Community Structure and Production of the Epiphytic Algae in the Barataria Bay Area of Louisiana.

Wilmer Charles Stowe

Louisiana State University and Agricultural & Mechanical College

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The Louisiana State University and Agricultural
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Botany

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COMMUNITY STRUCTURE AND PRODUCTION OF THE EPiphytic
ALGAE IN THE BARATARIA BAY AREA OF LOUISIANA

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in
The Department of Botany

by
Wilmer Charles Stowe
B. S., Louisiana Polytechnic Institute, 1965
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August, 1972

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12. Diagrammatic representation of possible energy flow for the water's edge epiphytic community; showing gross production, respiratory loss, and export from the community ........................................ 66

13. Diagrammatic representation of possible energy flow for the inland epiphytic community; showing gross production, respiration loss, and import into the community ........................................ 68
Annual primary production and community respiration were determined for the epiphytic algae associated with *Spartina alterniflora* Loisel. in the southwestern Barataria Bay area of Louisiana. Changes in production and respiration were related to changes in the algal standing crop.

The epiphytes were divided into two communities: (1) those associated with the *Spartina* located at the water's edge (the grass-water interface) and (2) those associated with the *Spartina* located 1.5 meters inland from the water's edge.

Structurally, the presence of macroscopic algae at the water's edge and their absence inland was one of the most noticeable differences between the two locations. At the microscopic level distinct diatom communities were observed at the two locations.

Productively the two locations were very different. The water's edge community exported 16.06 g C/m$^2$ annually; whereas, the inland community required the import of 63.44 g C/m$^2$ annually for maintenance.
INTRODUCTION

High production levels within the estuaries have been attributed to the large amount of organic detritus of higher plant-origin and to attached algae concentrated at the margins of the water (Russell-Hunter, 1970). The high turbidity found in many estuaries often reduces the effectiveness of phytoplankton as producers.

This study was undertaken to determine the significance of a group of attached algae (the epiphytes) to the general energy flow of the Barataria Bay ecosystem. These epiphytes are associated with the higher marsh plants.

The stimulus for this study was based on information from Wetzel (1964) and Jones (1968) which showed attached estuarine algae to be highly productive, and a study by Becker (1972) in which about 6,625 miles of streamside and lake-margin shore line were found in the Barataria Bay area of Louisiana. Most of this shore line is vegetated by the marsh grass Spartina alterniflora Loisel. When it is realized that Spartina increases by five times the surface area of the streamside, the tremendous area available to the attaching algae can be realized.

Studies of sessile communities have given rise to a great variety of terminology. Much of this terminology has been discussed in detail by Wetzel (1964) and Round (1964 b). For the purposes of this paper, two terms will be used to describe the sessile community. Periphyton, a general term, refers to those organisms living either attached to or upon any substrate. Epiphyton refers specifically...
to organisms living attached to or upon living plant substrates.

In this study culms of *Spartina alterniflora* and the pneumatophores of *Avicennia germinata* (L.) L. served as the host substrate. All organisms collected on the host substrate are classified as epiphytes.
DESCRIPTION OF THE AREA

The vegetation of the lower Barataria Bay system is typical of a saline marsh (Chabreck, et al., 1968). The entire system is bounded by the levees of the Mississippi River on the east and those of the Bayou Lafourche on the west. The southern border is formed by a series of barrier islands and salt marsh. This is a deltaic plain in a dynamic state of land flux (Gagliano and van Beek, 1970). The estuary is one of the interdistributary bays formed over the past 5,000 years by the changes in the course of the Mississippi River (Frazier, 1967). More detailed discussions of the geological processes are given by Russell (1936), Saucier (1963), and Gagliano and van Beek (1970) and others.

Supporting evidence, both physical and chemical, is also being collected by other persons within the sampling area. Instrument stations which continually monitor some of the physical parameters are permanently located in the area.

The saline marsh region (the location of this study) has eight permanent sampling stations and four instrument stations (Figure 1). The following stations were selected as permanent sampling sites for epiphytic algae: stations 6, 7, 12 and a station opposite instrument station number 2. Stations 6 and 7 are located at opposite ends of Airplane Lake. Stations 6 and 7 were selected for two reasons: (1) information from the Louisiana Wild Life and Fisheries Commission stated that Airplane Lake traditionally has an early development of large shrimp populations, and (2) these two stations have very
Figure 1. Location of sampling stations within the Barataria Bay area.

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different grass communities. Station 6 is located at the eastern end of the lake and has a vegetation composed almost exclusively of *Spartina alterniflora*. Station 7 is located at the western end of the lake and has mixed vegetation composed primarily of *Spartina alterniflora*, *S. patens*, and *Distichlis spicata*. *D. spicata* has a much denser growth than either species of *Spartina*, resulting in more intensive shading than in the other locations. Station 12 is in a "pure" stand of *Spartina* at the west end of Lake Palourde approximately 1.5 miles southwest of Airplane Lake. This station is located at a bend in the lake and does not receive the full force of waves blown the entire length of the lake. The sampling site located at instrument station 2 is also located in a "pure" stand of *Spartina alterniflora*. This station is in a bayou at the eastern end of Lake Palourde. This is an east-west bayou that is almost straight for three-quarters of a mile. Waves at this site could result from wind blowing the entire length of the lake.

Stations 7 and 12 are obviously different from the other two stations. Station 7 has a higher shore line relative to the other stations. The inland location at station 7 is the highest of all inland locations. Station 12 is the shallowest of all stations with a long sloping shoreline. Along the shore are numerous islands of *S. alterniflora* surrounded by water or bare marsh area. The island location appears to be flat in respect to the water's edge.

The annual variation in atmospheric temperature for the New Orleans area (approximately 60 miles north) shows a range from 12 C in the winter to a summer average high of 28 C (U.S. Dept. of Commerce, 1968). The average temperature for each month is shown in...
Figure 2A. The average water temperature (Day et al., in preparation) for the Barataria Bay area is also shown in figure 2A. Only two months have temperatures of less than 15 C while 4 months have an average water temperature greater than 25 C.

Salinity data provided by the Louisiana Wild Life and Fisheries Commission (Barrett, 1971) is shown in Figure 2B. This graph is the average of 16 or more samples taken each month from January 1968, to June 1969.

Daily tidal variations generally range from a few centimeters to 50 or 60 cm. There is a seasonality to the height of the tides also (Figure 2C). The average water depth in a nearby channel ranges from a maximum of 1.4 m in the summer to a low of 1.0 m in the winter. Also shown is the approximate marsh level relative to the depth of the water in the channel. The summer tides show two peaks: a lower spring peak and a larger late summer peak. During eight months of the year the average water level is equal to or higher than the level of the marsh floor.

Because of the host-epiphyte relationship, Figure 3 is included to show the seasonal changes in the live standing crop of Spartina alterniflora. This unpublished graph was adapted from Kirby (1971). Dead and dying material is most abundant during the fall and winter; however, in the spring there is a rapid initiation of new growth which generally reaches a peak in September. A rapid decline in live standing material occurs after flowering.
A. Average water temperature in the sampling area. Thirty year average atmospheric temperature for the southeastern area of Louisiana.

B. Average monthly salinity for the southern Barataria Bay area.

C. Average monthly water level and extremes in Airplane Lake for 1970. Water level is a measure of depth of water in the channel leading to the lake. Marsh line reference is shown.
Figure 3. Live standing crop of streamside and inland *Spartina* expressed as grams per square meter (from Kirby, 1971).
REVIEW OF LITERATURE

This review is divided into five sections: epiphytic production, ecology of littoral algae, epiphytic ecology, filamentous epiphytes, and organic nutrition.

