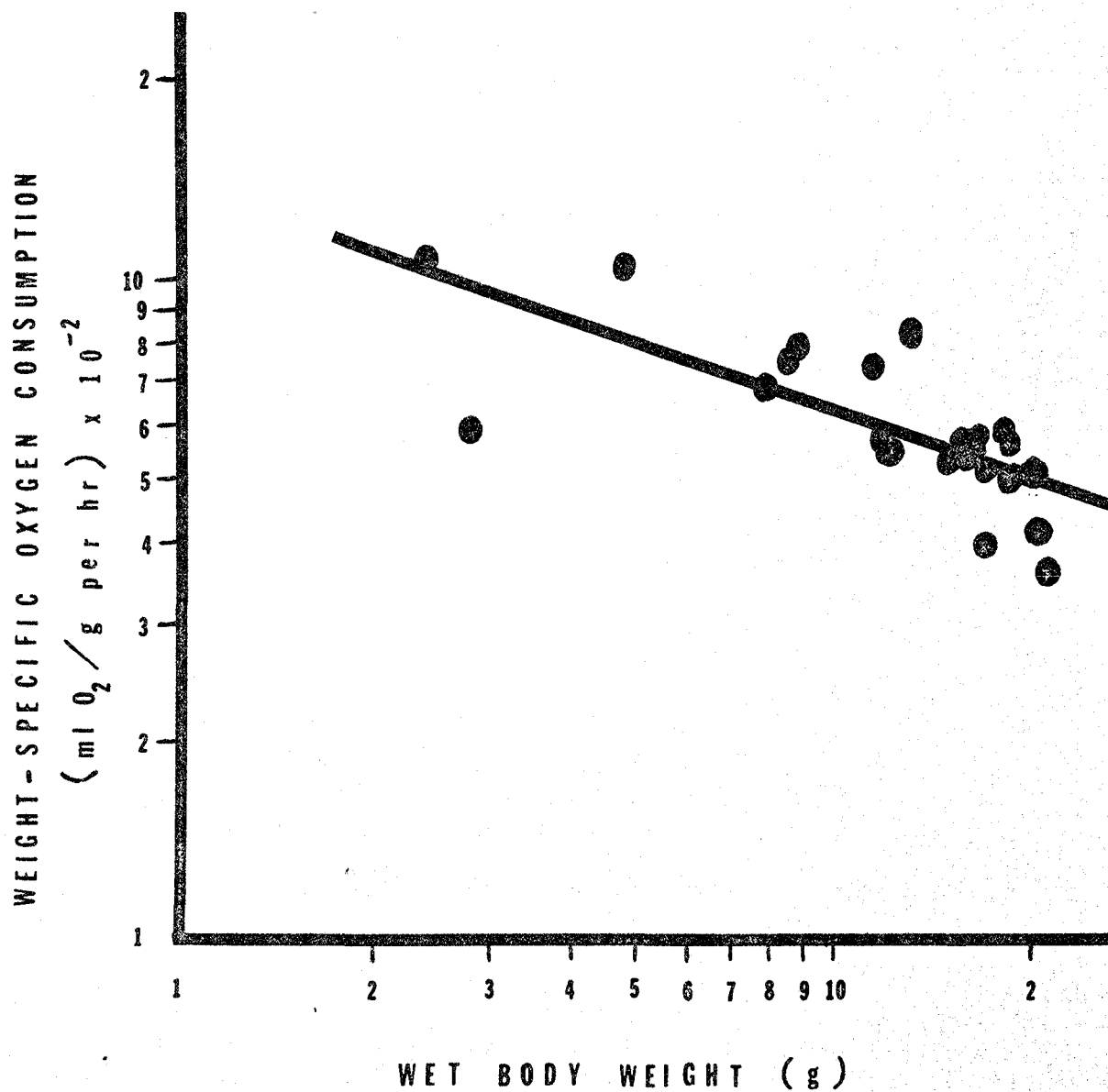


Figure 5. Double logarithmic plot of weight-specific oxygen consumption in water versus wet body weight of Sesarma reticulatum.



bath temperature was 24-25°C, similar to ambient air temperature measurements.

