COLOR-INFRARED AERIAL PHOTOGRAPHIC INTERPRETATION AND NET PRIMARY PRODUCTIVITY OF A REGULARLY-FLOODED NORTH CAROLINA SALT MARSH

Productivity Studies in North Carolina Salt Marshes

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ABSTRACT

Acreage of major community types in a regularly-flooded marsh at Oak Island in Brunswick County, North Carolina was determined by analyzing color-infrared aerial photographs. Vegetation type coverage of the entire marsh was also determined in this study. These values were used to determine net productivity on a whole-marsh basis.

An attempt to determine net primary productivity of the major vegetation types in the regularly-flooded marsh was also made. A harvest method was used to obtain standing crop estimates of dominant vegetation types. These standing crop values were used to calculate net productivity. Net production was determined by two methods: (1) using only living standing crop estimates and (2) using changes in living and dead standing crop estimates. Predicted standing crop values obtained by fitting the observed data (from both methods) to a fourth degree polynomial in time were also calculated to make estimates of net production. The goodness of fit values obtained in this method were good for all vegetation types.

Estimates of net primary productivity using changes in living and dead predicted standing crops obtained in this study were as follows: short *Spartina alterniflora* - 1106 kcal/m^2/yr, medium *Spartina alterniflora* - 1856 kcal/m^2/yr, tall *Spartina alterniflora* - 6471 kcal/m^2/yr and *Juncus roemerianus* - 5346 kcal m^2/yr. On a whole-marsh basis, net primary production was estimated to be 1534 kcal/m^2/yr. These estimates were the best obtained in this study.

The net primary production estimates obtained in this study were not as high as values obtained in previous salt-marsh studies. Reasons

for this apparent discrepancy could be: (1) length of growing season, (2) climate of study areas, (3) per cent estimates of vegetation coverage of marsh and (4) correction value for loss of dead material.

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INTRODUCTION

A present trend in ecological studies is to determine productivity and energy flow in various terrestrial and aquatic ecosystems. Such studies have been carried out in a number of ecosystems. Energy flow is perhaps best understood in the regularly-flooded salt marsh of the south Atlantic coast. The bulk of the data on which this knowledge is based has been gathered at Sapelo Island, Georgia, by ecologists from the University of Georgia.

From data collected in the Georgia estuarine studies, Odum (1961) estimates the estuarine ecosystem to be one of the most productive systems in the world. He states that the estuarine system must be considered in its entirety (tidal flats, creeks, rivers, submerged bottoms) and not as single components. Studies by Smalley (1959), Odum (1961), and Teal (1962) indicate that the productivity of the primary producers in the estuarine ecosystem is comparable to or greater than that of ecosystems cultivated by man. Odum (1961) suggests that a management system based on utilization rather than production is needed in order to avoid serious mistakes in conservation of the estuarine ecosystem.

Realizing the importance of the estuarine ecosystem, a need exists to determine the relative value of the various components of such areas in order to establish an effective program of estuarine management. This study was carried out in an effort to determine the general nature of net primary production in an area of regularly-flooded salt marsh in North Carolina.

Specific objectives were:

1. To develop a rapid method of determining the area occupied by major salt marsh community types using color-infrared photographs.

2. To estimate the magnitude of net primary production in an area of well-developed regularly-flooded salt marsh in North Carolina.

REVIEW OF LITERATURE

Salt marshes are areas of land which border the sea, which are dominated by grasses or grass-like plants, and which are subject to periodic tidal inundation (Chapman, 1960). In the eastern United States, marshes from New Jersey to Florida and Louisiana belong to the Coastal Plain type (Chapman, 1960). Kurz and Wagner (1957) report these marshes are formed on a sinking coastline. The substrate is a grey, soft silt.

Description of North Carolina Salt Marshes

Wilson (1962) classifies North Carolina marshes as regularly-flooded (low) and irregularly-flooded (high) salt marshes. Regularity of inundation by saline tides is the basic criterion of Wilson's classification.

Regularly-flooded marshes cover about 58,400 acres in North Carolina, extending from Oregon Inlet and Ocracoke on the Outer Banks to Beaufort, and south to the South Carolina state line (Wilson, 1962).

Spartina alterniflora Loisel[1] is the dominant vascular plant in the regularly-flooded marsh. It exhibits three height forms depending on its proximity to tidal inundation. It has been shown that the height of *Spartina alterniflora* decreases as salinity increases (Teal, 1958; Smalley, 1959; Adams, 1963). These authors note that the tall *Spartina alterniflora* (one meter or taller) grows on the streamside banks in the marshes. On the levees and in their immediate proximity, medium *Spartina alterniflora* (50 to 100 cm) grows. Short *Spartina alterniflora*

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[1]Nomenclature according to Radford *et al.*, 1964.

(10 to 50 cm) grows in intercreek areas in the highest part of the marsh. *Juncus roemerianus* Scheele occurs in the regularly-flooded marsh in dense patches generally at higher elevations (Adams, 1963).

In the regularly-flooded marsh, tidal inundation occurs twice daily. Bordeau and Adams (1956) studied the effects of environmental factors (elevation, soil texture, and salinity) on distribution of vegetation in a marsh at Southport, North Carolina. They studied vegetation zones in which Spartina patens, Juncus roemerianus, and tall, medium, and short *Spartina alterniflora* were dominant. Their results showed that a micro-relief gradient existed throughout the three zones, and soil texture was similar between the latter two zones but became more sandy in the *Spartina patens* zone. Salinity increased more than twofold landward from the tall to short *Spartina alterniflora* zone, and then decreased to a minimal level in the *Spartina patens* zone. Adams (1963) concluded that tidal elevation influences primarily control the distribution of saltmarsh species. He also stated that salinity is a primary factor in reducing growth of salt-marsh species.

The substrate of the regularly-flooded marsh, as described by Adams (1963), contains more silt than the substrate of the irregularly-flooded marsh. It is grey-colored and soft.

Irregularly-flooded marshes are the most extensive of the two marsh types in North Carolina, covering 100,450 acres, and primarily extending from Roanoke Island to Atlantic (Wilson, 1962).

Irregularly-flooded marshes are flooded at unpredictable intervals. These flooding tides are mostly controlled by high winds and severe storms. The substrate of these marshes is sand overlain with peat. The sand is more or less uniform but the peat varies in depth and composition depending on the vegetation type (Waits, 1967). Salinity in this type of marsh is directly related to the regularity of flooding by sound water (Waits, 1967).

Studies of irregularly-flooded marshes are not numerous. Brown (1959) listed the important vascular plant species found in the major habitats of the Outer Banks; dunes, sand flats, and marshes. Dominant vascular plant species described in the salt marsh habitat are *Spartina alterniflora*, *Juncus roemerianus*, *Spartina patens*, *Distichlis spicata*, and *Scirpus robustus* (Brown, 1959; Burke, 1962; Waits, 1967).

Aerial Photography

In 1942, Eastman Kodak Company introduced Kodak Ektachrome Aero film (High Contrast) and Kodak Ektachrome Aero film (Camouflage Detection) for military reconnaissance. These films were precursors to Ektachrome Aero (color) and Ektachrome Infrared Aero (color-infrared), the films used in this study.

In the area of scientific uses, Colwell has used these films in attempts to detect disease in cereal grains, finding that color-infrared film showed evidences of infestation earlier than color or panchromatic film. Colwell has effectively used color-infrared film for distinguishing soil types, mineral types, plant species, water depths, and timber stand insect attacks. (Colwell, 1956, 1960, 1964; American Society of Photogrammetry, 1960).

Additional studies in forest disease detection by color-infrared film have been in the specific analysis of Oak Wilt, Annosus root rot, and little leaf disease. (Roth *et al*., 1963; Cordell *et al*., 1965).

Leuder (1959) discussed possible application of color and color-infrared film to ecological and botanical studies. He proposed the use of color and color-infrared film in surveying tidal marshes to obtain correlations that may exist between the patterns of these areas and the location of organisms such as oysters which feed upon food from these marshes. He suggested use of these films to determine wet-material mosquito-breeding areas in inaccessible regions such as New Guinea.

Olson (1964) made one of the first studies in tidal marshes involving aerial photographic interpretation. He studied aerial photographs to determine the type of information which could be obtained from them and to determine the accuracy of photographic interpretation. Accuracy of identification in relation to experience of interpreters varied directly with their previous knowledge of vegetation and photographic interpretation. He noted that accuracy of identification varied little in relation to the type of film, panchromatic or color, used. Color-infrared film was not used in this study. An increase in scale increased the accuracy of identification of pure stands of marsh vegetation types. It was found that mixed types were less accurately identified than pure vegetation types. Olson concluded that aerial photographs are useful in determining general types of marsh vegetation, and broad ecological zones. Plant species and associations can also be recognized with a reasonable degree of accuracy.

Anson (1966) compared panchromatic, color, and color-infrared film in mapping the drainage, vegetation, soils, and culture in a Coastal Plain region of South Carolina. His results showed the latter two film types superior to panchromatic for all phases of interpretation except soils. In soils, similar results were obtained from each type of film. Color-infrared was superior to color or panchromatic for vegetation analysis and drainage mapping. Color was superior to color-infrared for mapping culture.

Strandberg (1966) used color-infrared photographs in a water quality analysis study. He found that algae and other aquatic growths can be detected on this film. Such growths may be indicative of irrigation return flows which may be polluting streams with pesticides and other harmful chemicals.

A newer technique in aerial photography is by using infrared and multispectral sensing (Holter, 1967). Photographic type films that are sensitive to infrared cannot be stored without fogging; therefore, a need for a more accurate image recorder is needed. An amplifier is used to transmit the radiation to the photo recorder. The radiation is broken into spectral bands and a computer prints the desired band forming a detailed image.

Productivity Studies in Salt Marshes

The necessity for determining the productivity of aquatic and terrestrial ecosystems is not a new realization. The actual determination of productivity values is, however, a relatively recent development. The approach to productivity studies in the ecosystem can be of two types with either the entire ecosystem on individual components being studied (Smalley, 1959).

Many productivity studies have been done in the area of terrestrial plants. Westlake (1963) listed productivity data for cultivated plants, forests, and uncultivated plants; Newbould (1963) reviewed productivity data of various terrestrial plants such as maize, grass in old fields, and prairies. Ovington (1962) noted the rate of accumulation of plant organic matter is dependent on many factors but that highly productive, intensively managed temperate woodland contains about 350 x 10^3 kg/ha organic matter at about 50 years of age. It averages about 7 x 10^3 kg/ha in annual accretion.

Pomeroy's study (1959) showed that algae, a primary producer in the estuarine ecosystem, contribute 1620 kcal/m^2/yr net production in a Georgia estuary. Schelske and Odum (1961) noted five factors that contribute to maintaining high productivity in the estuarine ecosystem. They are the tidal regime in the marsh; turnover, regeneration, and conservation of nutrients; abundance of nutrients; three types of primary producers; and year-around production of crops by primary producers.

Most of the research on productivity of salt marshes has been done at Sapelo Island, Georgia. Most of the primary production can be attributed to *Spartina alterniflora*. It is the only major higher plant in the marsh (Teal and Kanwisher, 1961). Teal (1962), using the data of Smalley (1959), estimated that marsh average net productivity of *Spartina alterniflora* was 6580 kcal/m^2/yr. Net production data were gathered from short and tall (levee and streamside) Spartina alterniflora in Smalley's study. Teal's estimate of net production using data collected by Smalley (1959) of short Spartina alterniflora was 2570 kcal/m^2/yr and an estimate of 8970 kcal/m^2/yr was obtained for tall *Spartina alterniflora*. An estimation of 5200 kcal/m^2/yr net production was made by Smalley (1959) for medium *Spartina alterniflora*. It was also noted that short *Spartina alterniflora* occupied 42% of the total marsh area and tall *Spartina alterniflora*, 58%. Gross production of this marsh was estimated at 34580 kcal/m^2/yr. Net production was calculated to be only 19% of gross production.

Harvest methods have been used to determine net primary productivity of vascular plants in all salt marsh productivity studies to date (Odum, 1959; Smalley, 1959; Waits, 1967). This method cannot be used for algae which produce many crops per year. Harvest methods are based on periodically harvesting the standing crop of grass. Dry weight of grass is determined and production is calculated by adding the increase in biomass during each sample period. Removal of dead grass by tidal action or animal feeding results in an underestimation of net productivity. Smalley used relationships based on changes in living and dead standing crops of *Spartina alterniflora* to improve the estimation of net primary production in *Spartina alterniflora*. With an increase in the standing crop of living and dead *Spartina alterniflora*, net production was the sum of the increase. With a decrease in the standing crop of living and dead *Spartina alterniflora*, net production was zero. With a decrease in the standing crop of living *Spartina alterniflora* and an increase in the standing crop of dead *Spartina alterniflora*, results were added algebraically. In the situation where there was an increase in the standing crop of living *Spartina alterniflora* and a decrease in the standing crop of dead *Spartina alterniflora* production was equal to the increase in living *Spartina alterniflora*.