Primary production is one of the two significant subjects of this paper. Because of the numerous reports on primary production, this review is restricted to production by the epiphytic algae. Similarly, algal ecology has been researched extensively; and for this reason, this literature review is restricted to ecology of littoral algae. The section on epiphyte ecology is designed to show the differences between living and non-living substrates. The filamentous epiphytes have been separated from the other sections because of their conspicuous nature and important contribution to the epiphytic community. Organic nutrition of algae is significant because (1) all organisms studied here are living on an organic substrate, (2) this organic substrate is subject to seasonal changes, and (3) heterotrophy by the epiphytic algal community appears to be present.

I. EPIPHYTIC PRODUCTION

Most reports of primary production by benthic organisms deal with total water body production, and give general compartmentalization of the community production (e.g. Pomeroy, 1960; and Pieczynska and Szczepanska, 1966), or, as in the case of Mann (1970), allude to higher levels of production by epiphytic algae.
Recently more detailed studies have measured epiphytic production: by Allen (1971) and Hickman (1971) in fresh water and by Jones (1968) and Wetzel (1964) in saline environments.

Epiphytic production has been found to vary in different environments. In a fresh water environment, Allen (1971) found $^{14}$C incorporation by the epiphytes to be 660 g C/m$^2$/yr. on submerged substrates and 71 g C/m$^2$/yr. on emergent substrates. Hickman (1971) reported 279 g C/m$^2$/yr. $^{14}$C incorporation by the epiphytes on Equisetum. In the saline environment Wetzel (1964) found that the $^{14}$C fixation by periphyton was 267 g C/m$^2$/yr. Jones (1968) who used the oxygen method found that the epiphytes on Thalassia produced 315 g C/m$^2$/yr. or about 35% of the total production of the host-epiphyte complex.

Attempts made to correlate periphyton production with chlorophyll have shown contradictory results. Szczepanski and Szczepanski (1966) showed a correlation of increasing production with increasing chlorophyll; however, Wetzel (1964) found a poor correlation between pigment levels and production. Only when there were high levels of both chlorophyll and production did the two correlate well (Wetzel, 1964). Hickman (1971) suggested partial correlation of production with total cell number and chlorophyll. At times he found correlation of production with cell number; at other times it appeared to correlate with chlorophyll levels. However, there was relatively poor correlation between total cell number and chlorophyll level. Allen (1971) found major pigment peaks to occur in the winter for the submerged vegetation. These peaks occurred at a time when production was undetectable. However, on emergent vegetation pigment
peaks nearly coincided with the production peaks.

Variation in production by attached algae is related to the degree of submergence. Wetzel (1964) found considerable variation between samples. He attributed this to fluctuation in water level. Allen (1971) found on emergent vegetation less variation in production with increasing depth.

While these production figures are significant on a unit area basis, epiphytic production, generally, is limited to regions of abundant host plants and is severely stressed by fluctuations in water level. Production by this group may be either a main source of energy production in shallow lakes, ponds, and marshes or a negligible source in larger, deeper lakes (Wetzel, 1964).

II. ECOLOGY OF LITTORAL ALGAE

The presence of organisms within an environment indicates their physiochemical selection over a wide variety of other organisms (Provasoli and Pintner, 1960). It is the adaptation of organisms to specific environmental situations that results in these organisms being used as environmental indicators (Provasoli and Pintner, 1960).

Algae within the littoral zone are exposed to widely varying environments (Round, 1965). Some of these variables are: length of exposure to desiccation, salinity, air and water temperatures, light, nutrients, and in the case of the epiphytes, condition of the host plant (Feldman, 1951; Biebl, 1962; Round, 1965).

A. Influences of Periodic Submersion and Emersion

Algae within the littoral belt are subject to periodic submersion and emersion. These organisms either can tolerate this
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A. Influences of Periodic Submersion and Emersion

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situation or actually require it for survival (Feldmann, 1951). The marine alga *Fucus*, for example, survives only when exposed to alternating periods of wetting and drying. With prolonged submersion it dies from anoxia (Biebl, 1962), whereas species of *Bostrychia* are capable of surviving long periods of submersion and exposure (Dawson, 1966).

The time and duration of emersion are also factors in water loss from marine algae. It has been observed that algae emersed during the night are subject to less dehydration than are those exposed during the day (Jenik and Lawson, 1967).

The width and height of the algal zone is influenced by the frequency and length of exposure (Castenholz, 1963). Its upper limits are determined by the tolerance of the juveniles to exposure and the ability of the substrate to retain moisture (Castenholz, 1967).

The ability to survive desiccation depends on cellular resistance to plasmolysis. Thickness of the cell wall (Feldman, 1951) and growth pattern (Round, 1965) are two factors involved in the survival against desiccation. Plants with thick cell walls and sheaths are capable of retaining large quantities of moisture, assuring survival during long periods of exposure. However, thick-walled plants such as *Fucus sp.*, also tend to hold waste metabolites in and require some aids such as tidal flushing to help eliminate the material. Thin-walled plants often lose large quantities of water and are subject to death by desiccation. On the other hand, plants such as *Bostrychia sp.* are capable of surviving prolonged submergence. Upon emersion their highly branched, spongy thalli hold water and enable them to survive prolonged exposure (Dawson, 1966).
Field and laboratory studies on algal desiccation have shown that the substrate plays a very important role in the retention of water by the alga. Laboratory experiments with substrate-free Caloglossa (Chapman, 1966) showed a 70% loss of water in 30 minutes in a wind of 8 ft/sec in high relative humidity and temperature. On a mangrove pneumatophore, at the same wind speed and temperature, it lost only 50% of the water in nine hours (Chapman, 1966).

The nature of the substrate influences the distribution of epiphytic diatoms. During periods of exposure to the air, the water-holding potential of the substrate determines the species composition (Hopkins, 1964). Substrates that can retain water for long periods of time stimulate the development of desiccation-sensitive species in the higher littoral zone (Hopkins, 1964). Chalk cliffs which have high water-holding capacity have been found to support the desiccation-sensitive diatoms Navicula ramosissima, Fragilaria striatula, and Licmophora (Hopkins, 1964).

B. Influence of Dehydration on Photosynthesis

Ogata and Matsui (1965) studying the influence of dehydration on the photosynthetic rate, found a gradation in tolerance related to the position in the algal band. Dehydration effects were also found to be species-variable. Prior dehydration of Porphyra tenera up to 91% loss of fresh weight had no effect on photosynthesis. However, prior dehydration up to 70% resulted in a declining rate of photosynthesis in Ulva pertusa; dehydration above 75% resulted in complete photosynthetic suppression. Gelidium was found to be more sensitive to prior dehydration than Ulva (Ogata and Matsui, 1965). Chapman (1966) found that upon reimmersion the rise in photosynthetic
rate only occurred if prior dehydration was slight. If dehydration had been severe, photosynthesis was repressed.

Photosynthesis and respiration of exposed intertidal algae are often dependent on their ability to retain water (Biebl, 1962). Because *Hormosira* is sensitive to desiccation, photosynthesis usually ceases within an hour of emergence (Chapman, 1966). The photosynthetic rate of *Carpophyllum maschalocarprum* falls 60% on emergence and drops to zero at 80% dehydration; whereas, respiration drops 35% on emersion and declines to 20% of the submerged value at 80% desiccation. Inhibition of photosynthesis under dehydrated conditions results from protoplasmic shrinkage and cytoplasmic changes in CO$_2$ and pH (Ogata and Matsui, 1965).

C. Influences of Salinity

Tidal cycles that bring stress by desiccation also contribute to salinity stress (Feldmann, 1951). Williams (1962) found that diatom reproduction took place throughout wide salinity ranges; however, the higher salt levels included numbers of dead cells or cells with deformed chromatophores. Drum and Webber (1966), in a Massachusetts salt marsh, found the greatest species diversity occurred at stations of the lowest salinity. Almost half of the taxa which they found in Massachusetts were reported in an earlier study in the Des Moines River in Iowa indicating that many diatoms have wide salinity tolerances.