B. Air

An initial blank run indicated stability of the manometer fluid without an animal present in the chamber. Although 25 measurements were subsequently made using 19 individuals, two later blank runs indicated an apparent oxygen uptake of a similar magnitude. Also, the Scholander apparatus did not appear to be completely water-tight in all cases. Taking this -- and the erratic data -- into account, it was felt that the data did not represent true respiration values. An S_b value was calculated for the data and tested with a t-test; the test indicated acceptance of the null hypothesis (i.e. b was not significantly from zero). Since a regression of respiration versus body weight would be expected to have a slope significantly different from zero, the data have been rejected and are not included in this report.

DISCUSSION

I. ENERGY BUDGET

An energy budget for Sesarma reticulatum can be constructed using data from the present study and the literature. Averaging Daiber and Crichton's (1967) caloric values of fresh Spartina and Spartina unassimilated by Sesarma gives 4.159 kcal/g dry weight and 3.226 kcal/g dry weight, respectively. These values are used to convert the g dry weight values of Table 2 into the caloric values seen in Table 3.

The respiration values of Figure 5 represent the resting metabolic rate, since crabs used in the respiration measurements were mostly inactive and were starved for about one day prior to the experiment (i.e. no increase in respiration due to digestion). Using data from the author's recording of one crab's spontaneous locomotor activity during an LD 12:12 light cycle and from Palmer (1967), it is estimated that Sesarma is active about 10 hours/day. Oxygen consumption of marsh crabs in air increases two- to threefold in going from resting to active metabolism (S. cinereum and Uca spp. -- Teal and Carey, 1967; Uca pugnax -- Brown et al., 1954). Hughes (1970) cites several respiration studies which use a factor of 2 to determine increased respiration during activity. The activity period and an assumed twofold increase in respiration of Sesarma are used to calculate daily respiration (R) as follows:

$$(11) R = (\text{ml } O_2/\text{g per hr} \times 2 \times 10 \text{ hr/day active}) \\ + (\text{ml } O_2/\text{g per hr} \times 14 \text{ hr/day resting})$$

Table 3. Total caloric values for Spartina alterniflora offered to and processed by the three Sesarma reticulatum groups during one lunar period. Values given as total kcal and kcal/g wet weight of crab.

Group	<u>Spartina</u> <u>Offered</u>	<u>Uningested</u> <u>Spartina</u>	<u>Ingested</u> <u>Spartina</u>	<u>Unassimilated</u> <u>Spartina</u>	<u>Assimilated</u> <u>Spartina</u>
I	148 kcal 1.48 kcal/g crab	89 0.89	59 0.59	22 0.22	37 0.37
II	369 kcal 1.52 kcal/g crab	309 1.27	60 0.25	15 0.06	45 0.19
III	296 kcal 1.24 kcal/g crab	90 0.37	206 0.87	91 0.38	115 0.49

Group	<u>Respiration</u>	<u>Production</u>
I	30 kcal 0.30 kcal/g crab	7 0.07
II	68 0.28	-23 -0.09
III	69 0.29	46 0.20

where ml O_2 /g per hr is that value found using the respiration regression (Equation 9) and the mean crab wet weight for each group (initial weight -- Table 2). The resulting R values are then multiplied by 30 days/month to give lunar-monthly respiration values.

Since a respiratory quotient (R.Q. = CO_2 produced/ O_2 consumed) was not calculated in the present study, the standard R.Q. of 0.85 common in energetics studies (Engelmann, 1966) is used. This assumes that a mixture of protein, fat, and carbohydrate is metabolized, giving a resulting oxycalorific coefficient of about 4.8 kcal/l O_2 , based upon the data of Ivlev (1934). Slobodkin (1962) indicates only a 5% variation in the coefficient over an R.Q. range of 0.71-1.00; a 4.4-7% difference exists in the caloric equivalent of oxygen calculated on the basis of a fat, protein, or carbohydrate energy source (Hughes, 1970; Swift and French, 1954). By multiplication, respiration is thus converted to the caloric values seen in Table 3. Respiration, as kcal/g crab, is similar for all three groups but is highest for Group I.

The regression line for weight-specific oxygen consumption versus wet body weight (Equation 9) has a calculated slope (-0.344) similar to that of -0.347 for S. reticulatum found by Teal (1959). The respiration estimates were based upon measurements in water. In the marsh, Sesarma may spend more time in air than in water. Since respiration rate is somewhat greater in water than in air (Teal, 1959), estimates of respiration for the three groups may be too great. However, exclusion of increased oxygen consumption due

to factors such as digestion (Wissing and Hasler, 1971) and molting (Roberts, 1957; Chandrashekar, 1965) may compensate for this over-estimate. S. reticulatum might adjust its oxygen consumption in response to variations in temperature, salinity (cf. S. plicatum -- Madanmohanrao and Rao, 1962), and oxygen concentration of the medium (Teal, 1959; Teal and Carey, 1967).