Morgan (1961) made net production estimates in Delaware using the clip quadrat harvest method. Estimates were made for the entire marsh for all species collectively. Morgan estimated net primary productivity to be 445 gms dry weight/m^2. This value is considerably lower than the productivity estimates from the Sapelo Island marshes. Morgan proposed the longer growing season in a warmer climate may account for this variation.

There are several studies of salt marsh production in North Carolina. Waits (1967) carried out a productivity study in an irregularly-flooded marsh on Bodie Island. He determined observed and predicted standing crops for the four principal vegetation types. Net production and net production efficiency were also calculated for these vegetation types. Net primary productivity values obtained were as follows: mean annual net production for the entire marsh was 5350 $kcal/m^2/yr$. Net production for Spartina patens was 5835 $kcal/m^2/yr$; and for Juncus roemerianus net production was 6123 $kcal/m^2/yr$.

These values for the irregularly-flooded salt marsh fall between the estimates of Teal (1962) for short and tall Spartina alterniflora.

Williams and Murdoch[2] have carried out studies of primary productivity in the estuary near Beaufort, North Carolina. Groups of primary producers for which they have determined net primary production are phytoplankton, Spartina alterniflora, and Juncus roemerianus. Net production of the dominant marsh species Spartina alterniflora

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[2] Williams, R. B., and Marianne B. Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Annual production of Spartina alterniflora and Juncus roemerianus in salt marshes near Beaufort, North Carolina. Presented at Association of Southeastern Biologists Meeting, April 15, 1966, Raleigh, North Carolina.

and *Juncus roemerianus* was determined by Williams[3] by a harvest method similar to that used at Sapelo Island, Georgia. He collected ten one-meter square samples every five weeks. Living and dead were separated, dead leaves and leaf scars were counted on the stems. A balance between living and dead material was calculated from these data. Williams estimates production of *Spartina alterniflora* to be 1 $kg/m^2/yr$. Using a slightly different method, he obtained a similar estimate of net primary production for *Juncus roemerianus*.

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[3]Williams, R. B. Oak Ridge National Laboratory, Oak Ridge, Tennessee. Primary production by marsh grass and eel grass at Beaufort, North Carolina. Presented at Atlantic Estuarine Research Society Meeting, November 12, 1965, Hampton, Virginia.

METHODS

Description of the Study Area

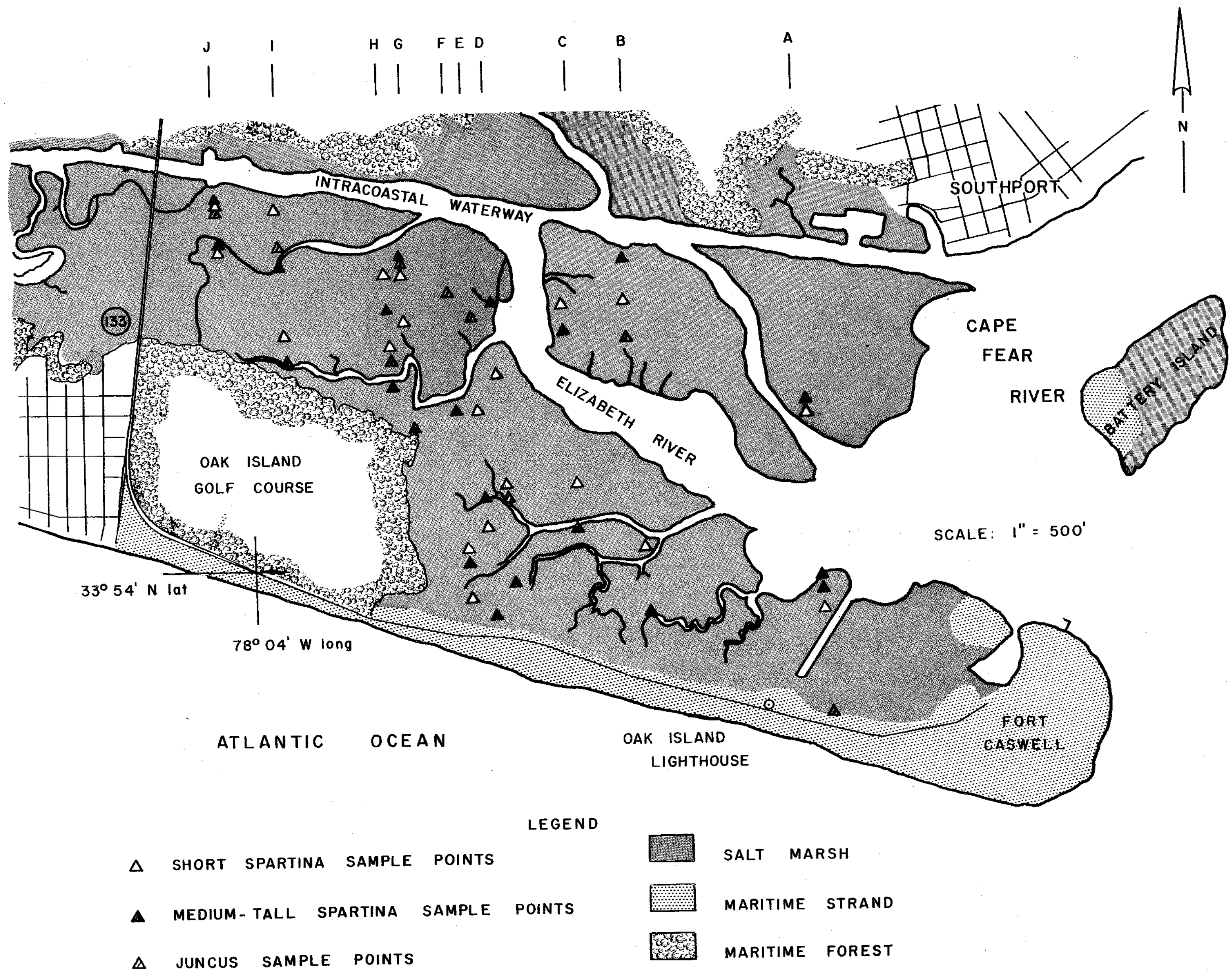
The area chosen for study is a regularly-flooded saltmarsh, covering approximately 2,000 acres, located on Oak Island in Brunswick County, North Carolina.(Figure 1). This study area is bounded on the west by the Southport-Oak Island Bridge, on the north by the Intracoastal Waterway, on the east by the Cape Fear River, and on the south by a narrow fringe of barrier beach and maritime forest. All major community types characteristic of regularly-flooded marsh are well represented in the study area.

Aerial Photography

Aerial photographs were used to identify community types, to determine their distribution, and to estimate acreage of community types within the study area. Two types of film were used: Ektachrome Aero (color) and Ektachrome Infrared Aero film (color-infrared). Both of these films are reversal color films of the subtractive type yielding a positive transparency when developed. Each film has three emulsion layers coated on a single film base. The emulsion layers of the color film are sensitive to wavelengths in the visible spectrum (400 to 700 mu). When developed, relatively true colors result (Tarkington, 1953; Leuder, 1959; American Society of Photogrammetry, 1960; Fritz, 1965).

In color-infrared film, the emulsion layers are sensitive to the visible spectrum plus the infrared spectrum (700 to 900 mu). Thus, the term "near infrared" film is more correct (Colwell, 1960;

Figure 1. Map of Oak Island, North Carolina showing location of transects and sample points



J
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N
INTRACOASTAL WATERWAY
SOUTHPORT
133
CAPE FEAR RIVER
BATTERY ISLAND
ELIZABETH RIVER
OAK ISLAND GOLF COURSE
SCALE: 1" = 500'
33° 54' N lat
78° 04' W long
ATLANTIC OCEAN
OAK ISLAND LIGHTHOUSE
FORT CASWELL
LEGEND
SHORT SPARTINA SAMPLE POINTS
MEDIUM-TALL SPARTINA SAMPLE POINTS
JUNCUS SAMPLE POINTS
SALT MARSH
MARITIME STRAND
MARITIME FOREST

Suits, 1960). Since color-infrared film is also sensitive to blue and violet emissions, a yellow filter such as a Wratten No. 12 or 15G must be used to filter these wavelengths. When developed, false colors result. The resulting colors are dependent on the infrared reflectance of the body photographed. Infrared reflecting surfaces appear red, non-infrared reflecting surfaces green, and blue features black. Healthy, green vegetation appears various shades of red due to its high infrared reflectance (Clark, 1946; Colwell, 1956; Leuder, 1959; Cordell et al., 1965).

Aerial photographs used in this study were taken by the North Carolina Highway Commission. A Wild RC 8 camera having a lens of focal length of 152.18 mm was mounted in an Aero Commander 500 plane. The photographs were taken at 3,000 feet elevation, and the resulting scale of the photographs was 1 inch = 500 feet. Deviation from this scale was probably within three percent of the altitude. Some tilt may have occurred. Measurements made from the photographs are within a five percent range of scale accuracy.

No filter was used on the Ektachrome Aero film. A filter which cuts off at a wavelength of 500 mu was used on the Ektachrome Infrared Aero film; thus the range of this film was from 500 to 900 mu. Both films were developed by the Aerial Photography Division at the North Carolina Highway Commission using the standard Ektachrome E-3 process.

Determination of Community Types

Six community types were interpreted within the study area. Four vegetation types were determined in the Oak Island marsh. The area occupied by each type was determined by an analysis of the color and color-infrared aerial photographs. In order to do this, the entire study area was divided into 75 transects 200 feet in width. Each ran parallel to the Oak Island Bridge over the Intracoastal Waterway. Based on general vegetation differences the area was divided into two sections, one with 54 transects and the other with 21. A total of 21 transects, 15 in the larger section and 6 in the smaller, were randomly selected for analysis. After the transects were selected and located on the photographs, a celluloid overlay having a transect 200 feet wide (based on the aerial photo scale) was placed over the selected transect on the photograph. A dot grid was then placed randomly over the overlay and the number of dots which fell on each community type were counted. The number of dots falling on each community type was then multiplied by the appropriate conversion factor (1 dot = 0.08967 acres) for a scale of 1 inch = 500 feet, to yield total acreage and percentage of each community type..

Net Primary Production

Vegetation Sampling

Net primary production of vascular plants in the study area was estimated by the clip plot method. An effort was made to develop a statistically valid sample design. The same transect design was used in collection of field data as was used in the aerial photographic analysis of community types. Ten transects were selected randomly from a table of random numbers. Restrictions placed on the selection of transects were that seven transects were to come out of the larger section and three out of the smaller. Sampling was without replacement.

A creek and its associated vegetation types were the basic sample units. Two creeks were selected from each of these transects by counting the total number of creeks in the transect. The creeks then were numbered, and two were selected at random. Positioning of the sample point on the right or left side of the creek when facing up-creek was determined by flipping a coin. If the right bank of the first creek was chosen, the left bank of the second creek was automatically taken.

The actual points for the collection of vegetation data were established as follows. Two sample locations were used in tall *Spartina*. A coin was flipped to determine whether the first point was to be on a bank or on the levee. If the bank was the site of sampling on the first creek, the levee was taken on the second creek. A medium *Spartina* sample point was placed halfway from each tall *Spartina* sample point to the short *Spartina* zone. Short *Spartina alterniflora* was sampled by numbering the short zones in the selected transect on the color-infrared photograph and then randomly choosing two such zones. The sample point was placed in the middle of the zone. Sample points were marked in the field with wooden stakes enabling a return to the same point for repetitive sampling.

Sites for sampling *Juncus roemerianus* were determined by selecting at random one clump of *Juncus* in each transect. The sample point was placed as nearly as possible in the center of the clump. There were only nine sample points for *Juncus roemerianus* due to the absence of this vegetation type in one transect.

The number of sample points and their distribution by vegetation types is summarized in Table 1.

Table 1. Number and distribution of sample points in Oak Island study area

Vegetation type	Number of sample points
Tall *Spartina alterniflora*	
Bank	10
Levee	10
Medium *Spartina alterniflora*	20
Short *Spartina alterniflora*	20
Juncus roemerianus	9

Standing Crop Estimates

The method used to obtain standing crop estimates was the clip plot method. Clip samples were taken during the period June 1966 to March 1967. Dates of sampling were: June 28 - 30, 1966; July 20 - 22, 1966; August 15 - 17, 1966; September 23 - 24, 1966; November 11 - 13, 1966; January 18 - 20, 1967, and March 13 - 15, 1967.