D. Influence of Temperature and Light

Littoral algae are subject to wide variations in temperature. While water temperature is less variable than atmospheric temperature (Feldmann, 1951), water in shallow bays and estuaries is much more...
greatly influenced by atmospheric temperatures than is the water in deeper bays (Reid, 1961). Thus, algae in the littoral region of the shallow bays can be exposed to as much temperature variation as takes place in the atmosphere.

Seasonal temperature variations have been suggested as factors responsible for the migration of algae from one location to another (Knight and Parke, 1931, cited by Feldmann, 1951).

Light and temperature have occasionally been shown to act in combination affecting the photosynthesis of marine littoral algae. The photosynthetic rate of the red alga Chondrus at 20 C demonstrates a logarithmic increase with increasing light up to about 1000 foot candles (Kanwisher, 1966). At 2.0 C, it reaches its photosynthetic peak near 750 foot candles.

Low respiration rates may be a survival mechanism allowing the algae to survive in dim light (Blinks, 1955). The suppression of respiration by low temperatures could account for the rapid build-up of filamentous algae during the colder months (Levring, 1969). Also associated with the lowering of temperature would be a reduction in the respiration and activity of the grazers. As Blinks (1955) suggests, high production and low grazing can mean a larger accumulation of organic carbon.

Light quality and intensity are also functions of water depth by the selective absorption of light with increasing depth (e.g. Reid, 1961). The selective absorption of various wave lengths of light in turbid water serves to restrict the distribution of algae (Dawson, 1966). In silty water some brown algae are found at depths receiving only 40 to 80 foot candles of light. This light intensity is near
their compensation point. Turbid waters have been found to reduce the P:R ratio for the phaeophytes (Levring, 1969).

Castenholz (1963) found a relationship between diatom density and light intensity as affected by depth of submersion. In the laboratory, McIntire and Wulff (1969) observed a relationship between light intensity, biomass of diatoms, and the length of the desiccation period. They also noticed some adaptation to different light intensities.

Diatom distribution is influenced by a multitude of environmental parameters. However, within an estuary, light and temperature may be the two most important ones (Patrick, 1967).

Within an estuary three types of diatoms are commonly found: benthic, neritic and planktonic (Patrick, 1967). Usually high turbidity in the estuary tends to repress the activities of the true planktonic forms, resulting in dominances by benthic and neritic forms (Russell-Hunter, 1970). Thus, within most estuaries true planktonic diatoms are not a significant component of the population.

E. Littoral Zonation

Hendey (1964) has divided the littoral area of the estuary into three zones dependent on tide level. Within these three zones—supra-littoral, littoral, and sub-littoral—can be found all extremes of environmental situations. Each zone has its own characteristic diatom flora. The littoral region has the greatest species diversity, followed by the sub-littoral. The supra-littoral zone has the smallest degree of diversity. Castenholz (1967) observed, however, that the sub-littoral community was the most stable. He observed that the populations in sub-littoral communities show little seasonal
variation in regions of moderate climatic variation. Patrick and Reimer (1966) observed that very stable environments show a relatively low population diversity and that a slightly varying environment is necessary to achieve the highest species diversity.

The sub-littoral diatom community is characterized by frondose colonies (e.g. the genera *Gramatophora* and *Licmophora*) forming ribbons or chains (Hendey, 1964). The supra-littoral zone usually has a relatively permanent community year-round (Hendey, 1964). *Pleurosigma* and *Surirella* are common components of the supra-littoral zone.

F. Influence of Sediment Type

Within the littoral zone, sediment type contributes greatly to the population variations (Moul, 1959). Highest algal density on tidal flats has been found on mud substrates, with fewer numbers on mud-sand and still fewer on sand (Leach, 1970). Desiccation on sand is a limiting factor, while organic sediments, even as high as the splash zone, hold water well (Round, 1965).

Williams (1962) found a direct correlation between the sediment make-up and the diatoms present. Generally, the members of the Monoraphidinae were found on the hard surfaces while the Bira- phidinae were common on a variety of substrata. The presence of Centric diatoms and Araphidinae on soft sediments are considered to be the result of planktonic settling.

G. Influence of Size and Numbers

The size of the organism is significant in the seasonal variation of population density (Round, 1960). The seasonal diatom variation in Georgia was due more to the change in the number of smaller diatoms than to a variation in the number of the more common
larger diatoms (Williams, 1962). Williams (1962) found that four genera dominate. The cell number may tend to indicate the dominance of one species, but examination of biomass may prove a less prominent species to be more significant than its number would indicate (Round, 1964a).

III. EPiphytic Ecology

A. Factors in Epiphyte Distribution

The vertical zonation of the littoral region described by Hendey (1964) has been extended to the epiphytic algae by Round (1971). This is a region in which communities vary in number and species composition; this variation is both seasonal and spatial (Round, 1971).

The scouring of the host plant by winds and waves often reduces epiphytic populations (Young, 1945). Knudson (1957) found that the influence of waves on the epiphytic community is not so great on large standing crops with rapid growth rates as on a low population. While working in a fresh-water stream, Douglas (1958) found the opposite effect. Flooding by heavy rains greatly reduced the populations in 2/3 of his stations with high populations, but the stations with low numbers did not demonstrate a reduction in number resulting from flood waters.

Sediments also influence the distribution of epiphytic diatoms. Hopkins (1964) found that slight amounts of sediment on the stipe of Fucus spiralis stimulated the development of a Pleurosigma community. Reyes-Vásquez (1970) reported that the sediment characteristically around and on the host plant had more influence on the epiphytic diatoms living on Thalassia than did salinity and temperature.
Morphology of the host plant is a significant factor in the attachment of epiphytes (Aleem, 1950). Epiphytes have been observed to grow best on red algae (Edsbergge, 1967) and cylindrical green algae (Aleem, 1950) with highly branched forms being most susceptible to epiphytosis (Prowse, 1959). The ability of these forms to protect their epiphytes from desiccation without seriously reducing available light has been suggested as one of the important factors in epiphytic selection (Hopkins, 1964).

Attachment of epiphytic algae is influenced by the species and age of the host plant (Young, 1945; Round, 1965). Dead standing stems have been found to have higher standing crops than live stems (Young, 1945; Jorgensen, 1957; Kowalczeski, 1965). Young attributed this to the fact that the surface of the young stems is slick and wax-like, while the surface of the older stems is usually rough and not waxy, favoring the development of epiphytes. Older leaves of Utricularia, Najas and Echadrias have been observed to have heavier epiphytic growths than the younger leaves (Prowse, 1959). However, Knudson (1957) found no significant difference between young and old stems during the various seasons. The observation that higher diatom densities were found on old stems of Phragmites communis and that the epiphyte maxima on Phragmites occurred when the dissolved silicon was low suggested that the diatoms were capable of using the silica from the host plant (Jorgensen, 1957).

Seasonality of epiphytic algae are influenced by the same factors as seasonality of phytoplankton plus the influence of the host substrate. Phytoplankton and epiphyte blooms have been observed to take place at different times in the year (Jorgensen, 1957). The
epiphyte bloom usually precedes the phytoplankton bloom (Jorgensen, 1957; Foerster and Schlichting, 1965). The seasonal distribution of *Tabellaria flocculosa* followed a typical phytoplankton sequence with spring and fall maxima and summer and winter lows (Knudson, 1957).

New substrata introduced into the aquatic environment are very rapidly colonized (Round, 1965). In the fresh-water environment this sequence of colonization has been found to be *Cocconeis*, *Synedra*, *Zenococcus*, *Achnanthes* and *Comphonea* (Whitford, 1956). The attached marine diatoms have been found to demonstrate a high degree of seasonality (Hopkins, 1964), with *Grammatophora marina* and *Striatella unipunctata* in the fall and early winter, *Grammatophora marina* and *Melosira* in the winter and *Achnanthes* and blue-green algae in the summer (Hopkins, 1964). However, Castenholz (1963), working on the Oregon coast, did not observe such seasonality.