Production (here meaning growth or tissue increase) is found by subtraction:

$$(12) \text{ Production} = (\text{assimilation}) - (\text{respiration})$$

The calculated values, given in Table 3, indicate some growth for Groups I and III but imply a decrease in biomass for Group II. Weight losses exhibited by several individuals may imply that a diet consisting solely of Spartina for extended periods of time can be nutritionally insufficient. During late spring, before Spartina has grown very tall in the marsh, Sesarma might be primarily a detritus-algae eater. Detritus-algae feeding, predation upon Uca (Crichton, 1960), and cannibalism (e.g. just after molting and under crowded conditions -- personal observation) may serve to supplement Sesarma's apparent basic summer diet of Spartina. A few Group II individuals which did not eat during the experiment still survived, thus implying that Sesarma can subsist for extended periods by apparently using energy sources stored within the body.

Extrapolation from results of the present study to an energy budget for the entire S. reticulatum population of Canary Creek Marsh would require knowledge of such factors as population size and actual distribution within the marsh, size (in terms of carapace

width and/or weight) of animals within that population, variations in ingestion and assimilation with crab size and sex, respiration rate in air versus in water, time spent in air versus water, and Spartina productivity and total standing crop.

II. EFFICIENCIES OF ENERGY UTILIZATION

Efficiencies of energy utilization by Sesarma (Table 4), based upon the calculated monthly caloric values for each group (Table 3), are found using the following ratios (after Kozlovsky, 1968):

Consumption or utilization efficiency	$\frac{I_n}{NP_{n-1}}$
Assimilation efficiency	$\frac{A_n}{I_n}$
Ecological growth efficiency	$\frac{NP_n}{I_n}$
Growth or tissue growth efficiency	$\frac{NP_n}{A_n}$
Respiration/assimilation	$\frac{R_n}{A_n}$

where I = ingestion

A = assimilation

R = respiration

NP = net production (i.e. A - R)

n = 2° trophic level (i.e. Sesarma)

n - 1 = 1° trophic level (i.e. Spartina)

The consumption efficiencies imply that the amount of Spartina offered to the crabs was not limiting in Groups I and II but might

Table 4. Efficiencies of energy utilization by Sesarma reticulatum feeding upon Spartina alterniflora. All ratios multiplied by 100% to give percent.

Group	$\frac{I_n}{NP_{n-1}}$	$\frac{A_n}{I_n}$	$\frac{NP_n}{I_n}$	$\frac{NP_n}{A_n}$	$\frac{R_n}{A_n}$
I	40%	63%	12%	19%	81%
II	16%	76%	-36%	-47%	14%
III	70%	56%	23%	41%	59%

have been limiting in Group III. Consumption of all the Spartina offered to a few Group III crabs on some days implies that the amount offered limited the amount ingested (i.e. the actual amount ingested was less than the amount which could have been ingested had a greater amount of Spartina been offered). The difference between consumption efficiencies of Groups I and III may reflect the different mean crab size of the two groups. On a per gram of crab basis (Table 2), the amounts ingested and assimilated are greater for Group III, whose total wet body weight and mean weight are greater than those of Group I. Group II is an exception, since several crabs ate inconsistently and many molted. Comparison of total grams dry weight of Spartina utilized by each Group III individual during the entire test period indicates a general increase in total amount ingested with increased wet body weight of crab; a lesser increase in total amount assimilated occurs with increased body weight.