A circular sample plot $0.1m^2$ in area (35.6 cm diameter) was used. Samples were taken in the vicinity of the sample point by dropping a peg to determine the plot center. The peg was re-dropped if it fell on a previously clipped area.

After the point of collection was determined, vegetation was clipped as close to the surface of the ground as possible and placed in a bag marked with the transect number, sample number, and name of the community type. Dead material and any loose material in the clip area was also placed in the bag.

After collection, the samples were taken to the laboratory for analysis. The Spartina alterniflora material was treated in the following manner. The average height of the plant material in the bag, and thus of the sample, was estimated and the material was then separated into living and dead (based on color). The dead material was labeled as standing dead and any loose dead material was treated as dead debris. The living material was then separated into new and old groups (based on height and leaf condition). In the November collection, it was noted that stems which could not be classified as either new or old were present. These stems were labeled as intermediate. The same basis (height and leaf color) was used to classify this group as in the previous groups. The new, intermediate, and old stems were each arranged in order of height and counted. From a table of random numbers, ten stems were selected from each group. These ten stems were then measured for height, number of living and dead leaves, and diameter of stem (first three collections). Dead material was removed from the stem after the diameter was measured. Each of the selected ten stems was labeled individually and weighed.

Juncus roemerianus was handled differently due to its growth habit. The average height of the leaves was estimated. The leaves were then separated into three categories: all living, green-dead, and all dead. The all dead was labeled as standing dead. The leaves in the all living category were arranged in order of increasing height, counted, and ten were randomly selected for height measurement. The green-dead category was measured for total height, the length of the dead was then removed, measured, and tagged. The living portion was also tagged.

Dry weights of all plant materials were determined by wrapping the samples, labeling them, and placing them in an oven at 105°C for 24 hours at which time the samples were removed and weighed.

Calorimetry

Caloric values were calculated for all species in this study in order to express productivity data on an energy basis. Caloric determinations were made on living plant material collected in June 1966, September 1966, and March 1967. Methods of caloric determination were essentially those of Waits (1967). Aerial portions of the plants were used for these determinations. Random samples of the plant material were taken from the entire collection of oven-dried material. All of these stems were lumped to form a composite sample. The sample was then ground in a Waring blendor, and placed in a desiccator over anhydrous $CaCl_2$, and left to dry until caloric determinations were made. A Gallenkamp Adibatic Bomb Calorimeter, Model CB-040, was used to burn the plant material and to make the caloric determinations. Two samples, each weighing approximately one gram, were burned. Calculations were reported as gram-calories per gram dry weight of plant material.

Statistical Analysis

Aerial Photography

Statistical analysis of acreage data obtained from color-infrared photographs was done using standard statistical methods (Steele and Torrie, 1960).

Standing Crop Data

A simple analysis of variance ("between months" and "within months") was computed using the standard ANOV program for the IBM 360/75 computer at the Triangle Universities Computation Center. This analysis established an estimate of the sampling error from the "within months" source and allowed an overall test of significance of the "between months" variability. The sampling error was also expressed as a relative standard error, the coefficient of variability (CV).

A second analysis was performed to express the "between months" variability in production as a fourth degree in time (t), where the time variable was the serial number of the months (t = 1, 2, ..., 12). This fourth degree polynomial was used by Waits (1967). A standard regression program was used for this analysis. To facilitate computations, the variable (t) was coded as $t - \bar{t}$ where $\bar{t}$ is the mean value of t over all months ($\bar{t} = 6.47$ for all Spartinas and $\bar{t} = 5.43$ for the Juncus).

Thus, the prediction equation becomes:

$$\hat{y}\ (t) = bo + b_1\ (t - \bar{t}) + b_2\ (t - \bar{t})^2 + b_3\ (t - \bar{t})^3 + b_4\ (t - \bar{t})^4$$

$$\hat{y}\ (x) = bo + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4$$

where the increasing powers of $(t - \bar{t})$ are represented by X_1 to X_4. The y-values were the observed weights for plots at each sampling date. The b-values, the partial regression coefficients, have no meaning when interpreted independently, but are of importance in the calculation of the prediction equation of $\hat{y}$. The predicted values obtained by the use of this equation are represented as standing crop estimates. The values were also used to estimate net primary production.

RESULTS

Aerial Photography

Six community types were recognized in the study area. Each was distinguishable on the aerial photographs by a unique combination of color, texture, and position (Table 2).

Table 2. Aerial photograph color and texture properties of community types in Oak Island Study area

Type	Color	Infrared
Short *Spartina alterniflora*	Light yellowish-green	Light pink to grey
Medium *Spartina alterniflora*	Not distinguishable	Pink to red
Tall *Spartina alterniflora*	Dark green	Brilliant red
Juncus roemerianus	Grey	Pink, orange to green
Other	Clear	Clear
Water	Grey	Black to bluish

In order to determine the relative value of color versus color-infrared photography for mapping purposes, four transects were mapped by dot grid. The results (Table 3) show that medium *Spartina alterniflora* was not distinguishable from tall on the color photographs. For this reason, color-infrared was used to make the final acreage determinations of each community type in the Oak Island marsh.

Tall *Spartina alterniflora* grows along streams with medium *Spartina alterniflora* behind it. The color of the medium *Spartina alterniflora*

Table 3. Comparison of acreage of community types in four transects on color and color-infrared photographs in Oak Island Marsh by dot grid analysis

Color Photographs

Transect number	Short *Spartina alterniflora*	Tall *Spartina alterniflora*	*Juncus roemerianus*	Water	Total
	Community types				
5	13.8	4.1	0	1.0	18.9
6	21.0	6.4	0.1	1.6	29.1
9	8.2	2.3	4.5	2.8	17.8
10	9.0	2.8	3.5	1.6	16.9
Total	52.0	15.6	8.1	7.0	82.7

Color-infrared Photographs

Transect number	Short *Spartina alterni-flora*	Medium *Spartina alterni-flora*	Tall *Spartina alterni-flora*	*Juncus roemerianus*	Water	Total
	Community types					
5	13.4	2.9	1.6	0	1.0	18.9
6	21.4	4.0	2.2	0	1.7	29.3
9	7.1	2.2	1.4	4.3	3.0	18.0
10	8.7	2.1	2.0	3.0	1.8	17.6
Total	50.6	11.2	7.2	7.3	7.5	83.6

on the color-infrared photograph is less red than the tall Spartina alterniflora. Short Spartina alterniflora, which occurs in the highest parts of the marsh between creeks, has some grey color on the infrared photographs due to reflection from the sediments. Juncus roemerianus forms a "fungus-like" patch on photographs of both types making it clearly recognizable. Types of communities classified under the term "other" included spoil areas and bare areas in the marsh.

The results of the final analysis of the Oak Island area, determined on color-infrared photographs, are shown as total acreage and relative importance of marsh community types (Tables 4 and 5). Short Spartina alterniflora is the most important community type in the marsh ranging in relative importance from 9.9% - 62.6% (1.6 - 21.4 acres) in 21 sample transects. Medium and tall Spartina alterniflora are next in importance. They are more evenly distributed than Juncus roemerianus which has importance in only one section of the marsh. Water has larger acreage and higher importance values than any community type except short Spartina alterniflora (6.6% - 41.4%).

In analyzing these 21 transects, it seems that distribution of the community types is related to gross habitat characteristics. Away from the inlet as water area decreases and tidal creeks finger out into the marsh upstream, tall Spartina alterniflora acreage decreases. As the streams narrow (transects 54 - 73) away from the inlet, short Spartina alterniflora and Juncus roemerianus become increasingly important. Thus, two distinct areas of distribution of community types can be seen in this marsh, one large area of Spartina alterniflora dominance and the other a smaller area of Juncus roemerianus.

Table 4. Acreage of marsh community types in Oak Island Marsh by dot grid analysis of 21 sample transects on color-infrared aerial photographs

Transect number	Acreage of community type						
	Short *Spartina alterniflora*	Medium *Spartina alterniflora*	Tall *Spartina alterniflora*	*Juncus roemerianus*	Other	Water	Total
5	1.6	1.7	0.5	0.7	5.1	6.5	16.2
7	6.0	0.6	1.0	0.0	3.4	8.3	19.2
12	7.6	1.9	1.4	0.0	6.2	12.1	29.4
17	12.5	2.5	1.3	0.0	5.6	11.8	33.7
26	17.4	2.5	1.2	1.5	0.0	11.6	34.2
27	18.5	2.3	1.8	0.6	0.0	11.2	34.5
28	16.6	4.1	1.5	1.7	0.0	10.3	34.2
29	17.4	4.5	2.1	0.6	0.0	10.1	34.8
32	20.2	3.5	2.3	0.9	2.1	5.5	34.5
33	21.4	4.0	2.1	0.0	0.4	6.2	34.2
40	15.5	3.6	3.0	0.0	1.9	9.4	33.4
41	13.4	3.5	1.4	0.0	1.1	13.2	32.6
47	18.7	5.6	2.9	1.3	0.7	3.0	32.1
54	7.1	2.1	1.4	4.3	0.0	3.0	17.9
55	8.7	2.1	2.0	3.0	0.0	1.7	17.5
60	6.9	2.3	1.2	4.0	0.6	2.1	17.3
61	7.0	1.7	0.8	4.3	1.5	1.5	16.8
65	5.7	1.6	0.8	4.1	1.3	1.3	14.9
66	5.6	0.9	0.7	4.7	2.0	1.0	14.9
67	3.8	2.4	0.5	5.0	1.3	1.2	14.3
73	2.6	0.9	0.6	8.4	0.0	1.7	14.2

Table 5. Relative importance (percent of communities in transect) of marsh community types in 21 sample transects in Oak Island Marsh

Transect number	Community type					
	Short *Spartina alterniflora*	Medium *Spartina alterniflora*	Tall *Spartina alterniflora*	*Juncus roemerianus*	Other	Water
5	9.9	10.5	3.3	4.4	31.3	40.4
7	31.2	3.0	5.1	0.0	17.5	43.1
12	25.9	6.6	4.9	0.0	21.2	41.4
17	37.2	7.3	3.8	0.0	16.5	35.1
26	50.8	7.4	3.6	4.3	0.0	33.8
27	53.6	6.7	5.3	1.8	0.0	32.5
28	48.6	12.0	4.4	4.8	0.0	30.1
29	50.1	13.0	6.2	1.8	0.0	29.0
32	58.5	10.1	6.6	2.6	6.2	15.9
33	62.6	11.8	6.3	0.0	1.2	18.1
40	46.4	10.7	9.0	0.0	5.6	28.2
41	41.0	10.7	4.4	0.0	3.3	40.6
47	58.3	17.3	9.0	3.9	2.2	9.2
54	39.5	12.0	8.0	24.0	0.0	16.5
55	49.8	11.8	11.3	17.2	0.0	10.0
60	40.1	13.5	7.0	23.3	3.6	12.4
61	42.0	10.1	4.5	25.4	9.1	8.8
65	38.2	10.9	5.4	27.4	9.1	9.0
66	37.9	6.0	4.8	31.3	13.2	6.6
67	26.7	17.0	3.4	35.2	9.5	8.2
73	18.4	6.6	4.1	59.2	0.0	11.7

The data for the 21 transects were converted to derive an estimate of total acreage of each community type in the entire marsh. These values (Table 6) show that short Spartina alterniflora covers 837 acres (44.2%) of the estimated total of 1,895 acres in the marsh. Medium and tall Spartina alterniflora occupy 195 acres (10.3%) and 110 acres (5.8%) of the total marsh respectively. Water covers 25% of the marsh. Juncus roemerianus covers only 161 acres (8.5%) of the marsh area.

Coefficients of variation (relative variability) (Table 6) are ten percent or lower for the widely and regularly distributed Spartina alterniflora and water types. These values are higher for the more sporadic Juncus roemerianus and "other" types.

Net Primary Production

Calorimetry

Caloric values determined for the four vegetation types in the community types in the Oak Island marsh are presented in Table 7. Duplicate values for each sample period are recorded. In order to calculate net productivity on an energy basis, the individual means for each vegetation type reported in this table in gcal/g dry weight of plant material will be used. These values obtained in this study are comparable to values reported for salt marsh species by others (Smalley, 1959; Golley, 1961; Waits, 1967; Foster, 1968).