IV. FILAMENTOUS EPiphyTES

Salt marshes with heavy sedimentation generally have a macroscopic algal flora associated with the angiosperm population (Round, 1965). The same factors that influence the distribution of other algae also are significant in the distribution of filamentous epiphytes.

Since four genera of macroscopic algae comprise the bulk of the epiphytic macrophytes, these will be emphasized in this discussion. The four genera are the following: *Bostrychia*, *Polysiphonia*, *Enteromorpha* and *Ectocarpus*. *Bostrychia* has been reported growing epiphytically on *Spartina* in the Mississippi Sound (Humm and Caylor, 1957) and on mangrove pneumatophores in the West Indies (Chapman, 1963). Taylor (1960) describes *Bostrychia* as a common epiphyte from
Louisiana to Brazil in the eastern section of the western hemisphere. He gives the range of Polysiphonia as being from North Carolina to British Honduras.

The spongy nature of Bostrychia enables it to hold water during long periods of emersion. This and its habit of growing in protected areas are two of the factors that help it to adapt to a high intertidal habitat (Dawson, 1966).

The genera Enteromorpha and Ectocarpus are the two common winter epiphytes in the Louisiana salt marsh. They are found in great abundance on the mudflats and intertwined in the Spartina at the water's edge. Earle (1969) has found three epiphytic species of Ectocarpus in Louisiana. She described E. intermedius, E. dasycarpus, and E. Siliculosus as cool-water plants whose presence is almost exclusively limited to the winter months.

Three species on Enteromorpha (E. intestinalis, E. prolifer, and E. flexuosa) have been found lining the mudbanks and growing as epiphytes on Spartina alterniflora and mangrove pneumatophores (Kapraun, personal communication). The same three species were also found in Texas, occupying calm water below the low tide line (Kapraun, 1970). All three are considered to be cold-weather organisms, since they are most abundant during the winter.

In the relationship of temperature and salinity, lower temperatures favor algal growth at suboptimal salinities (Doty and Newhouse, 1954). The genus Enteromorpha grows best at salinities in excess of 40 ppt with sporulation occurring at salinities varying greatly from this optimum (Kapraun, 1970). E. flexuosa grew best at 50 ppt although sporulation occurred best at 17.5 and 27.5 ppt. E. lingulata demonstrated sexual
dimorphism at salinities between 25-40 ppt with optimal sporulation for the male plant at 27 ppt and for the female plant 35-55 ppt. *E. prolifera* was found to be similar to *E. flexuosa* in response of the vegetative plant to salinity, but *E. prolifera* sporulated in a range of 25-45 ppt.

V. ORGANIC NUTRIENTS

Various inorganic nutrient requirements of algae have been known and studied for a long time (see Provasoli et al., 1957). These earlier studies led to the realization that additional organic growth factors are required. The vitamin requirements of algae are reviewed by Provasoli (1958). Provasoli and Pinter (1960) found that 78 of 124 species of algae tested required exogenous vitamin sources. Vitamins B$_{12}$, thiamine and biotin were required most often by both photosynthetic and colorless algae (Provasoli and Pintner, 1960). Literature cited by Lewin and Lewin (1960) indicates high levels of B$_{12}$ in estuarine muds account for the high number of B$_{12}$-requiring organisms in the estuaries.

More recently, the phenomena of heterotrophy and photoheterotrophy have been recognized among pigmented algae. Lewin (1963) noted that many species of diatoms found in sediments rich in organic matter are capable of heterotrophic growth. Heterotrophy can be important from two aspects: (1) as a mechanism allowing survival of the organisms during long periods in reduced or not light (Sloan and Strickland, 1966) and (2) as a short-cut in the mineralization process through the use of organic compounds as energy sources (Provasoli and McLaughlin, 1963).

Amino acids, such as arginine and asparagine, have been shown...
to be nitrogen sources for heterotrophic growth of three species of Gyrodinium and two species of Amphidinium (Provasoli and McLaughlin, 1964). Sugars have also been shown to be heterotrophic energy sources. An interdependence of carbohydrates and amino acids has been shown in nine organisms tested (Lewin, 1963). All grew heterotrophically on a combination of glucose and tryptone, while four grew heterotrophically on glucose alone and only two grew on tryptone alone.

The phenomenon of photoheterotrophism is also significant among the epiphytic and littoral communities. Photoheterotrophy takes place when light energy below the compensation point is used to enable growth on exogenous organic material (Parker, 1971). Bunt (1969) does not take such a narrow view in his definition; he includes any stimulation of organic uptake by radiant energy. He found that Cocconeis could grow phototrophically but grew better on organic substrates in light. This same organic substrate was incapable of supporting growth of Cocconeis in the dark.

Allen (1971) demonstrated the release of dissolved organic material (DOM) by macrophytic plants and uptake of the DOM by epiphytic algae and bacteria. A comparative study showed that in a five-hour period unepiphytized plants released twice as much DOM to the water as epiphytized plants, indicating immediate utilization of DOM by the epiphytic community (Allen, 1971).

Culture experiments demonstrated uptake of macrophytically released DOM by axenic cultures of a diatom and bacterium (Allen, 1971). Uptake for the diatom was greater in the dark than in the light. In mixed cultures there was stimulation of algal uptake while the bacterial rate remained constant. Other experiments indicated
bacterial stimulation of algal uptake to be due to the bacterial pre-treatment of the DOM. This bacterial-algal interaction indicates a probable cycling of DOM within the epiphytic community.
MATERIALS AND METHODS

Stems of *Spartina* were collected from the water's edge and inland 1.5 m at the sampling stations previously described. Twelve to 20 stems were collected at each site for enumeration of epiphytic algae. An equal number of stems were collected from station 6 and selected sites in Airplane Lake for primary production measurements. All stems from each location were placed intact in large plastic bags and returned to the field laboratory under refrigeration. The stems for algal enumeration were refrigerated and returned to Baton Rouge for processing; the stems for measurement of production were used immediately upon return to the field laboratory, usually within 1.5 hours.

The epiphytic community was divided into two categories: the macroscopic forms and microscopic forms (almost exclusively diatoms). The non-diatoms were identified by the examination of wet mounts from stem scrapings.

The density of macrophytic forms was determined by collecting the algae from the surface of stems of known surface area. The removed algae were then dried to a constant weight at 68 °C and weighed.

Diatom density was determined by suspending stems of known surface area in 200 ml of distilled water, blending for two minutes in a Waring blender, and counting aliquots of this sample with a bright-line hemacytometer\(^1\) under a bright-field microscope. Millipore

---

\(^1\)American Optical Corporation.
filters (McNabb, 1960) were later used, which resulted in higher population counts. For the latter analysis, stems of known surface area were suspended by blending them in 300 ml of distilled water. Then 0.5 ml aliquots or a 1/10 dilution of the diatom-stem suspension was filtered through a .45 μ HA millipore filter. The filter was dried, rendered transparent by xylene, and then permanently mounted with Permoun on 3" x 1" glass slides. Cell counts were made with a phase-contrast microscope at 500X. Twenty-five fields were counted or, if the density of the cells was great, 350+ cells were counted. Cell density was determined by a modification of the equation found in "Techniques for Microbiological Analysis, ADM 40" (Millipore Corporation, 1967).

\[
\text{Number cells/cm}^2 = \frac{C \times T_f \times a}{V_s \times (V_f \times \text{area of one field}) \times \# \text{ (of fields counted)}}
\]

- \(C\) = Total number of cells counted
- \(T_f\) = Total filtering area
- \(V_s\) = Volume of water used to suspend sample
- \(V_f\) = Volume of \(V_s\) filtered

Permanent mounting of the millipore filters was highly desirable, since it gave a permanent counting reference. Also, it preserved many of the delicate diatoms that might have been destroyed by the conventional methods of preparing diatom slides.