Assimilation efficiency is greatest for Group II and lowest for Group III. Comparison with consumption efficiencies (Table 4) and total amounts of Spartina ingested and assimilated (as kcal/g crab -- Table 3) implies that when more Spartina is consumed, less is assimilated. Assimilation efficiencies of the three groups fall within the range of 22.4-86.2% calculated from Daiber and Crichton's (1967) data for Sesarma, but they are all greater than the calculated average of 48.6%. The three efficiencies are also high compared with those of other invertebrate herbivores (e.g. a composite winter percentage for detritus-feeding marsh crabs,

including S. reticulatum, Uca pugilator, and U. pugnax, 23-31% -- Teal, 1962; Orchelimum fidicinum, a Spartina-feeding grasshopper, 36% -- Odum and Smalley, 1959; Fissurella barbadensis, an algal-feeding mollusk, 33.6% -- Huges, 1971). However, they are close to the range of 65-75% given by Engelmann (1966) as common for most herbivores (based upon mammalian studies). Efficiency of Group III is similar to 61% for the deposit-feeding bivalve mollusk Scrobicularia plana (Hughes, 1970) and 62% for the carnivorous gastropod Navanax inermis (Paine, 1965). Factors such as possible incomplete defecation of uningested Spartina prior to fecal collection might give a high estimate of assimilation efficiency.

The amounts of Spartina consumed and assimilated by Sesarma might vary with the quality of the blades, especially in relation to the maturity of the plants. The major biochemical components of mature Spartina leaves from a low marsh area, as percent of total dry weight, are 47.4% N-free extract, 30.2% crude fiber, 9.2% protein, 2.6% fat, and 10.6% ash (averages based upon Burkholder, 1956). Young leaves contain greater proportions of protein and ash but less N-free extract. Teal (1962) states that the N-free extracts of a Spartina/mud mixture are carbohydrates and the crude fiber is primarily cellulose. It would seem that, on the basis of efficiency not greater than about 60%, assuming that cellulose and ash are ingested but not assimilated and that the other components are ingested and assimilated. It is not known whether Sesarma can utilize cellulose. If Sesarma feeds selectively, discarding fibrous matter (as suggested by O. W. Crichton, personal

communication), an assimilation efficiency greater than 60% could result. Orchelimum (Marples, 1966) was observed to feed upon the upper part of Spartina blades, eating the soft tissues while avoiding the harder fibers. In the laboratory, Orchelimum ate the entire blade if no additional blades were available for selective feeding.

Ecological growth efficiency of Group I is similar to those of about 10% for Orchelimum (calculated from Smalley, 1960), 8% for Fissurella (Hughes, 1971), and 13% for a freshwater crustacean, Daphnia (Slobodkin, 1962). Group II displays a negative efficiency; this reflects the low amount of Spartina ingested by this group in relation to the energy demands of respiration. The efficiency of Group III is higher than the given literature values.

Tissue growth efficiency of Group I is similar to that of 17% for detritus-feeding marsh crabs (Teal, 1962), 22% for Scrobicularia (Hughes, 1970), and 14% for Littorina irrorata, a detritus-aufwuchs feeding marsh snail (Odum and Smalley, 1959). Group II's efficiency is again negative, reflecting the energy needed for respiration in excess of that assimilated, thus requiring utilization of energy stored in the body rather than yielding energy for production of new body tissue. A more thorough analysis of Group II's actual weight loss (Table 1), converted to calories, might serve as a check on this apparent weight loss. Efficiency of Group III is similar to that of 37% for Orchelimum (Odum and Smalley, 1959). Odum and Smalley relate the difference in efficiencies of Littorina and Orchelimum to their different

growth patterns (i.e. the "slow-growing, long-lived" Littorina versus the rapidly-growing, short-lived Orchelimum). In the case of the Sesarma studied, it may be that Group I displays the usual summer tissue growth efficiency, while Group III may exhibit a greater efficiency related to increased storage of energy in the body prior to winter hibernation.

The proportion of assimilated energy used in respiration by Group I is high compared to that of approximately 63% for Orchelimum (calculated from Smalley, 1960) and 70% for Scrobicularia (Hughes, 1970) but is close to that of 83% for detritus-feeding marsh crabs (calculated from Teal, 1962) and 86% for Littorina (Odum and Smalley, 1959). Group II's efficiency again reflects the excessive respiratory demand. The efficiency of Group III is similar to that of Orchelimum.

Biological efficiency, as defined by Daiber and Crichton (1967) is similar to the trophic level production efficiency of $\frac{A_n}{NP_{n-1}}$ (after Kozlovsky, 1968). Again using monthly group totals, biological efficiency is found to be 25% for Group I, 12% for Group II, and 39% for Group III. The average (25%) is high compared to that of 18% found by Daiber and Crichton (1967), but all three efficiencies are within their range of 4-47%. In both the present study and that of Daiber and Crichton, the term NP_{n-1} of the consumption and biological efficiencies does not represent total production of Spartina in the marsh but rather the amount of Spartina offered to crabs under the experimental conditions.