Standing Crop Data

Although the data gathered covered only a 12-month period, they spanned parts of two consecutive growing seasons. For purposes of

Table 6. Acreage determinations for Oak Island Marsh by dot grid analysis

Community type	Short *Spartina alterniflora*	Medium *Spartina alterniflora*	Tall *Spartina alterniflora*	*Juncus roemerianus*	Other	Water	Total
Estimated total (acres)	837	195	110	161	118	474	1,895
N	21	21	21	21	21	21	21
CV (%)	10.6	9.2	9.3	20.1	40.3	13.0	6.5
% Total	44.2	10.3	5.8	8.5	6.2	25.0	100.0
$\bar{x} \pm t_{.05}(S_{\bar{x}})$ (acres)	837 ± 184	195 ± 37	110 ± 21	161 ± 78	118 ± 74	474 ± 129	1,985 ± 258

Table 7. Caloric values of whole-plant samples for four vegetation types[a]

Collection data		gcal/g dry weight			
		Vegetation types			
Year	Month	Short *Spartina alterniflora*	Medium *Spartina alterniflora*	Tall *Spartina alterniflora*	*Juncus roemerianus*
1965	August[b]	4127.0	3931.8	4017.7	4590.7
		4051.4	4006.2	4196.1	4411.2
1966	June	3843.4	3944.0	4048.1	4352.2
		3809.4	3942.1	3977.1	4432.4
1966	September	4128.7	4184.0	4764.0	4340.5
		4054.9	4080.9	4674.0	4397.4
1967	March	3760.0	3809.4	3616.4	4354.4
		3805.0	3620.2	3787.3	4297.6
$\bar{X}$		3947.5	3939.8	4135.1	4397.1

[a]Determinations of above-ground parts only.

[b]Collection of plant material by Paul Sykes, Department of Zoology, North Carolina State University at Raleigh.

computing production estimates, the data were arranged so as to represent one growth cycle from January to November.

The observed mean living standing crop values ($g/0.1m^2$) for each vegetation type are presented in Table 8. The standing crop values are listed for old, intermediate, and new categories. The values are also totaled to obtain a standing crop value for each vegetation type.

Table 8. Observed mean living standing crop for each vegetation type in the Oak Island Marsh

Vegetation type	Mean standing crop ($g/0.1m^2$)						
	January	March	June	July	August	September	November
Spartina alterniflora							
Short							
Old	1.7	0.2	19.1	22.7	23.2	20.5	9.2
Intermediate	1.1	3.0	0	0	0	0	2.2
New	0.9	0.6	0.4	1.1	2.7	4.4	1.9
Total	3.7	3.8	19.5	23.8	25.9	24.9	13.3
Medium							
Old	1.3	0.3	26.5	35.7	43.3	43.2	22.0
Intermediate	3.1	9.0	0	0	0	0	2.4
New	1.8	0.6	0.1	0.2	1.8	4.5	2.3
Total	6.2	9.9	26.6	35.9	45.1	47.7	26.7
Tall							
Old	3.1	1.5	67.1	81.1	104.4	124.8	104.7
Intermediate	11.2	12.8	0	0	0	0	9.9
New	3.1	0.5	0.2	1.0	4.6	7.2	4.2
Total	17.4	14.8	67.3	82.1	109.0	132.0	118.8
Juncus roemerianus	65.1	60.5	85.3	95.7	117.3	86.6	52.0

The observed mean dead standing crop value for the categories, old, intermediate, new, and dead debris in each vegetation type are shown in Table 9. These values for the four categories are lumped to obtain a total dead value for each vegetation type.

Net primary production was initially calculated by using mean observed standing crop values. The peak standing crop for each vegetation type minus the minimal standing crop was used to estimate net primary production. Net production estimates for each vegetation type are shown in Table 10.

Table 9. Observed mean dead standing crop for each vegetation type in the Oak Island Marsh

	Mean standing crop (g/0.1m^2)						
Vegetation type	January	March	June	July	August	September	November
Spartina alterniflora							
Short							
Old	28.1	19.4	5.0	16.0	15.6	20.5	20.9
Intermediate	2.1	1.5	0	0	0	0	1.6
New	0.8	0.2	0	0.1	0.2	1.2	1.1
Debris	9.7	13.3	15.1	7.4	3.8	6.2	5.2
Total	40.9	34.4	20.1	23.5	19.6	27.9	28.8
Medium							
Old	63.2	36.1	7.0	27.5	29.8	28.2	32.6
Intermediate	3.3	4.7	0	0	0	0	1.8
New	0.9	0.2	0	1.1	0	0.1	0.6
Debris	19.0	17.9	29.4	11.2	11.1	4.1	8.0
Total	86.4	58.9	36.4	39.8	40.9	32.4	43.2
Tall							
Old	96.4	79.2	26.2	34.5	34.4	39.6	39.1
Intermediate	10.0	7.2	0	0	0	0	6.9
New	1.4	0.2	0	0.8	0.1	0.5	1.8
Debris	21.8	22.8	72.8	9.1	13.6	3.2	17.3
Total	129.6	109.4	99.0	44.4	48.1	43.3	65.1
Juncus roemerianus	97.1	110.6	88.0	77.6	91.5	101.8	99.5

Table 10. Net primary production for each vegetation type using net production estimates calculated from standing crop values

Vegetation type	$g/0.1m^2$	g/m^2	kcal/g	$kcal/m^2$
Spartina alterniflora				
Short	22.3	223	3.95	881
Medium	41.5	415	3.94	1635
Tall	117.1	1171	4.14	4848
Juncus roemerianus	65.4	654	4.40	2878

The standing crop values for each vegetation type are presented in $g/0.1m^2$, then converted to g/m^2 to calculate production. The g/m^2 production values are converted to $kcal/m^2$ for the purpose of comparison of these values with the results obtained in other productivity studies. Production estimates on an energy basis ($kcal/m^2$) were converted from production estimates on a weight basis (g/m^2) by using the mean caloric values in Table 7.

The data show tall Spartina alterniflora to be the most productive vegetation type followed by Juncus roemerianus. Net production of medium Spartina alterniflora was less than one-half that of tall and short Spartina alterniflora production was only one-fifth of the value for the tall form.

Percentage of marsh covered by each vegetation type and net production values are presented in Table 11. Net production on a whole-marsh basis is also presented in Table 11. This table shows that short Spartina alterniflora covers the most area of the marsh (44.2%) but

Table 11. Calculations of net primary production on a whole-marsh basis using net production estimates calculated from observed living standing crop values

Vegetation type	Percentage of marsh	Net production ($kcal/m^2/yr$)
Spartina alterniflora		
Short	44.2	881
Medium	10.3	1635
Tall	5.8	4848
Juncus roemerianus	8.5	2878
	Weighted mean	1084

has the lowest net production (881 $kcal/m^2/yr$) of any vegetation type. Tall *Spartina alterniflora* occupies the least area in the marsh (5.8%) but is the most productive (4848 $kcal/m^2/yr$). Net production on a whole-marsh basis was calculated to be 1084 $kcal/m^2/yr$.

Efficiency of net production (percentage of incident light utilized in net production) was calculated for each vegetation type (Table 12). These values were calculated by using the values of 818,730 $kcal/m^2/yr$ (Waits, 1967) and 600,000 $kcal/m^2/yr$ (Teal, 1962) as the incident light energy values. The net production value for each vegetation type was divided by the mean of these two incident light energy values to obtain efficiency of net production. Tall *Spartina alterniflora* had the highest efficiency of net production of 0.7% followed by *Juncus roemerianus* at 0.4%. An estimate of 0.2% efficiency was obtained

Table 12. Net primary production efficiency of each vegetation type and of whole-marsh using net production estimates calculated from observed living standing crop values

Vegetation type	Efficiency per cent
Spartina alterniflora	
Short	0.1
Medium	0.2
Tall	0.7
Juncus roemerianus	0.4
Whole-marsh	0.2

for the whole marsh. These values are comparable to those obtained by Waits (1967) but considerably lower than those by Teal (1962).

There has been criticism of the previous method of calculating net primary production as it uses only the observed living standing crop and does not account for mortality before the peak standing crop is reached or growth occurring after the peak standing crop is reached (Weigert and Evans, 1964).

Smalley (1959) proposed a method involving changes of living and dead standing crops in order to meet this problem. If the change in the standing crop increased from one collecting date to the next, the increase was positive. If the change decreased, the decrease was negative. If both the living and dead categories increased, the values were added. If both living and dead standing crops decreased, net production was zero. If the living increased and the dead decreased, the sum of these two values was the increase of the living. If the dead increased and the living decreased, the negative value was subtracted from the positive value.

The mean living and mean dead standing crops were determined for each vegetation type in each sample period. The changes in these crops were then determined. By treating the changes as proposed by Smalley, annual net production was calculated (Tables 13 - 16).

Estimates of net primary production calculated using changes in living and dead standing crops are higher than those calculated from living standing crops alone. Comparison of Tables 13 - 16 with Table 10 shows an underestimation of approximately 400, 200, and 500 kcal/m^2/yr for short, medium and tall Spartina alterniflora respectively. Juncus roemerianus was underestimated by 600 kcal/m^2/yr.

A summary of net production estimates for each vegetation type and percentage of marsh coverage is presented in Table 17. Net production on a whole-marsh basis is estimated to be 1370 kcal/m^2/yr, a value approximately 300 kcal/m^2/yr greater than that obtained from changes in living standing crop alone. Calculations using changes in both living and dead standing crops are thought to be a better method of estimating net primary production.

Efficiency of net primary production for each vegetation type is presented in Table 18. These values were determined in the same manner as previously described. Tall Spartina alterniflora (0.8%) followed by Juncus roemerianus vegetation type (0.5%) had the highest efficiencies of net production. Efficiency of net production on a whole-marsh basis was 0.2%. The efficiency values obtained by using net production

Table 13. Calculation of net primary production for short *Spartina alterniflora* using changes in observed living and dead mean standing crops

Sample date Year	Month	Standing crop (living) (g/0.1m^2)	Standing crop (dead) (g/0.1m^2)	Change living	Change dead	Net production (g/0.1m^2)
1967	January	3.6	40.8			
				0.2	- 6.5	0.2
	March	3.8	34.3			
				15.7	-14.1	15.7
1966	June	19.5	20.2			
				4.3	3.3	7.6
	July	23.7	23.5			
				2.2	- 3.9	2.2
	August	25.9	19.6			
				- 1.0	8.2	7.2
	September	24.9	27.8			
				-11.6	0.9	0
	November	13.3	28.7			
		Annual Net Production				32.9 g/0.1m^2/yr 329 g/m^2/yr 1300 kcal/m^2/yr

Table 14. Calculation of net primary production for medium <u>Spartina alterniflora</u> using changes in observed living and dead mean standing crops

Sample date Year	Month	Standing crop (living) ($g/0.1m^2$)	Standing crop (dead) ($g/0.1m^2$)	Change living	Change dead	Net production ($g/0.1m^2$)
1967	January	6.2	86.4			
				3.8	-28.8	3.8
	March	10.0	57.6			
				16.6	-21.2	16.6
1966	June	26.6	36.4			
				9.3	3.4	12.7
	July	35.9	39.8			
				9.3	1.2	10.5
	August	45.2	41.0			
				2.5	- 8.7	2.5
	September	47.7	32.3			
				-21.1	10.8	0
	November	26.6	43.1			
	Annual Net Production					46.1 $g/0.1m^2/yr$ 461 $g/m^2/yr$ 1816 $kcal/m^2/yr$

Table 15. Calculation of net primary production for tall *Spartina alterniflora* using changes in observed living and dead mean standing crops

Sample date Year	Month	Standing crop (living) $(g/0.1m^2)$	Standing crop (dead) $(g/0.1m^2)$	Change living	Change dead	Net production $(5/0.1m^2)$
1967	January	17.4	118.2			
				- 2.6	- 8.9	0
	March	14.8	109.3			
				52.6	-10.3	52.6
1966	June	67.4	99.0			
				14.6	-54.7	14.6
	July	82.0	44.3			
				27.0	4.0	31.0
	August	109.0	48.3			
				22.9	- 5.0	22.9
	September	131.9	43.3			
				-13.2	21.7	8.5
	November	118.7	65.1			

Annual Net Production	$129.6\ g/0.1m^2/yr$
	$1296\ g/m^2/yr$
	$5365\ kcal/m^2/yr$

Table 16. Calculation of net primary production for <u>Juncus roemerianus</u> using changes in observed living and dead mean standing crops

Sample date Year	Month	Standing crop (living) ($g/0.1m^2$)	Standing crop (dead) ($g/0.1m^2$)	Change living	Change dead	Net Production ($g/0.1m^2$)
1967	January	65.1	97.1			
				- 4.6	13.5	8.9
	March	60.5	110.6			
				24.8	-22.6	24.8
1966	June	85.3	88.0			
				10.4	-10.4	10.4
	July	95.7	77.6			
				21.6	13.9	35.5
	August	117.3	91.5			
				-30.7	10.3	0
	September	86.6	101.8			
				-34.6	- 2.3	0
	November	52.0	99.5			

Annual Net Production

79.6 $g/0.1m^2/yr$
796 $g/m^2/yr$
3502 $kcal/m^2/yr$

Table 17. Calculations of net primary production on a whole-marsh basis using net production estimates calculated from observed living and dead standing crop values

Vegetation type	Percentage of marsh	Net production ($kcal/m^2/yr$)
<u>Spartina alterniflora</u>		
Short	44.2	1300
Medium	10.3	1816
Tall	5.8	5365
<u>Juncus roemerianus</u>	8.5	3502
	Weighted mean	1370

Table 18. Net primary production efficiency of each vegetation type and of whole-marsh using net production estimates calculated from observed living and dead standing crop values

Vegetation type	Efficiency per cent
<u>Spartina alterniflora</u>	Oak Island, North Carolina
Short	0.2
Medium	0.3
Tall	0.8
<u>Juncus roemerianus</u>	0.5
Whole-marsh	0.2

estimates based on changes in living and dead standing crops were higher for all vegetation types than efficiencies of observed living standing crop net production values. On a whole-marsh basis, the efficiency estimate was the same.