To study the vertical distribution of epiphytic algae, the stems

---

were divided into three 10 cm lengths from the mud surface up.

The surface area of the stems was determined by measuring length and diameters and converting to surface area by use of the mathematical equation for determination of the surface area of a cylinder. The area of the leaves was determined by doubling the product of the length times the width. Summing the leaf and stem surface areas gave the total surface area of the plant segment.

Acid-cleaned diatoms mounted in Hydrax\(^3\) (Patrick and Reimer, 1966) were identified following the taxonomic scheme of Hendey (1964). The diatoms were cleaned with hot dichromate solution. The material was washed by settling in a series of distilled water rinses until a pH of 6.5 to 7.0 was obtained. The neutralized diatom suspension was then mounted in Hydrax. Duplicate copies of the slides were placed in the herbarium of the Department of Marine Sciences, Louisiana State University, with Dr. W. G. Smith.

Production of the epiphytic community was measured by a modification of the light-dark bottle method (Howard and Menzies, 1969). Stems were collected at the water's edge and inland 1.5 meters. Two 10 cm lengths of the lower portion of the stems were incubated for two hours in BOD bottles filled with aged seawater. Samples from the water's edge were incubated in direct sunlight in a number 3 washtub filled with tap water to control the temperature. The inland stems were incubated in moderate shade of *Distichlis spicata* near the lab. This shade closely approximated the shade condition in the field.

\(^3\)Custom Research and Development, Inc., Richmond, Calif.
At the end of the two-hour incubation period, dissolved oxygen was determined by the modified Winkler titration (Strickland and Parsons, 1968) with sodium azide added to the alkaline iodine. Later dissolved oxygen was determined with a Martek polarographic dissolved-oxygen meter. The oxygen probe fit directly into the BOD bottle so that the membrane was approximately 1/3 of the way down into the bottle. The water was stirred with a magnetic stirrer set at a moderate speed. After determination of the dissolved oxygen concentration, the total volume of the water was determined to the nearest ml.

The dissolved oxygen reading was converted to amount of carbon fixed by the following formula:

**Gross production** -

\[
\text{mgC/stem/hr} = \frac{O_2^{\text{LB}} - O_2^{\text{DB}}}{1000} \times V \text{ Bot.} \times \frac{0.375}{1.2} \times T \times \text{No. stems/bottle}
\]

**Net production** -

\[
\text{mgC/stem/hr} = \frac{O_2^{\text{LB}} - O_2^{(0)}}{1000} \times V \text{ Bot.} \times \frac{0.375}{1.2} \times T \times \text{No. stems/bottle}
\]

- \(O_2^{\text{LB}}\) = Oxygen in ppm in light bottle at end of experiment
- \(O_2^{\text{DB}}\) = Oxygen in ppm in dark bottle at the end of experiment
- \(O_2^{(0)}\) = Original oxygen concentration in ppm before the beginning of experiment
- \(V \text{ Bot.}\) = Volume of water in the BOD bottle in ml
- 0.375 = C/O\(_2\) ratio
- 1.2 = suggested photosynthetic quotient by Strickland and Parsons, (1968)
Community respiration was calculated as the difference between gross and net production.

To relate the production and respiration rates per stem to marsh surface area, it was necessary to determine the stem density. Average stem density was determined by counting ten 0.1 m² areas of erect *Spartina* stems from the water's edge and inland locations in the summer and winter.

Annual gross and net productions were calculated by (1) assuming the hourly rates to be constant for 12 hours per day, (2) determining the daily average from production means for all measurements, and (3) multiplying by 364. Annual respiration was calculated by using the same procedure as above except a constant hourly rate for 24 hours per day was assumed.
ARTIFICIAL SUBSTRATES

In view of the wide spread use of artificial substrates, some comments regarding their desirability for this study is appropriate. Artificial substrates come in all shapes and sizes (see Sladeckova, 1962), but glass slides, as earlier used by Butcher (1932) and later made popular by Patrick, et al. (1954), are often used. Glass slides and other substrates appear to be good for comparative work in water quality analysis (Szczepanski and Szczepanski, 1966; Arthur and Horning, 1969). They have been found to be selective against non-diatomaceous epiphytes (Castenholz, 1961) and even among the diatoms; they seem to favor sand grain-inhabiting diatoms (Round, 1965).

Substrates which vary from the natural environment tend to give misleading ecological pictures (Wetzel, 1964). Foerster and Schlichting (1965) found periphyton peaks on glass slides to occur before the same organisms peaked on the host plant. The glass slides were also found to extend this peak beyond the period of dominance on the natural host. Tippett (1970) found that the glass slide technique tended to shift population cycles; whereas it either extended or compressed the species cycles. He found the diatom maximum on *Elodea* to occur in winter from November to February, but on the glass slides the cycle was shifted so that the maximum numbers occurred between February and October. *Diatoma elongatum* on *Elodea* was found to be an early winter form found between November and March; on the glass slides it did not occur until January. *Cocconeis placentula*, common on *Elodea*, with a winter maximum was found to...
have a summer maximum on the glass slides.

Because of these results and a few personal observations, it was decided to work with the natural substrate.
RESULTS AND DISCUSSION

I. PRODUCTION

Primary production was compartmentalized into water's edge and inland communities. To reduce interference caused by the host plant chlorophyll, production measurements were limited to the lower 10 cm of the stems. During almost all year the host plant chlorophyll was not noticeably present in the sheaths of the lower portions of the plants. The presence or absence of chlorophyll was determined by the sheath color. Production was converted to mg C/m^2 of marsh surface/hour. This conversion was made after determining the average number of stems per m^2 of marsh surface.

Seasonally gross production values for the water's edge and inland communities are opposite (Figure 4). Gross production for the water's edge community followed the seasonal pattern of summer highs and winter lows. Conversely, the inland community showed a production pattern of winter highs and summer lows.

The average range for gross water's edge production was a summer high of 38 mg C/m^2/hr. and a winter low of 8 mg C/m^2/hr. The inland community had the following reading: an early fall low of 3 mg C/m^2/hr., a late fall and early spring high of 16 mg C/m^2/hr., and a late spring low of 2 mg C/m^2/hr.

Only during the winter did the production rates of the two locations become nearly equal. During the winter the reduction of the filamentous algal density contributed to the reduction of water's
Figure 4. Gross epiphytic production on stems of *Spartina* collected at the water's edge and inland 1.5 m.
edge production; whereas, the thinning of the *Spartina* influenced the increased inland gross production.

Significant differences in net production between the water's edge and inland locations have been found (see the Analysis of Variance Tables, Table 1). The environmental differences between locations have been discussed earlier (see the Description of the Area). The water's edge production was naturally restricted to an active zone averaging 30 cm wide. Productively the remainder of the marsh is inland.

Table 1

<table>
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</tr>
<tr>
<td>Error</td>
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<td>283,087.158</td>
<td>10,110.255</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>29</td>
<td>729,295.628</td>
<td></td>
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</tr>
</tbody>
</table>

Highly significant F values of 14.736, 21.943, and 25.365 for the linear, quadratic, and cubic effects, respectively, indicated real seasonal variations in net production. These F values were calculated by multiple regressional analysis (regression of production on time). The $R^2$ of 0.248 indicates highly variable results. Factors that contribute to production variations were the same as those that influence filamentous algal and diatom distributions.
Annual net production ranged from 0–37 mg C/m²/hr. in the winter and early fall respectively. The largest range of 2 to 35.7 mg C/m²/hr. was observed on October 31, 1970 (Figure 5). The variations in production can be attributed to the lack of uniformity in stem colonization. Occurrence of a small range in production would indicate a state of uniform colonization. The alternation of small with larger ranges in production illustrated that the epiphytic community was in a continual state of flux.