Sesarma apparently contributes to the food web of the marsh in two basic ways (excluding saprophytic decomposition). In feeding upon Spartina, Sesarma adds to the detritus pool of the marsh through Spartina fragments cut from leaves but not ingested and through unassimilated Spartina in the form of feces. However, digestive processes in Sesarma would be expected to change the biochemical composition and caloric content of Spartina. By serving as a prey, Sesarma contributes to the third of carnivore trophic level. Crichton (1959) indicates possible predation of Sesarma by birds and mammals in Canary Creek Marsh. The present author has noted mammalian tracks and Sesarma remains at the entrance of Sesarma burrows. Predators in Georgia marshes are the raccoon and the clapper rail (Teal, 1962) and possibly the rice rat, Oryzomys palustris (Sharp, 1967).

III. TEST PROCEDURES

Crabs used in the feeding experiments were not truly random samples of the Sesarma population in Canary Creek Marsh. The samples were biased to include only adult males, of similar size. The transect choice of a drainage ditch in close proximity to the mouth of the Creek excluded population variations which might exist in marsh areas near the upper reaches of the Creek. However, the transect yielded crabs exposed to slightly different tidal regimes (assuming areas farther from the Creek were exposed for longer periods of time than were those nearer the Creek).

The energy pathway used in this study requires two main assumptions. First, the dry weight difference between Spartina

offered to Sesarma and that which is uningested is assumed to equal the amount ingested. This does not take into account a possible change in weight of Spartina caused by factors other than ingestion (e.g. microbial decomposition or physico-chemical breakdown). Weight measurements of Spartina taken on days when some Group II crabs did not eat showed either a decrease or an increase in dry weight over the daily test period. The average weight change of Spartina offered but uningested, based upon various daily sample numbers over 25 days, was about a 1.3% decrease. Weight changes due to decomposition were probably slight except in cases where several days elapsed between collection and actual drying and weighing of uningested Spartina. To lessen this error, lunar-monthly weight totals for each group were used for construction of the energy budget and for determination of efficiencies of energy utilization.

A second assumption is that the weight difference between ingested Spartina and unassimilated Spartina (i.e. feces) is equal to the weight of assimilated Spartina. This does not take into account fecal matter such as mucus which is actually derived from assimilated substances or ingested matter which is egested in other than fecal form (e.g. soluble organic material) (Johannes and Satomi, 1967). Caloric losses via urine were also not included in the present study. It is assumed that these errors would be slight (cf. Paine, 1965; Hughes, 1971).

The exact time and duration of feeding of Sesarma are not know. Sesarma has been occasionally observed feeding in the

marsh during the daytime (O. W. Crichton, personal communication), near a daytime low tide (W. H. Amos, personal communication), and at mid-flood tide (Teal and Teal, 1969). These observations seem to contradict the findings of Palmer (1967) concerning activity of Sesarma mainly during nighttime and high-tide hours. Although Sesarma is not usually seen on the surface of the marsh during the daytime, it might feed near high tide, whether during daytime or nighttime hours. During the present study, general observations indicated that crabs fed during the afternoon did not eat during the afternoon, but crabs fed in the evening (about 1900-2100 h) ate shortly after being fed. Crabs fed in the late afternoon ate by 1000 h the next day. Thus, although Sesarma may sometimes eat during the daytime, it must be assumed that, during the feeding experiments, Sesarma's main feeding period occurred at night.

The average percent dry weight of Spartina found for Groups I and II is close to the average of 28.3% calculated from Daiber and Crichton's (1967) data and 28.0% for tall Spartina from Canary Creek Marsh found during a class project in August, 1971. Spartina plants used in testing Group III were collected in early autumn, at the end of the growing season. The greater percent dry weight of these plants, in comparison with those of Groups I and II, may reflect the more mature condition of the plants.

Caloric determinations were not undertaken in the present study. Literature values for caloric content of Spartina (Smalley, 1960; Golley, 1961; Teal, 1962; Cummins and Wuycheck, 1971) and feces containing Spartina (Smalley, 1960) are in relatively close

agreement with the calculated averages based upon Daiber and Crichton's (1967) data. Teal (1962) shows an initial slight increase in caloric content of Spartina in seawater, followed by a gradual decline.