Statistical Analysis of Standing Crop Data

A simple analysis of variance and F-test of the data were run on the computer (Table 19). The F-test shows that there is significant variation, over and above sampling error, due to time throughout the year. All F-values proved to be highly significant.

Relative variability values (coefficients of variation) are presented in Table 20. Relative variability characterizes the inherent variability of the experimental material. In absolute terms, variability is expressed as s^2, in relative terms as the coefficient of variation. Relative variability expresses where variability other than that due to sampling error is located. These values show that the greatest variability occurs in dead categories which may be a problem of classification and growth pattern. Classification of categories and tidal removal of dead material from sample points may account for some of this variability.

The standing crop data for the time period June 1966 - March 1967 were fitted to a fourth degree polynomial in the time variable. The data were summed for living old, intermediate, and new stems to get a total living value for short, medium, and tall *Spartina alterniflora*. The same procedure was followed to obtain a total dead value for each of these vegetation types. *Spartina alterniflora* was also lumped to get a predicted value for all vegetation types in which this species occurred. *Juncus roemerianus* also was totaled to obtain a total living and total

Table 19. Analysis of variance and F-test to test overall variation between months

Vegetation type	Variable	Source	df	MS	F-ratio
Short *Spartina alterniflora*	Live (old)	Total	138		
		Regression	6	2056.9	31.3[a]
		Deviations	132	65.8	
	Live (intermediate)	Total	138		
		Regression	6	28.4	46.0
		Deviations	132	0.6	
	Live (new)	Total	138		
		Regression	6	38.9	24.1
		Deviations	132	1.6	
	Dead (old)	Total	138		
		Regression	6	631.2	5.4
		Deviations	132	115.9	
	Dead (intermediate)	Total	138		
		Regression	6	18.1	31.9
		Deviations	132	0.6	
	Dead (new)	Total	138		
		Regression	6	7.1	8.7
		Deviations	132	0.8	
	Dead (debris)	Total	138		
		Regression	6	3.6	7.2
		Deviations	132	0.5	
Medium *Spartina alterniflora*	Live (old)	Total	135		
		Regression	6	6102.6	46.8
		Deviations	129	130.4	
	Live (intermediate)	Total	135		
		Regression	6	127.5	42.6
		Deviations	129	3.0	
	Live (new)	Total	135		
		Regression	6	46.7	20.8
		Deviations	129	2.2	
	Dead (old)	Total	135		
		Regression	6	5860.8	30.7
		Deviations	129	190.7	

Table 19 (continued)

Vegetation type	Variable	Source	df	MS	F-ratio
	Dead (intermediate)	Total	135		
		Regression	6	66.7	15.8
		Deviations	129	4.2	
	Dead (new)	Total	135		
		Regression	6	3.9	7.4
		Deviations	129	0.5	
	Dead (debris)	Total	135		
		Regression	6	13.8	21.6
		Deviations	129	0.6	
Tall *Spartina alterniflora*	Live (old)	Total	139		
		Regression	6	4707.0	11.8
		Deviations	133	3797.5	
	Live (intermediate)	Total	139		
		Regression	6	749.9	23.3
		Deviation	133	32.2	
	Live (new)	Total	139		
		Regression	6	135.8	14.4
		Deviation	133	9.4	
	Dead (old)	Total	139		
		Regression	6	14024.0	15.7
		Deviation	133	895.0	
	Dead (intermediate)	Total	139		
		Regression	6	15.3	12.1
		Deviation	133	1.3	
	Dead (debris)	Total	139		
		Regression	6	25.5	10.5
		Deviation	133	2.4	

Table 19 (continued)

Vegetation type	Variable	Source	df	MS	F-ratio
Juncus roemerianus	Live (all)	Total	62		
		Regression	6	18.9	7.9
		Deviations	56	2.4	
	Live (green-dead)	Total	62		
		Regression	6	19.5	7.1
		Deviations	56	2.7	
	Dead (all)	Total	62		
		Regression	6	37.3	4.6
		Deviations	56	8.1	
	Dead (green-dead)	Total	62		
		Regression	6	0.5	5.0
		Deviations	56	0.1	
	Dead (debris)	Total	62		
		Regression	6	8.7	3.0[b]
		Deviations	56	2.9	

[a]All ratios highly significant at $P \leq 0.005$ except b.

[b]Significant at $0.005 \leq P \leq 0.01$.

Table 20. Relative variability of variables in vegetation types in Oak Island Marsh

Vegetation type	Variable	s^2	GM[a]	RV (per cent)
Short *Spartina alterniflora*	Live (old)	65.8	13.7	59.3
	Live (intermediate)	0.6	0.9	91.2
	Live (new)	1.6	1.7	76.3
	Dead (old)	115.9	18.6	57.7
	Dead (intermediate)	0.6	0.7	101.5
	Dead (new)	0.8	0.6	149.9
	Dead (debris	0.5	0.9	76.7
Medium *Spartina alterniflora*	Live (old)	130.4	1.7	104.3
	Live (intermediate)	3.0	25.6	44.6
	Live (new)	2.2	1.6	91.8
	Dead (old)	190.7	33.3	41.5
	Dead (intermediate)	4.2	1.3	159.0
	Dead (new)	0.5	0.4	177.9
	Dead (debris)	0.6	1.5	55.0
Tall *Spartina alterniflora*	Live (old)	3797.5	68.8	89.6
	Live (intermediate)	32.2	4.9	116.7
	Live (new)			
	Dead (old)	895.0	50.0	59.9
	Dead (intermediate)	17.8	3.3	127.5
	Dead (new)	1.3	0.7	152.0
	Dead (debris)	2.4	1.8	86.3
Juncus roemerianus	Live (all)	2.4	2.8	56.2
	Live (green-dead)	2.7	5.2	31.8
	Dead (all)	8.1	6.6	43.2
	Dead (green-dead)	0.1	0.6	51.2
	Dead (debris)	2.9	2.5	68.4

[a]General mean.

dead prediction estimate for calculation of net primary production. Coefficients of determination (R^2) were also calculated. These values express the percentage of variability in the standing crop explainable by the prediction equation.

A test of the hypothesis of no relationship is contained in the F-values associated with the reduction due to the regression on the model in Table 21. This test explains month-to-month variations. A significant F-value indicates that some relationship exists. The F-values are all highly significant at the .005 level, except the dead debris category in the *Juncus roemerianus* type which is significant at the .01 level. The R^2-values are considered to be a more quantitative expression of the extent of this relationship. The R^2-values are considered to be significant in all instances of a significant F-value.

It may be noted in Table 22 that the R^2-values are highest in the living categories of short, medium, and tall *Spartina alterniflora*. The R^2-values drop in the dead categories of all vegetation types. The R^2-values are lower in *Juncus roemerianus* in all categories than in *Spartina alterniflora* vegetation types. When *Spartina alterniflora* vegetation types are combined, the R^2-values drop radically.

By fitting the observed standing crop values to the prediction model, it was possible to determine standing crop estimates in $g/0.1m^2$ (Table 23). The values for February, April, May, October, and December are determined by calculation from the prediction equations shown in Appendix Table 1 since no data were collected for these months.

The predicted standing crop values in Table 23 were used to estimate net primary production for each vegetation type. Both methods used to

Table 21. Analysis of variance and F-test to test the reduction of sum of squares due to regression on the model for significance (for each living category and each dead category in each vegetation type)

Vegetation type	Variable	Source	df	MS	F-ratio
Short *Spartina alterniflora*	Live (old)	Total	138		
		Regression	4	3085.3	47.6[a]
		Deviations	134	64.8	
	Live (intermediate)	Total	138		
		Regression	4	41.3	63.9
		Deviations	134	0.6	
	Live (new)	Total	138		
		Regression	4	57.5	35.6
		Deviations	134	1.6	
	Dead (old)	Total	138		
		Regression	4	880.8	7.6
		Deviations	134	116.2	
	Dead (intermediate)	Total	138		
		Regression	4	26.8	47.2
		Deviations	134	0.6	
	Dead (old)	Total	138		
		Regression	4	9.0	10.5
		Deviations	134	0.9	
	Dead (debris)	Total	138		
		Regression	4	292.1	5.2
		Deviations	134	56.2	
Medium *Spartina alterniflora*	Live (old)	Total	135		
		Regression	4	9146.9	71.1
		Deviations	131	128.6	
	Live (intermediate)	Total	135		
		Regression	4	185.6	59.6
		Deviations	131	3.1	
	Live (new)	Total	135		
		Regression	4	63.7	26.5
		Deviations	131	2.4	

Table 21 (continued)

Vegetation type	Variable	Source	df	MS	F-ratio
	Dead (old)	Total	135		
		Regression	4	7471.1	32.8
		Deviations	131	338.1	
	Dead (intermediate)	Total	135		
		Regression	4	97.9	23.2
		Deviations	131	4.2	
	Dead (new)	Total	135		
		Regression	4	4.5	8.0
		Deviations	131	0.6	
	Dead (debris)	Total	135		
		Regression	4	1380.8	16.4
		Deviations	131	84.1	
Tall *Spartina alterniflora*	Live (old)	Total	139		
		Regression	4	70363.5	18.8
		Deviations	135	3748.4	
	Live (intermediate)	Total	139		
		Regression	4	1103.6	34.2
		Deviations	135	32.3	
	Live (new)	Total	139		
		Regression	4	199.1	21.1
		Deviations	135	9.4	
	Dead (old)	Total	139		
		Regression	4	20450.9	22.8
		Deviations	135	899.0	
	Dead (intermediate)	Total	139		
		Regression	4	547.7	31.0
		Deviations	135	17.7	
	Dead (new)	Total	139		
		Regression	4	22.8	18.4
		Deviations	135	1.2	
	Dead (debris)	Total	139		
		Regression	4	2586.8	9.4
		Deviations	135	276.0	

Table 21 (continued)

Vegetation type	Variable	Source	df	MS	F-ratio
Combined *Spartina alterniflora*	Live (old)	Total	414		
		Regression	4	53865.5	25.1
		Deviations	410	2148.9	
	Live (intermediate)	Total	414		
		Regression	4	918.9	48.6
		Deviations	410	18.9	
	Live (new)	Total	414		
		Regression	4	282.0	54.1
		Deviations	410	5.2	
	Dead (old)	Total	414		
		Regression	4	21478.7	33.3
		Deviations	410	645 4	
	Dead (intermediate)	Total	414		
		Regression	4	481.1	46.0
		Deviations	410	10.5	
	Dead (new)	Total	414		
		Regression	4	28.5	28.5
		Deviations	410	1.0	
	Dead (debris)	Total	414		
		Regression	4	3318.9	31.0
		Deviations	410	158.4	
Juncus roemerianus	Live (all)	Total	62		
		Regression	4	2755.3	11.7
		Deviations	58	236.6	
	Live (green-dead)	Total	62		
		Regression	4	2471.1	8.3
		Deviations	58	296.4	
	Dead (green-dead)	Total	62		
		Regression	4	54.7	6.2
		Deviations	58	8.9	

Table 21 (continued)

Vegetation type	Variable	Source	df	MS	F-ratio
	Dead (all)	Total	62		
		Regression	4	5514.2	7.0
		Deviations	58	787.2	
	Dead (debris)	Total	62		
		Regression	4	836.6	2.7[b]
		Deviations	58	309.8	

[a]All ratios highly significant at $P \leq 0.005$ except b.

[b]Significant at $0.005 \leq P \leq 0.01$.