A fitted curve of net production for the water's edge community has been superimposed on the actual data points. The curve coincides well with the summer and winter highs and lows. However, it does not show the speed at which the production decreased following the loss of the summer macroscopic algae. The calculated equation for the fitted curve and the \( R^2 \) value are also shown on Figure 5.

Included in Figure 5 as a comparison is the net production for the inland community. Unlike the gross production figure, net production for the inland community revealed a consuming population with greatest consumption occurring during the warmer, summer months. Only twice, in late October-November and late February, did the net production of the inland community demonstrate this environment to be truly productive.

Gross and net production for the water's edge community closely followed the seasonal patterns of the summer algae. Gross production reached a peak in early September with the fall decline beginning in mid-October and continuing to the low in mid-November. Production rates showed a significant rise with the development of the winter flora, but the rapid spring rise occurred following the development
Figure 5. Net epiphytic production on stems of Spartina collected at the water's edge and inland 1.5 m. With the averages and extremes for the net water's edge production and a fitted curve for water's edge production superimposed.

\[ Y = 111.85 + 3.728D - 0.0372D^2 + 0.000087D^3 \]

\[ R = 0.2480 \]

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of Bostrychia sp. and Polysiphonia sp.

Gross production often exceeded net production by 50% or more. Generally the relationship of gross to net production is 10 to 20% (Kanwisher, 1966); however, these results showed a high level of consumer activity. The only time during the year that gross and net production approached the expected relationship for algae was during the latter part of the fall production decline. The large gap between gross and net production can be more readily understood when it is realized that these are community measurements and that there was consumption by bacteria, fungi, and animals taking place at the same time photosynthesis was proceeding.

A comparison of gross and net production for the inland communities illustrated even more startling differences than that for the water's edge community. Gross production for the inland community showed a seasonal trend that could be associated with the winter algal flora or temperature. However, when net production for the inland community was examined, it was revealed as a consuming community. This consumption could be attributed to the facts that the inland epiphytic community was submerged less frequently than the water's edge community and that the inland community had no appreciable filamentous algae, although it had a high bacterial population (Hood and Colmer, 1971) and a lower diatom density.

High community respiration is indicated by the gap between gross and net water's edge production and the negative net production for the inland community. Community respiration for the two locations was determined by the dark bottle method. Seasonally (see Figure 6) the respiratory rate for both of the locations had a tendency to
Figure 6. Seasonal respiration rate for epiphytes on stems of *Spartina* collected at the water's edge and inland 1.5 m.
follow the temperature cycle with the highest rates of respiration occurring during the warmer months and the lower rates occurring during the colder months.

The respiration rate of the water's edge community also corresponded with the density pattern of the summer filamentous algal community. The branches of *Bostrychia* and *Polysiphonia* (the summer flora) are often inhabited by large numbers of amphipods, worms, and protozoans. Although the number of animals found within the epiphytic community was not assessed, animal density appeared to be related to the length of time the algae had been exposed to colonization. The inland community, not having a dense animal population, had a high microbial population that contributed to the high respiratory rate.

Annual respiration of 87.84 and 90.72 g C/m² was found for the water's edge and inland communities respectively. However, when examined on an individual stem basis, the water's edge community had the highest rate of respiration. The water's edge community had an average of 220 stems per square meter of marsh surface; whereas the inland region had an average of 360 stems per square meter of marsh surface. The higher water's edge respiration per stem could be attributed to the following: the density of the algal population, large animal populations, a large number of microbes, or the effect of wave action moving water over the community. The speed of water movement in an aquatic environment has been shown to influence the rate of respiration in aquatic communities (Schumacher and Whitford, 1965). Since the water's edge community was continually being exposed to moving water, its rate of respiration would be expected to be higher per unit surface of stems than the inland area which was not exposed.
Annual gross and net production and respiration for the water's edge community were determined to be 103.9, 59.97, and 87.84 g C/m² respectively; however, the annual gross and net production and respiration for the inland community were determined to be 27.28, -18.36, and 90.72 g C/m² respectively. The results show the water's edge community was a producing community which annually contributed 16.06 g C/m² to the water column. Conversely, the inland community was a consuming community requiring 63.44 g C/m² annually to maintain itself. Since these two communities are essentially isolated from each other, the water's edge community is not likely to have provided directly the necessary energy for the inland community. Also, the inland community is several hundred times more extensive than the water's edge community; thus it was impossible for the water's edge community to provide the necessary energy. The most obvious source of energy for the inland community is the *Spartina* itself.

Productively, the inland and water's edge communities were very distinct. The water's edge community, flooded and washed by tidal action often, contributed organic products to the water column. The inland area, flooded irregularly, required exogenous energy.

Net production of 10 cm sections of epiphytized mangrove pneumatophores and exposed stolons was determined (see Table 2). Only those pneumatophores which extended toward the water were examined for production. These data are presented in mg C/10 cm stem segment/hour.

The major, filamentous epiphytic algae follow the same seasonal pattern on mangroves as they did on *Spartina*. However, due to the fact
Table 2

NET PRODUCTION OF ALGAE ATTACHED TO MANGROVE PNEUMATOPHORES. mg C/10 cm section/hr.

<table>
<thead>
<tr>
<th>Date</th>
<th>High</th>
<th>Low</th>
<th>Av.</th>
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<tbody>
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<td>.070</td>
<td>.098</td>
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<tr>
<td>10-17-70</td>
<td>.044</td>
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<td>1-22-71</td>
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<td>.018</td>
<td>.028</td>
</tr>
<tr>
<td>3-27-71</td>
<td>.278</td>
<td>.122</td>
<td>.203</td>
</tr>
<tr>
<td>4-24-71</td>
<td>.240</td>
<td>.108</td>
<td>.142</td>
</tr>
</tbody>
</table>

that many of the pneumatophores and stolons were more frequently covered by tide water than was Spartina, they were often more densely colonized than the Spartina. In contrast, inland mangrove pneumatophores are generally not colonized by the larger filamentous algae. Often the density of the filamentous epiphytes resulted in a retardation of production. For example, on January 22, 1971, there was approximately 0.5 grams dry weight of Ectocarpus sp. attached to the pneumatophores. Net production for this date averaged 0.037 mg C/10 cm stem/segment/hour, the lowest ever recorded. This low net production could be attributed to the self-shading and crowding that occurred when the stems were placed in the BOD bottles.

In an attempt to evaluate maximum primary production available to this community, photosynthesis and respiration of cultures of the red alga Bostrychia sp. were measured by manometry. Photosynthesis and respiration were measured under both wet and dry conditions. After approximately 14 hours under dry conditions, the dry tissues in the...
reaction vessels were flooded with a nutrient solution to simulate conditions that would occur when the alga undergoes resubmersion.

The results of the wet and dry experiments are shown in Figure 7. During the initial stages of drying, the alga photosynthesized at a rate similar to that of the wet alga. The effects of drying began to appear within the second 15 minute period, and by the end of the first hour, the dry alga was photosynthesizing at a rate appreciably lower than the wet material. After 2.25 hours in the light the respiration rate of the dry material exceeded its photosynthetic rate. Respiration rates of the wet and dry alga showed essentially the same repression phenomenon as did photosynthesis. The respiratory rate for the wet material exceeded that of the dry material by almost 1.75 times. After 14 hours in the closed reaction flask, the dry alga was flooded with 3/4 ASP-2 to simulate resubmersion. Initially the respiration rate of the alga was reduced, but observable oxygen evolution occurred within the second 15 minute period. By the end of the first hour, the wetted material had increased its rate of photosynthesis to a rate almost equal to that of the wet material.