Studies of energy utilization on a seasonal basis are valuable in constructing annual energy budgets for populations. However, daily records of such factors as ingestion and assimilation can give a more detailed picture of energy utilization in relation to physiological factors such as molting.

IV. FEEDING IN RELATION TO MOLTING

Environmental conditions of the feeding experiment were similar to those required for molting of terrestrial crabs (i.e. "darkness, moderate temperatures, and often privacy", as found in the crab's burrow -- Bliss, 1968). Although conditions were apparently suitable for proecdysis of Sesarma, factors such as water level or lack of necessary nutrients of minerals (particularly calcium -- e.g. Prosser and Brown, 1966) may have led to death of many animals during ecdysis. The carapaces of preserved crabs which had died in molting were not closed over the gills, such that the extended gills fringed the carapace. This may indicate a structural abnormality or some response to possibly insufficient oxygen levels in the water.

There was no apparent correlation between molting and type of feeding behavior (i.e. constant eaters, occasional eaters, or non-eaters). Starvation was found to inhibit molting of Pachygrapsus crassipes at 16°C and above; however, this inhibition is

apparently not universal among decapod crustaceans (Roberts, 1957).

Records of ingestion and assimilation for individual crabs indicate that Sesarma stops feeding about 9-11 days before molting. Prior to that, however, a gradual decline in amount ingested occurs, over about an 11-day period. Again, this is reflected in the composite picture of Figure 3. The gradual decline in amount ingested is apparently not caused by a decrease in the number of crabs eating; Group II individuals which ate consistently display a similar declining pattern. The increase in amount ingested may reflect storage of energy within the body prior to the onset of ecdysis. Assuming that Sesarma exhibits an increase in oxygen consumption as ecdysis approaches, similar to that of Pachygrapsus (Roberts, 1957), the decrease in amount ingested during this time would appear to cause a more rapid depletion of the body's energy stores.

The fact that most Group II crabs molted, within a particular time period, suggests retention of some physiological rhythm. This apparent rhythm may have been endogenous (in view of the fairly constant laboratory conditions) or exogenous (possibly in response to some environmental factor such as mechanical disturbance associated with changing of the container water and feeding, exposure to the red lights and associated slight temperature increase, or possible natural light leaks).

V. PATTERN OF FOOD UTILIZATION

Figures 2-4 indicate the possibility of an increase in

amounts of Spartina ingested and assimilated occurring between the first-quarter and full-moon lunar phases. Data from Daiber and Crichton (1967) display a similar lunar relationship. However, testing of all three groups in the present study was begun near the first quarter lunar phase, thus making it difficult to discount a pattern initiated by testing procedures rather than a naturally-occurring pattern.

The possible environmental entraining agents mentioned with respect to molting, in addition to varying salinity of the medium, may have caused an apparent pattern for Groups I and II. The absence of an extended pattern in Group III may reflect the more constant laboratory conditions or the insufficient amount of Spartina offered on certain days.

Biweekly rather than monthly sampling of the Sesarma population might have given results more indicative of field conditions. If Sesarma displays a definite pattern of food ingestion and assimilation in the marsh, this pattern may fade with time when observed under laboratory conditions. The lighting conditions of the present study were employed to lessen the chances of artificially inducing a rhythm of food utilization. However, exposure of the crabs to natural illumination (e.g. window exposure) might yield results more indicative of food utilization in the marsh, particularly with respect to possible cyclic patterns.

In view of fluctuations in various external factors in the feeding experiments, the existence of a lunar-monthly cycle of food utilization remains questionable. Patterns of ingestion and

assimilation might occur in response to either quantity of Spartina available (i.e. under certain environmental conditions of light and tidal state) or quality of Spartina (i.e. biochemical composition, particularly in relation to seasonal changes associated with development and maturity). It was thought that cyclic patterns of oxygen consumption and locomotor activity might be coupled with cyclic feeding patterns, especially in relation to illumination and tidal cycles, perhaps resulting in peaks of food ingestion and/or assimilation during the lunar phases when tidal and diurnal maxima in the other rhythms occurred. Variation of the amount ingested in relation to the amount offered may support the possibility that, when environmental conditions of daylight and/or tidal stage make Spartina plants more accessible to Sesarma, more is ingested. Further study of the apparent pattern of food utilization in relation to molting of Sesarma may help clarify the question of lunar-monthly rhythms.

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