Table 22. Goodness of fit (R^2-values) of the model for each variable of each vegetation type

Variable	Short *Spartina alterniflora*	Medium *Spartina alterniflora*	Tall *Spartina alterniflora*	Combined *Spartina alterniflora*	*Juncus roemerianus*
Live (old)	0.5869[a]	0.6847	0.3574	0.1965	
Live (intermediate)	0.6562	0.6455	0.5029	0.3216	
Live (new)	0.5150	0.4470	0.3845	0.3455	
Dead (old)	0.1846	0.5000	0.4026	0.2451	
Dead (intermediate)	0.5851	0.4141	0.4788	0.3097	
Dead (new)	0.2351	0.1954	0.3523	0.2241	
Dead (debris)	0.1345	0.3340	0.2174	0.1697	0.1570[b]
Live (all)					0.4454
Live (green-dead)					0.3651
Dead (green-dead)					0.2988
Dead (all)					0.3257

[a] All values highly significant at $P \leq 0.005$ except b.

[b] Significant at $0.005 \leq P \leq 0.01$.

Table 23. Predicted standing crop estimates for each vegetation type

Date	Standing crop (g/0.1m^2)									
	Short *Spartina alterniflora*		Medium *Spartina alterniflora*		Tall *Spartina alterniflora*		Combined *Spartina alterniflora*		*Juncus roemerianus*	
	Live	Dead	Live	Dead	Live	Dead	Live	Dead	Live	Dead
January	1.9	40.3	7.0	86.1	17.3	151.7	7.7	84.8	55.4	96.4
February	3.8	40.6	8.8	82.4	16.4	106.0	9.4	81.9	53.8	124.7
March	3.6	36.7	8.1	71.8	15.5	97.7	8.7	73.4	58.6	114.0
April	8.5	31.7	12.2	55.7	26.6	76.5	16.7	61.7	67.7	109.9
May	14.8	27.2	19.1	47.0	43.6	67.0	25.8	50.9	78.9	93.8
June	19.6	24.1	27.3	38.6	63.9	58.9	36.9	41.7	89.9	83.5
July	24.0	23.0	36.6	35.0	87.7	54.7	49.4	36.3	98.3	82.3
August	26.0	24.1	44.7	35.8	109.9	55.1	60.1	34.7	101.6	89.7
September	24.9	25.9	48.3	39.5	125.1	61.7	66.1	36.3	97.4	100.9
October	20.6	29.4	44.6	43.9	130.7	76.5	65.2	41.1	83.0	121.0
November	12.4	39.2	28.7	45.0	119.7	101.7	53.1	45.3	55.8	96.4
December	5.0	26.6	1.2	38.5	89.0	137.5	29.7	50.2	82.7	51.1

calculate primary production were used with the predicted estimates of standing crop. Net primary production estimates for each vegetation type and a combined *Spartina alterniflora* estimate, both based on peak standing crop values are given in Table 24. The values for short and medium *Spartina alterniflora* are higher than those obtained in a similar fashion from standing crop values. However, the values for tall *Spartina alterniflora* and *Juncus roemerianus* are lower. These latter types remain, however, the most productive of the four vegetation types in the marsh.

Estimates of net primary production on a whole-marsh basis using predicted living standing crop values are given in Table 25. These calculations were made in the same manner as previously described. This value, 1067 kcal/m^2/yr, is lower than the value in Table 11 of 1084 kcal/m^2/yr net production for the whole-marsh calculated from observed standing crop data.

Efficiency of net primary production for each vegetation type and on a whole-marsh basis using predicted living standing crop values only are shown in Table 26. Efficiency values obtained were about the same as those obtained in Table 12 except for the tall *Spartina alterniflora* and *Juncus roemerianus* types which are slightly lower. On a whole-marsh basis, estimates were the same.

Tables 27 through 31 present net primary production estimates obtained by use of the method of determining net primary production based on changes in predicted living and dead standing crop values. Calculations were made in the same manner as in Tables 13 - 16.

Values obtained using the predicted changes in living and dead standing crop are higher than any previously obtained. Tall *Spartina*

Table 24. Net primary production for each vegetation type using predicted living standing crop values

Vegetation type	$g/0.1m^2$	g/m^2	kcal/g	$kcal/m^2$
Spartina alterniflora				
Short	24.1	241	3.95	951
Medium	47.1	471	3.94	1856
Tall	115.2	1152	4.14	4769
Combined	58.4	584	4.01	2342
Juncus roemerianus	47.8	478	4.40	2103

Table 25. Calculation of net primary production on a whole-marsh basis using net production estimates calculated from predicted living standing crop values

Vegetation type	Percentage of marsh	Net production ($kcal/m^2/yr$)
Spartina alterniflora		
Short	44.2	951
Medium	10.3	1856
Tall	5.8	4769
Combined	60.3	2342
Juncus roemerianus	8.5	2103
	Weighted mean	1067

Table 26. Net primary production efficiency of each vegetation type and of whole-marsh using net production estimates calculated from predicted living standing crop values

Vegetation type	Efficiency per cent
Spartina alterniflora	Oak Island, North Carolina
Short	0.1
Medium	0.3
Tall	0.7
Combined	0.3
Juncus roemerianus	0.3
Whole-marsh	0.2

Table 27. Calculation of net primary production for short *Spartina alterniflora* using changes in predicted living and dead standing crops

Sample date	Standing crop living ($g/0.1m^2$)	Standing crop dead ($g/0.1m^2$)	Change living	Change dead	Net production ($g/0.1m^2$)
January	1.9	40.3			
			1.9	0.3	2.2
February	3.8	40.6			
			-0.2	-3.9	0
March	3.6	36.7			
			4.9	-5.0	4.9
April	8.5	31.7			
			6.0	-4.5	6.0
May	14.5	27.2			
			5.1	-3.1	5.1
June	19.6	24.1			
			4.4	-0.9	4.4
July	24.0	23.0			
			2.0	1.1	3.1
August	26.0	24.1			
			-1.1	1.8	0.7
September	24.9	25.9			
			-4.3	3.5	0
October	20.6	29.4			
			-8.2	9.8	1.6
November	12.4	39.2			
			-7.4	-12.6	0
December	5.0	26.6			

Annual Net Production: 28.0 $g/0.1m^2/yr$; 280 $g/m^2/yr$; 1106 $kcal/m^2/yr$

Table 28. Calculation of net primary production for medium *Spartina alterniflora* using changes in predicted living and dead standing crops

Sample date	Standing crop living ($g/0.1m^2$)	Standing crop dead ($g/0.1m^2$)	Change living	Change dead	Net production ($g/0.1m^2$)
January	7.0	86.1			
			1.8	- 3.7	1.8
February	8.8	82.4			
			-0.7	-10.6	0
March	8.1	71.8			
			4.1	-16.1	4.1
April	12.2	55.7			
			6.9	- 8.7	6.9
May	19.1	47.0			
			8.2	- 8.4	8.2
June	27.3	38.6			
			9.3	- 3.6	9.3
July	36.6	35.0			
			8.1	0.8	8.9
August	44.7	35.8			
			3.6	3.7	7.3
September	48.3	39.5			
			-3.7	4.4	0.6
October	44.6	43.9			
			-15.9	1.1	0
November	28.7	45.0			
			-27.5	-6.5	0
December	1.2	38.5			
Annual Net Production					47.1 $g/0.1m^2/yr$ 471 $g/m^2/yr$ 1856 $kcal/m^2/yr$

Table 29. Calculation of net primary production for tall <u>Spartina alterniflora</u> using changes in predicted living and dead standing crops

Sample date	Standing crop living ($g/0.1m^2$)	Standing crop dead ($g/0.1m^2$)	Change living	Change dead	Net production ($g/0.1m^2$)
January	17.3	151.7			
			- 0.9	-45.7	0
February	16.4	106.0			
			- 0.9	- 8.3	0
March	15.5	97.7			
			11.1	-21.2	11.1
April	26.6	76.5			
			17.0	- 6.5	17.0
May	43.6	70.0			
			20.3	-11.1	20.3
June	63.9	58.9			
			23.8	- 4.2	23.8
July	87.7	54.7			
			22.2	0.4	22.6
August	109.9	55.1			
			15.2	6.6	21.8
September	125.1	61.7			
			5.6	14.8	20.4
October	130.7	76.5			
			-11.0	25.2	14.2
November	119.7	101.7			
			-30.7	35.8	5.1
December	89.0	137.5			

Annual Net Production: 156.3 $g/0.1m^2/yr$; 1563 $g/m^2/yr$; 6471 $kcal/m^2/yr$

Table 30. Calculation of net primary production for combined <u>Spartina alterniflora</u> using changes in predicted living and dead standing crops

Sample date	Standing crop living ($g/0.1m^2$)	Standing crop dead ($g/0.1m^2$)	Change living	Change dead	Net production ($g/0.1m^2$)
January	7.7	84.8			
			1.7	- 3.1	1.7
February	9.4	81.9			
			- 0.7	- 8.5	0
March	8.7	73.4			
			8.0	-11.7	8.0
April	16.7	61.7			
			9.1	-10.8	9.1
May	25.8	50.9			
			11.1	- 9.2	11.1
June	36.9	41.7			
			12.5	- 5.4	12.5
July	49.4	36.3			
			10.7	- 1.6	10.7
August	60.1	34.7			
			6.0	1.6	7.6
September	66.1	36.3			
			- 0.9	4.8	3.9
October	65.2	41.1			
			-12.1	4.2	0
November	53.1	45.3			
			-13.4	4.9	0
December	29.7	50.2			
	Annual Net Production			64.6 $g/0.1m^2/yr$ 646 $g/m^2/yr$ 2590 $kcal/m^2/yr$	

Table 31. Calculation of net primary production for _Juncus_ _roemerianus_ using changes in predicted living and dead standing crops

Sample date	Standing crop living $(g/0.1m^2)$	Standing crop dead $(g/0.1m^2)$	Change living	Change dead	Net production $(g/0.1m^2)$
January	55.5	96.4			
			- 1.6	28.3	26.7
February	53.8	124.7			
			4.8	-10.7	4.8
March	58.6	114.0			
			9.1	- 4.1	9.1
April	67.7	109.9			
			11.2	-16.1	11.2
May	78.9	93.8			
			11.0	-10.3	11.0
June	89.9	83.5			
			8.4	- 1.2	8.4
July	98.3	82.3			
			3.3	7.4	10.7
August	101.6	89.7			
			- 4.2	11.2	7.0
September	97.4	100.9			
			-14.4	20.1	5.7
October	83.0	121.0			
			-27.2	-24.6	0
November	55.8	96.4			
			26.9	-45.3	26.9
December	82.7	51.1			
Annual Net Production				121.5 $g/0.1m^2/yr$ 1215 $g/m^2/yr$ 5346 $kcal/m^2/yr$	

alterniflora and Juncus roemerianus, in that order, still remain the most productive of all vegetation types. Short *Spartina alterniflora* is the least productive.

Net primary production was calculated on a whole-marsh basis in the same manner as previously described (Table 32). Values obtained based on prediction estimates and using changes in living and dead standing crop values were much higher than any of the previous methods of estimating net production.

Table 32. Calculations of net primary production on a whole-marsh basis using net production estimates calculated from changes in predicted living and dead standing crops

Vegetation type	Percentage of marsh	Net production ($kcal/m^2/yr$)
Spartina alterniflora		
Short	44.2	1106
Medium	10.3	1856
Tall	5.8	6471
Combined	60.3	2590
Juncus roemerianus	8.5	5346
	Weighted mean	1534

This method showed an increase of 1100 $kcal/m^2/yr$ for tall *Spartina alterniflora* type and 2200 $kcal/m^2/yr$ in *Juncus roemerianus* type. On a whole-marsh basis, an increase of about 200 $kcal/m^2/yr$ was noted (Tables 32 and 17).

The data obtained using changes in predicted living and dead standing crops appear to be the most nearly correct data obtained in this study. Estimates obtained are much higher and are more comparable with other salt marsh studies than any of the previous results in this study.

Efficiencies of net production for each vegetation type, and the entire marsh, based on net production data calculated from changes in predicted living and dead standing crop values are the highest obtained in this study (Table 33). Tall *Spartina alterniflora* was the most efficient vegetation type with an efficiency of 0.9%. *Juncus roemerianus* type followed with an efficiency of 0.8%. On a whole-marsh basis, however, efficiency was the same as all others reported in this study (0.2%).