Although it is difficult to correlate laboratory and field experiments (see Chapman, 1966; and literature review), some attempted projections based on laboratory work are reasonable.

To project annual net production attributable to production by Bostrychia, the day was divided into four six-hour sections. Six hours of dry light, six hours wet light, six hours dry dark, and six hours wet dark. An average standing crop of Bostrychia of 0.05 grams dry weight per stem, 220 stems per m² of marsh surface and an average standing crop lasting for 180 days was assumed. Based on these
Figure 7. Influence of drying on photosynthesis and respiration of *Bostrychia*. Positive is in the light (photosynthesis) negative is in the dark (respiration). The rewet material was in the light at the time of flooding.
assumptions Bostrychia would have an annual production of 1,310 and 941.6 g C/m\(^2\) gross and net production respectively.

Field results were an order of magnitude smaller than the projected laboratory results. Obviously factors such as grazing, self-shading, drying, secondary epiphytes, and possible nutrient limitations act to reduce greatly the field production of Bostrychia.

A comparison of epiphytic production shows a wide range of results: 660 g C/m\(^2\)/yr. epiphytes on submerged substrates (Allen, 1971), 279 g C/m\(^2\)/yr. epiphytes on Equisetum (Hickman, 1971), and 71 g C/m\(^2\)/yr. epiphytes on emergent substrates (Allen, 1971). In the marine environment a production of 315 g C/m\(^2\)/yr. was measured for the epiphytes on Thalassia (Jones, 1968). In comparing the results of this report with those mentioned above, it appears as if the stress due to the fluctuation of water level caused a large drop in the productivity of attached algae in both the fresh water and marine environments.

II. SEASONAL DISTRIBUTION OF MAJOR MACROSCOPIC ALGAE

Among the larger epiphytic algae in the Barataria Bay area of Louisiana, four genera dominate. These genera are Bostrychia, Polysiphonia, Enteromorpha and Ectocarpus. Bostrychia and Polysiphonia have always been found attached to plant material while Enteromorpha and Ectocarpus grow attached to mud flats and other substrates as well as on plant material. A more extensive listing of filamentous algae found on Spartina alterniflora is presented later in this section.

The filamentous epiphytes were found only along the water's
edge, in bands ranging from 10 to 70 cm wide. The width of the band is influenced by the slope of the shore. The gently sloping banks such as at stations 6 and 12 had wide bands while station 7 and instrument platform number 2 had undercut bands, creating a sharp transition between the water and the marsh grass.

Seasonal water level (see Figure 2C) influences the vertical distribution of the filamentous epiphytes. During the low winter water, almost all algae were found on the lower 5 cm of the stem; during the high summer water, they were found as high as 15 to 20 cm on the stem. Rarely did erect stems have visible macroscopic algae higher than 20 cm on the stem.

At frequent intervals the pneumatophores of *Avicennia germinia* were examined for filamentous algae. The larger algae on pneumatophores and *Spartina* stems appeared to be similar species. A comparison of microscopic algae was not undertaken.

The four dominant genera form two distinct seasonal communities (see Figure 8). *Bostrychia* and *Polysiphonia* are dominant during the warm months while *Ectocarpus* and *Enteromorpha* dominate during the cooler months. The summer forms show a bimodal curve for a seven-month period with the first peak in April-May and the second peak in October. *Bostrychia* and *Polysiphonia* appear initially during the middle of March and coincide with the first average flooding of the marsh floor. The May-June decline corresponds with a temporary lowering of water levels (see Figure 2C), followed by an increase in standing crop associated with the rise of the water level in July and August. The water remains over the marsh floor until mid-October. At that time, the average level is below the marsh floor and is
Figure 8. Seasonal distribution and standing crop of the major filamentous epiphytes.
associated with a simultaneous loss of Bostrychia and Polysiphonia as conspicuous components of the epiphytic community.

It appears as if the controlling factor in the seasonal distribution of these two genera is the average water level in relation to the marsh floor. When average water levels are above the marsh floor, extensive growths of Bostrychia and Polysiphonia can be found.

Another possible explanation for the low population levels in May-June is nutrient limitation. The work of Ho (1971) and Mulligan and Baranowski (1969) suggests a possible explanation for the May-June decline of the summer flora. In the early spring the total nitrogen level of .20 mg/L is probably not limiting. By May, however, the inorganic nitrogen level has dropped rapidly to less than 0.04 mg/L which is possible within the limiting range (Mulligan and Baranowski, 1969). The nitrogen remains low until mid-September. The mud and stems themselves are two potential sources of nitrogen. If the mud were the major source of the nitrogen, the nitrogen should show up in the water. However, if a nitrogenous film diffuses from the stem, a microzone of highly concentrated nitrogenous material would be formed. From early spring until early summer Spartina grows actively, but by mid-June, the outer sheaths are beginning to decay. By mid-July, the rate of sheath decay could be great enough to provide a micro-zone of nitrogen in sufficient concentration to allow the growth of the filamentous algae. By October and November, low temperatures are low tidal level cause the die-off of summer forms.

While cultural studies were not studied in the laboratory, the seasonal abundance corresponds well with the cultural work of Edwards (1969) on Polysiphonia boldii. Optimum growth was found to
be between 25.5 and 30 C with death occurring at 10 C. Growth rate has been found to increase with temperatures from 15 C and up, reaching the optimum near 25 C. The abundant growth of Bostrychia and Polysiphonia occurs during April and September-October, when temperatures range in the low- to mid-twenties.

The winter community of Ectocarpus and Enteromorpha is more abundant on the mudflats below the level of the marsh floor than on the Spartina culms. Often, however, these algae become attached to the Spartina stems and the mangrove pneumatophores. The weight of the winter flora on mangrove pneumatophores was measured on two occasions and found to be 0.5 g dry weight per 10 cm section of a pneumatophore and stolon for those found below the level of the marsh floor and 0 g for those above the marsh floor. When these algal genera grow on the Spartina stems, they are usually limited to the lower 5 cm of the stem.

Earle (1969), Edwards (1969) and Kapraun (1970) have shown these genera to be cold weather organisms by field and/or laboratory studies. Edwards (1969) and Kapraun (1970) have also shown a relationship between salinity tolerance and temperature, confirming the earlier work of Boyle and Doty (1949).

The fact that extensive growth of Ectocarpus and Enteromorpha occurs on the Spartina stems and on the mud banks during the winter while the salinity ranges from 18 to 25 ppt supports the work of Boyle and Doty (1949).

Thus, temperature and tide level appear to be the factors controlling the growth of filamentous algae on Spartina. During the winter, temperature levels are lower than the minimal levels tolerated by Bostrychia and Polysiphonia; the same temperature levels
are also responsible for the ability of *Enteromorpha* and *Ectocarpus* to tolerate the low salinities.

**III. NUMERICAL DISTRIBUTION OF DIATOMS**

Significant differences in annual diatom numbers were found between stations, locations, heights on the stems, and sampling dates (trips). Significant differences were also found for the two-way interactions of locations and heights, locations and trips, and heights and trips. However, the three-way interaction of locations, heights, and trips was found not to be a significant factor in annual distribution of diatom number. (See Analysis of Variance Table, Table 3.)

The F value of 17.68 shows a highly significant difference among the four stations. The annual average diatom number for the four stations is shown in Figure 9. The significant differences among stations are based on stations 7 and 12 which had significantly fewer diatoms than the other two stations. Stations 7 and 12 have an annual mean number of $0.62 \times 10^5$ and $0.97 \times 10^5$ diatoms per cm$^2$ of stem surface respectively. Station 6 and the instrument platform number 2 were found to be similar, each having an annual mean number of $1.15 \times 10^5$ diatoms per cm$^2$ of stem surface.