Table 33. Net primary production efficiency of each vegetation type and of whole-marsh using net production estimates calculated from changes in predicted living and dead standing crops

Vegetation type	Efficiency per cent
Spartina alterniflora	Oak Island, North Carolina
Short	0.2
Medium	0.3
Tall	0.9
Combined	0.4
Juncus roemerianus	0.8
Whole-marsh	0.2

DISCUSSION AND CONCLUSIONS

Aerial Photography

Color and color-infrared aerial photographs were used in this study to determine acreage of community types within the Oak Island marsh. Analyses of marsh vegetation by color and color-infrared photographs are limited. Olson (1964) used color and panchromatic films to interpret marsh vegetation in Maine. He found that color films had a higher potential than panchromatic films, noting that a slight increase in accuracy of interpretation occurred with color films. Olson concluded in his study that volume and accuracy of information varied with vegetation types being studied, experience of interpretors, and scales of the photographs. Overall, Olson felt that volume and accuracy of information were not related to film type used.

Anson (1966) used panchromatic, color, and color-infrared film to obtain information about the potential usefulness of these films in photogrammetric applications in an area of the South Carolina Coastal Plain. Of interpreted items on three films, Anson's results showed correct analyses to be 20% greater on color film and 22% greater on color-infrared film. He concluded that color-infrared photography was superior to the other films for mapping drainage and vegetation.

The conclusion of this study is that mapping of relatively pure stands of salt marsh vegetation can be carried out successfully on color-infrared photographs. Entire acreage and distribution patterns of vegetation in an area of salt marsh may be analyzed in the laboratory from such photographs. However, in area of mixed vegetation, care must be taken to make adequate ground checks so that subtle variation patterns on the photographs may be correctly interpreted (Foster, 1968).

Net Primary Production

A harvest technique was used to obtain standing crop estimates for the four vegetation types in the regularly-flooded marsh at the Oak Island study area. Once standing crop estimates were determined, net production estimates were then calculated using two methods of calculation. These methods involved the use of: (1) living standing crop values only, both observed and predicted, and (2) changes in living and dead standing crop values, both observed and predicted. The results obtained from these two methods are summarized in Table 34.

Calculation of annual net production estimates for vegetation types based on living standing crop values only, both observed and predicted, are the lowest (Table 34). These estimates can be considered to be minimum estimate values of annual net production. Sampling error and changes in standing crop data such as death or consumption by herbivores of material between sampling periods are not taken into this method of estimating net productivity.

A second method used to calculate net production took into account changes in both living and dead standing crops (Smalley, 1959). It is assumed in this method that any net increase in living material between sampling periods is due to growth of new or existing stems. This increase is theoretically greater than death of stems or consumption by herbivores. If death and/or herbivore consumption of the standing crop exceeds an increase of the living standing crop, net production is zero.

Table 34. Summary of estimates of annual net primary production for each vegetation type and of whole-marsh in the Oak Island marsh using two methods of calculation

Vegetation type	Based on changes in living standing crop (kcal/m^2/yr)	Based on changes in living and dead standing crops (kcal/m^2/yr)
	Observed standing crops	
Spartina alterniflora		
Short	881	1300
Medium	1635	1816
Tall	4848	5365
Juncus roemerianus	1878	3502
Whole-marsh	1084	1370
	Predicted standing crops	
Spartina alterniflora		
Short	951	1106
Medium	1856	1856
Tall	4769	6471
Combined	2342	2590
Juncus roemerianus	2103	5346
Whole-marsh	1067	1534

If a decrease in the dead standing crop occurs, net production is considered as zero because processes which decrease the dead category were not studied.

Estimates of annual net production obtained using changes in living and dead standing crop values are higher than those using only living standing crop values (Table 34). Tall *Spartina alterniflora* (5365 kcal/m^2/yr) is the most productive of all vegetation types in the marsh. Net primary productivity was estimated to be 1300 kcal/m^2/yr for short *Spartina alterniflora*, 1816 kcal/m^2/yr for medium *Spartina alterniflora*, and 3502 kcal/m^2/yr for the *Juncus roemerianus* type. On a whole-marsh basis, the net primary productivity estimate was 1370 kcal/m^2/yr. It should be noted at this point that estimates on a whole-marsh basis were calculated from vegetation type per cent coverage presented in Table 6. All vegetation types totaled cover only 68.8% of the entire Oak Island marsh. The remaining percentage is covered by water (25%) and other community types, such as bare sand (6.2%). Productivity estimates therefore are based on 68.8% vegetation coverage instead of 100% coverages as in other marsh productivity studies.

Efficiency of net production was highest for the tall *Spartina alterniflora* type (0.8%) and *Juncus roemerianus* (0.5%). On a whole-marsh basis net production efficiency was 0.2%. Comparison of net production efficiencies with those reported in other studies will be discussed later.

Net production estimates obtained in the regularly-flooded marsh on Oak Island using observed changes in living and dead standing crops can be compared to the results obtained in other studies. Estimates obtained in the Oak Island study were determined using essentially the techniques of Smalley (1959) and Waits (1967). Teal (1962) using the data of Smalley (1959) showed net production estimates for the regularly-flooded marsh on Sapelo Island, Georgia as follows: short _Spartina alterniflora_ - 2570 kcal/m^2/yr (643 g/m^2/yr), levee-streamside (medium and tall) _Spartina alterniflora_ - 8970 kcal/m^2/yr (2243 g/m^2/yr). On a whole-marsh basis, total net production was 6580 kcal/m^2/yr.

Net production estimates for all vegetation types on Oak Island were much lower than those obtained on Sapelo Island. There are several reasons for this difference. In the first place no measurements were made to estimate the removal of leaves and stems between sample periods as they died or were broken. No correction factor was determined for losses of dead material due to tidal action, for decomposition rate, or for herbivore consumption. Smalley (1959) used a correction value of 26.6% to compensate for the loss of material in his net productivity estimate. In addition, the growing season in the Sapelo Island region is somewhat longer and more subtropical than that in the Oak Island study area. Perhaps the major reason is the difference in percent coverage of the marsh by tall and short _Spartina alterniflora_ in the two areas. In the Sapelo Island marsh, levee-streamside _Spartina alterniflora_ (equivalent to tall and medium _Spartina alterniflora_ in this study) occupies 58% of the total area and short _Spartina alterniflora_ occupies 42% of the total area. In the Oak Island marsh, tall and medium _Spartina alterniflora_ occupy only 16.1% (5.8 and 10.3% respectively) of the total marsh, with short Spartina alterniflora occupying 44.2%, and Juncus roemerianus 8.5%. Short Spartina is much less productive than tall Spartina and thus total production is much less in the Oak Island marsh as compared to Sapelo Island marsh.

Comparison of Oak Island estimates with those obtained by Waits (1967) on Bodie Island, North Carolina, show estimates of net primary productivity to be lower for Oak Island. Theoretically the reverse should be true since the Bodie Island study is in an irregularly-flooded marsh. Estimates of net production obtained by Waits (1967) are as follows: Spartina patens - 5835 kcal/m^2/yr, Mixed (several species) - 5981 kcal/m^2/yr, Juncus roemerianus - 6123 kcal/m^2/yr, and Marginal type - 3702 kcal/m^2/yr. On a whole-marsh basis, there is considerable difference in mean annual net production. Bodie Island had a net production of 5350 kcal/m^2/yr, and Oak Island measured 1370 kcal/m^2/yr Part of this difference may be due to the method of of estimates of per cent vegetation coverage of marsh. Calculations by Waits (1967) were based on 100% vegetation cover. Vegetation cover in the Oak Island marsh is only 68.8% of the total area.

Studies by Williams and Murdoch[4] of net primary production by Spartina alterniflora at Beaufort, North Carolina, were made by a

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[4]Williams, R. B. and Marianne B. Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Annual production of Spartina alterniflora and Juncus roemerianus in salt marshes near Beaufort, North Carolina. Presented at Association of Southeastern Biologists Meeting, April 15, 1966, Raleigh, North Carolina.

harvest technique similar to the one used at Sapelo Island, Georgia. Their estimates were made on the entire species Spartina alterniflora instead of the individual height forms. Ten one-meter squares of Spartina alterniflora were harvested every five weeks. All living and dead plants were removed. Dead leaves and number of leaf scars were counted, thus determining a balance between living and dead material. A correction value is thus used to account for the missing dead leaves. Williams and Murdoch also noted that development of new sprouts (intermediate) in Spartina alterniflora is subtracted from the peak value of the standing crop to obtain annual production. Williams and Murdoch[5] estimated 800 g dry matter (400 gC/m^2) as annual production of Spartina alterniflora.

In harvesting Juncus roemerianus, Williams and Murdoch[6] harvested two one-meter square samples each five weeks. Separation of leaves of Juncus roemerianus was as previously described in the METHODS section of this paper. This method of annual net production determination yielded estimates of 1 kg/m^2. Using a "compartmental model"

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[5]Williams, R. B. and Marianne B Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Annual production of Spartina and Juncus in North Carolina salt marshes. Presented at American Institute of Biological Sciences Meeting, August 15, 1966, College Park, Maryland.

[6]Ibid.

(transfer of standing crop between categories) annual net production of Juncus roemerianus was refined to 735 $g/m^2/yr$ by Williams and Murdoch[7].

Comparison of these data to values obtained in the Oak Island study show that the overall estimates (from predicted changes of living and dead standing crops) of 645 $g/m^2/yr$ is slightly lower than the 800 $g/m^2/yr$ obtained by Williams and Murdoch[8] for Spartina alterniflora. Values obtained for Juncus roemerianus range from 478 to 1306 $g/m^2/yr$ net production in the Oak Island marsh. The value obtained by Williams and Murdoch[9] using the "compartmental model" 735 $g/m^2/yr$ compares closely to 796 $g/m^2/yr$ obtained in this study using observed changes in living and dead standing crops.

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[7]Williams, R. B. and Marianne B. Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Compartmental alanysis of production and decay of Juncus roemerianus. Presented at Association of Southeastern Biologists Meeting, April 19, 1968, Athens, Georgia.

[8]Williams, R. B. and Marianne B. Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Annual production of Spartina and Juncus in North Carolina. Presented at American Institute of Biological Sciences Meeting, August 15, 1966, College Park, Maryland.

[9]Williams, R. B. and Marianne B. Murdoch. Oak Ridge National Laboratory, Oak Ridge, Tennessee, and U. S. Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina. Compartmental analysis of production and decay of Juncus roemerianus. Presented at Association of Southeastern Biologists Meeting, April 19, 1968, Athens, Georgia.

Foster (1968) made net primary production estimates on *Juncus roemerianus* using a slightly different method of estimating net production. He determined net leaf productivity by using rates of transfer of leaves between categories and by using rates of growth and of die-back of leaves. Once the number of leaves transferred in all intervals was summed, the number of leaves produced per year was determined. This value was then multiplied by the mean weight of green-dead leaves to calculate productivity in grams. In the second method, growth or die-back (in cm) for each interval (time) was multiplied by the unit weight of green-dead leaves to obtain productivity per interval. Annual production was obtained by summing all interval production values. Estimates obtained by Foster (1968) for net leaf productivity calculated from rates of transfer between categories were 550 leaves/m^2/yr (1028 g/m^2/yr). Annual production calculation from rates of growth was 553 g/m^2 and from rates of die-back was 571 g/m^2. Mean annual production of these values was 560 g/m^2/yr. Foster considered this value to be a minimum estimate of productivity and the larger value of 1028 g/m^2/yr to be a maximum estimate. He stated that the minimum estimate is the best estimate of net productivity of *Juncus roemerianus*.

These values are within the range of values obtained in this study. A minimum estimate of 478 g/m^2/yr and a maximum value of 1215 g/m^2/yr were calculated depending upon the method of estimating net primary production.

When net production is calculated using changes in observed living and dead standing crops, some of the standing crop changes included in the calculations may be errors due to sampling error or other unconsidered factors. The observed data obtained in this study were fitted to a fourth degree polynomial in time to obtain a smoother growth pattern over time. The goodness of fit of the standing crop data (R^2-values) was determined for all vegetation types (Table 22). The R^2-values for all categories except dead debris of the Juncus roemerianus type were highly significant at the .005 level. The dead debris category of Juncus roemerianus type was significant at the .01 level.

Even though the R^2-values were highly significant (the highest being 0.6847), there is still a considerable amount of variability in standing crop not accounted for by the regression in the model. Factors other than time would have to be considered to explain the remaining variability. Such factors could be tidal effects and local growth pattern. Surely the movement of the material in the dead categories is dependent on the tidal regimes in the regularly-flooded marsh. The R^2-values in dead debris categories in all vegetation types are generally lower (in size) than other categories. These R^2-values for the study in general fall in a range considered to be quite high for biological material. Therefore, predicted estimates of net primary production are considered to be reliable, despite the fact that considerable variation remains unexplained.

The R^2-values obtained in this study are much higher and more significant overall than those obtained by Waits (1967) in the Bodie Island study. The highest value obtained by Waits was 0.5265 which was highly significant at the .01 level. The predicted standing crop values obtained from fitting the observed standing crop data to the fourth degree polynomial in time do not include some fluctuations associated with the observed means. It is for the above reasons that the net production estimates calculated from changes in predicted living and dead standing crops are considered to be the best estimates obtained in this study.

Net primary production estimates obtained from changes in predicted living and dead standing crops are presented in Table 34. These estimates show that tall *Spartina alterniflora* type is the most productive (6471 kcal/m^2/yr) followed by *Juncus roemerianus* type (5345 kcal/m^2/yr). Net production on a whole-marsh basis is 1534 kcal/m^2/yr. These results are the highest obtained in this study. Waits (1967) obtained the following values using the same method of net production calculations in the Bodie Island marsh: *Spartina patens* - 6152 kcal/m^2/yr, *Juncus roemerianus* - 4028 kcal/m^2/yr, and whole-marsh basis - 4324 kcal/m^2/yr. Values for individual vegetation types are approximately equal. Higher estimates were obtained in the Oak Island study for the *Juncus* type. Tidal regimes in the regularly-flooded marsh theoretically remove waste products and increase nutrient circulation. The growing season being longer in the Oak Island marsh than in the Bodie Island marsh could account for the increased production of *Juncus roemerianus*.

Efficiency of net primary production values obtained in this study are low compared to the 1.4% efficiency obtained by Teal (1962). Regardless of the method of calculation of net primary productivity, efficiency on a whole-marsh basis (Tables 12, 18, 26, and 33) was estimated to be 0.2% in the Oak Island study. The highest percentages obtained (using predicted changes in living and dead standing crops) was 0.9% for tall *Spartina alterniflora* and 0.8% for *Juncus roemerianus*. Waits (1967) obtained estimates of 0.3 to 0.5% efficiencies of net production on a whole-marsh basis. Estimates of 0.8% for Spartina patens and 0.5% for Juncus roemerianus net production efficiencies (using predicted changes in living and dead standing crops) were the highest values obtained in the Bodie Island study. These values are approximately the same for both irregularly and regularly-flooded marshes in North Carolina.

No estimates of respiration rates were obtained and thus no estimate of gross primary production is available for the Oak Island study. As this study was concerned with calculation of net primary productivity in a regularly-flooded salt marsh, several sources of error are not compensated for in estimating net primary production. First of all, sample error must be admitted. No corrections are made for this error. Another source of error is that no compensation was allowed for herbivore activity. Waits (1967), Teal (1962), and Smalley (1959) feel that this is negligible. Teal (1962) reports only 305 kcal/m^2/yr are consumed by insects. Smalley (1959) states that grasshoppers feed on Spartina alterniflora only about four months out of the year. He feels that most organisms which feed in the marsh such as the fiddler crab, the marsh mussel, and the salt marsh periwinkle are detritus feeders. Smalley proposes that most of the Spartina alterniflora production is thus passed on to the decomposers in the marsh and the estuary.

No estimates were made in the Oak Island marsh for other producers. Other producer sources in the marsh would be algae on the exposed mud surfaces and stems of the vascular plants. Some algae may be suspended in the water in the marsh. Ragotzkie (1959) estimated net production of phytoplankton in the estuary water around Sapelo Island to be zero. Estimate of net production of algae in the marsh is 1620 kcal/m^2/yr.

No estimates of production of roots and rhizomes were made in this study. Only above-ground parts of plants were considered in net primary productivity estimates. This is another possible source of error.

A final source of error is no estimation of decomposition rate. Removal of material by decomposition between sampling periods means unmeasured production, thus underestimation of net productivity. No attempt was made to compensate for such material in this study.

Statements as to exactly how much net primary productivity is exported from the marsh to the estuary cannot be made on the basis of data from this study. Based on other studies, it is reasonable to suppose that much of this productivity goes to the estuary and is used by organisms in the estuary.

SUMMARY

This study was carried out in an effort to determine the general nature of net primary production in an area of regularly-flooded salt marsh at Oak Island, Brunswick County, North Carolina. The specific objectives were: (1) to develop a rapid method of determining the area of major salt marsh community types using color-infrared aerial photographs, and (2) to estimate the magnitude of net primary production of major vascular vegetation types within the marsh. Aerial photographs and vegetation samples were taken to determine net primary production.

Short, medium, and tall *Spartina alterniflora*, and *Juncus roemerianus* compose the vegetation in this regularly-flooded marsh. Water and other types (bare sand and mud) were also considered in determination of the total acreage of the various community types in the marsh. Acreage determinations for each of the community types are made on color-infrared photographs. Color-infrared photographs can be used in the laboratory to interpret community types over large areas.

The primary purpose of this study was to obtain estimates of net primary production of vegetation types within the regularly-flooded salt marsh. Standing crop values, obtained using a harvest technique, were used to calculate net production. Net production was calculated using two methods: (1) use of only living standing crop values, and (2) use of both changes in living and dead standing crops. The first method when compared to the second method showed an underestimation of net production. Estimates of net primary production obtained using the second method of calculation are as follows: short *Spartina alterniflora* - 1300 kcal/m^2/yr, medium *Spartina alterniflora* -

1816 $kcal/m^2/yr$, tall Spartina alterniflora - 5365 $kcal/m^2/yr$, and Juncus roemerianus - 3502 $kcal/m^2/yr$. Mean annual net production on a whole-marsh basis was estimated to be 1370 $kcal/m^2/yr$. Efficiency of net production ranged from 0.8% for tall Spartina alterniflora to 0.2% for short Spartina alterniflora. On a whole-marsh basis, efficiency of net production was 0.2%. These values were lower than those reported by Teal (1962) or Waits (1967).

The observed standing crop data were fitted to a fourth degree polynomial in the time variable to provide a smoother fit of the data to a growth curve. The goodness of fit (R^2-values) of the standing crop data to the polynomial was good in this study. These values were better than those obtained by Waits (1967). The predicted values obtained from fitting the observed data to the polynomial were used to calculate net production. Changes in both predicted living and dead standing crops were also calculated. Net production values obtained by this method of calculation are as follows: short Spartina alterniflora - 1106 $kcal/m^2/yr$, medium Spartina alterniflora - 1856 $kcal/m^2/yr$, tall Spartina alterniflora - 6467 $kcal/m^2/yr$ and Juncus roemerianus - 5746 $kcal/m^2/yr$. On a whole-marsh basis, net primary production was estimated to be 1544 $kcal/m^2/yr$. These values are thought to be the most reliable estimates obtained in this study. Sampling error and other processes not studied in this investigation represent sources of error in these estimates of net production.

An energy export value to the estuary was not obtained in this study. However, there is no reason to suppose that energy is not exported into the estuarine system just as at Sapelo Island, Georgia.

It is also reasonable to suppose that this exported energy is available to organisms in the estuarine system.

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APPENDIX

Appendix Table 1. Prediction equations for each variable in each vegetation type obtained from fitting observed standing crop estimates to a fourth degree polynomial in time

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Short *Spartina alterniflora*

Live (old)

$$\hat{y}(X_2) = 21.153 + (3.613)t + (-1.383)t^2 + (-0.114)t^3 + (0.024)t^4$$

Live (intermediate)

$$\hat{y}(X_3) = 0.00003 + (-0.526)t + (0.219)t^2 + (0.023)t^3 + (-0.005)t^4$$

Live (new)

$$\hat{y}(X_4) = 0.590 + (1.164)t + (0.304)t^2 + (-0.054)t^3 + (-0.013)t^4$$

Dead (old)

$$\hat{y}(X_5) = 12.717 + (0.938)t + (0.862)t^2 + (-0.062)t^3 + (-0.017)t^4$$

Dead (intermediate)

$$\hat{y}(X_6) = 0.005 + (-0.245)t + (0.093)t^2 + (0.010)t^3 + (-0.0004)t^4$$

Dead (new)

$$\hat{y}(X_7) = -0.068 + (0.343)t + (0.114)t^2 + (-0.014)t^3 + (-0.003)t^4$$

Dead (debris)

$$\hat{y}(X_8) = 10.523 + (-1.977)t + (0.052)t^2 + (0.055)t^3 + (-0.005)t^4$$

Medium *Spartina alterniflora*

Live (old)

$$\hat{y}(X_2) = 31.294 + (9.421)t + (-0.931)t^2 + (-0.321)t^3 + (-0.003)t^4$$

Live (intermediate)

$$\hat{y}(X_3) = (0.035) + (-1.152)t + (0.562)t^2 + (0.032)t^3 + (-0.016)t^4$$

Live (new)

$$\hat{y}(X_4) = (-0.061) + (1.191)t + (0.371)t^2 + (-0.054)t^3 + (0.013)t^4$$

Appendix Table 1 (continued)

Dead (old)

$$\hat{y}(X_5) = 17.592 + (1.812)t + (2.629)t^2 + (-0.207)t^3 + (-0.063)t^4$$

Dead (intermediate)

$$\hat{y}(X_6) = (-0.020) + (-0.709)t + (0.344)t^2 + (0.018)t^3 + (-0.009)t^4$$

Dead (new)

$$\hat{y}(X_7) = (-0.109) + (0.241)t + 90.097)t^2 + (-0.012)t^3 + (-0.003)t^4$$

Dead (debris)

$$\hat{y}(X_8) = (18.622) + (-5.175)t + (0.666)t^2 + (0.184)t^3 + (0.024)t^4$$

Tall *Spartina alterniflora*

Live (old)

$$\hat{y}(X_2) = 73.934 + (23.483)t + (-1.096)t^2 + (-0.560)t^3 + (-0.002)t^4$$

Live (intermediate)

$$\hat{y}(X_3) = 0.002 + (-2.140)t + (0.893)t^2 + (0.082)t^3 + (-0.015)t^4$$

Live (new)

$$\hat{y}(X_4) = 0.483 + (2.091)t + (0.522)t^2 + (-0.089)t^3 + (-0.018)t^4$$

Dead (old)

$$\hat{y}(X_5) = 30.640 + (-3.092)t + (3.660)t^2 + (-0.140)t^3 + (-0.094)t^4$$

Dead (intermediate)

$$\hat{y}(X_6) = 0.008 + (-1.076)t + (0.438)t^2 + (0.035)t^3 + (0.004)t^4$$

Dead (new)

$$\hat{y}(X_7) = 0.039 + (0.161)t + (0.041)t^2 + (0.002)t^3 + (0.001)t^4$$

Dead (debris)

$$\hat{y}(X_8) = 25.497 + (-8.059)t + (-2.067)t^2 + (0.383)t^3 + (0.086)t^4$$

Appendix Table 1 (continued)

Combined *Spartina alterniflora*

Live (old)

$$\hat{y}(X_2) = 42.126 + (12.162)t + (-1.131)t^2 + (-0.331)t^3 + (0.006)t^4$$

Live (intermediate)

$$\hat{y}(X_3) = -0.012 + (-1.291)t + (0.568)t^2 + (0.046)t^3 + (-0.013)t^4$$

Live (new)

$$\hat{y}(X_4) = 0.338 + (1.482)t + (0.399)t^2 + (0.066)t^3 + (-0.015)t^4$$

Dead (old)

$$\hat{y}(X_5) = 20.309 + (-0.241)t + (2.453)t^2 + (-0.134)t^3 + (-0.061)t^4$$

Dead (intermediate)

$$\hat{y}(X_6) = -0.003 + (-0.683)t + (0.295)t^2 + (0.021)t^3 + (-0.004)t^4$$

Dead (new)

$$\hat{y}(X_7) = -0.046 + (0.249)t + (0.084)t^2 + (-0.008)t^3 + (-0.002)t^4$$

Dead (debris)

$$\hat{y}(X_8) = 18.215 + (-5.055)t + (-0.902)t^2 + (0.207)t^3 + (0.035)t^4$$

Juncus roemerianus

Dead (debris)

$$\hat{y}(X_2) = 33.353 + (0.755)t + (-1.652)t^2 + (0.003)t^3 + (0.039)t^4$$

Live (all)

$$\hat{y}(X_3) = 24.573 + (9.970)t + (1.760)t^2 + (-0.446)t^3 + (-0.096)t^4$$

Live (green-dead)

$$\hat{y}(X_4) = 69.362 + (-1.237)t + (-3.576)t^2 + (0.040)t^3 + (0.093)t^4$$

Appendix Table 1 (continued)

Dead (green-dead)

$$\hat{y}(X_5) = 6.66 + (-1.190)t + (0.042)t^2 + (0.035)t^3 + (-0.005)t^4$$

Dead (all)

$$\hat{y}(X_6) = 41.792 + (-1.419)t + (6.474)t^2 + (-0.088)t^3 + (-0.203)t^4$$