The factors responsible for the difference in cell number at the four stations are more geographic than chemical. The physical differences between stations have been discussed earlier in the description of the area.

The highly significant difference in diatom number between locations at each station is shown by the F value of 111.27. The
Table 3

ANALYSIS OF VARIANCE TABLE

<table>
<thead>
<tr>
<th>Sources</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>Prob.</th>
</tr>
</thead>
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<td>Station</td>
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<td>266062.28</td>
<td></td>
<td>17.68**</td>
<td>.0001</td>
</tr>
<tr>
<td>Location</td>
<td>1</td>
<td>558099.76</td>
<td></td>
<td>111.27**</td>
<td>.0001</td>
</tr>
<tr>
<td>Height</td>
<td>2</td>
<td>1736481.95</td>
<td></td>
<td>173.10**</td>
<td>.0001</td>
</tr>
<tr>
<td>Trip</td>
<td>21</td>
<td>1582767.82</td>
<td></td>
<td>15.026**</td>
<td>.0001</td>
</tr>
<tr>
<td>Location and Height</td>
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<td>77331.87</td>
<td></td>
<td>7.709**</td>
<td>.0008</td>
</tr>
<tr>
<td>Location and Trip</td>
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<td>310078.31</td>
<td></td>
<td>2.943**</td>
<td>.0001</td>
</tr>
<tr>
<td>Height and Trip</td>
<td>42</td>
<td>1287899.35</td>
<td></td>
<td>6.11374**</td>
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</tr>
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<td>195146.82</td>
<td></td>
<td>0.926</td>
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<td>8314531.28</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Error</td>
<td>349</td>
<td>1750456.06</td>
<td>5015.63</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 9. Annual average diatom number per square centimeter of stem surface as influenced by station, height, and location.
average annual standing crop of $1.36 \times 10^5$ and $0.60 \times 10^5$ diatoms per cm$^2$ were found for stems collected at the water's edge and inland respectively (Figure 9).

Heavy shading due to the grass growth and desiccation due to elevation above the water are two factors which contribute to the variation between the two locations. The grass in the inland area has been found to be almost twice as dense as at the water's edge, resulting in heavy shading on all sides. At the water's edge the stems are less dense and have one side exposed to direct sunlight. The inland grass is elevated by the slope of the land. The elevation 1.5 meters inland is from 18 to 24 cm above the water's edge. This elevation, consequently, reduces the frequency of submersion.

The highly significant effect on population numbers by height above the sediment is indicated by an F value of 173.116 (also see Figure 9). The annual average number was $1.86 \times 10^5$, $0.78 \times 10^5$, and $0.25 \times 10^5$ diatoms per cm$^2$ of stem surface area for the three height classes of 0-10 cm, 10-20 cm, and 20-30 cm respectively. Each 10 cm increase in height results in a three-fold reduction in diatom number. This reduction is presumably due to the decreasing frequency of submergence.

A significant F value of 7.709 indicates an interaction between location and height. The water's edge stations averaged $2.40 \times 10^5$, $1.18 \times 10^5$, and $0.47 \times 10^5$ diatoms per cm$^2$ for each of the height classes respectively while the inland locations had an annual average of $1.31 \times 10^5$, $0.37 \times 10^5$, and $0.10 \times 10^5$ diatoms per cm$^2$ of stem surface area for each of the height classes respectively. The frequency of submersion is determined by the location and height of a
specific sample. Vertically, 0-10 cm at the water's edge and 20-30 cm inland 1.5 m comprise the extremes without overlap into other samples. These two samples have the highest and lowest numbers respectively. The 10-20 cm water's edge height and 0-10 cm height inland sample, receive approximately equal amounts of flooding and have approximately equal total numbers of organisms. This is true also of the 20-30 cm water's edge and 10-20 cm inland samples. Based only on the annual average number of diatoms, it appears that the 10-20 cm elevation at the water's edge and the 0-10 cm elevations at the inland location are comparable. The same also holds true for the 10-20 cm elevation inland and the 20-30 cm elevation at the water's edge.

Figure 10 shows the seasonal variation is standing crop of epiphytic diatoms collected at the three different height classes at the water's edge location. The data fit a bell-shaped curve with fall highs and winter lows in diatom number.

There is some general correlation of diatom number and seasonal tidal cycle. The seasonal fluctuation in the average water level results in the vertical shifting of the littoral zone. During the winter the Spartina zone is the supra-littoral zone, but with the shifting of the water level from winter to spring it is in the littoral zone.

Phytoplankton show two seasonal peaks—a major spring peak and a minor fall peak (Raymont, 1963). The same observation has been made for the epiphytic diatoms by Jorgensen (1957), Knudson (1957), and Jones (1968). However, Figure 10 shows only a single diatom bloom for the epiphytes in Barataria Bay, occurring in the fall. While this seems contrary to previous reports, Pomeroy et al. (1972)
Figure 10. Seasonal distribution of diatom number per square centimeter of surface area of *Spartina* stems collected at the water's edge.
has found a single phytoplankton peak in the late summer or early fall to be common for shallow estuaries. The work of Brkich (cited by Day et al. in preparation) shows that a single late summer phytoplankton bloom occurs in the Barataria Bay area.

Seasonally nitrogen and phosphorus in the Barataria Bay area have been found to reach high levels in the early fall, with a winter peak (Ho, 1971; Ho and Lane, in preparation). Pomeroy et al. (1972) have described similar fall nutrient maxima as common for shallow estuaries.

The occurrence of an epiphytic maximum prior to the phytoplankton bloom has been observed in fresh-water lakes (Jorgensen, 1957; Forester and Schlichting, 1965). In the Barataria Bay area the epiphytic maximum follows the phytoplankton bloom. This may be interpreted as a response to two factors--the state of Spartina growth and the temperature.

The live standing crop of Spartina is at its lowest level during January and February and at its maximum in August (Kirby, 1971). During the spring new growth is replacing dead material which is being rapidly washed from the marsh by the rising tides. Spartina grows vegetatively until August, at which time it flowers and the above-ground portion of the plant dies (Kirby, 1971). Jorgensen (1957), found the epiphytic diatom density to be much greater on old Phragmites stems than on new stems. Considering that diatoms are most often considered to be cool-weather organisms, a system of interactions can be seen. Diatom density during the winter months is low because the average water level is below the marsh floor. With the onset of spring and new Spartina growth and the rise of the water
level, there is colonization of live and dead stems. Meanwhile, the dead stems which have been decaying during the winter are rapidly removed from the marsh. The lower growth of *Spartina* is young and waxy. The attaching epiphytes are easily subject to removal by wave action. The temperature at this time is between 20-25 °C which favors diatom growth, but the presence of new stems does not. In the late spring the higher water gives rise to longer periods of submersion allowing increased periods of colonization.

During the summer, high water and the initiation of *Spartina* sheath decay should give rise to increasing populations, but temperature levels are relatively high for optimal diatom growth. This results in a relatively static standing crop during the summer. With the death of *Spartina*, lower temperatures, and high water, the epiphytes reach a peak bloom in October. Following the October peak, the rapidly lowering water accounts for the reduction of diatom numbers on the upper regions of the stems.

Figure 11 compares the seasonal distribution and stem distribution of diatoms collected from the inland stations. These diatoms are subject to the same factors as the water's edge community with two exceptions. The inland stems are generally elevated at least 15 cm above the water's edge location due to the slope of the land and the shading of the stems. The reduced amount of water and increased shading accounts for lower standing crops inland.

For four of the six height-classes, the number of diatoms show the bell-shaped curve (Figure 11) characteristic of the seasonal cycle. Only the 0-10 cm height-class at each location varies from this pattern. In both cases diatom number reaches a high level in
Figure 11. Seasonal distribution of diatom number per square centimeter of surface area on stems of *Spartina* collected inland 1.5 m.
late fall which is maintained into the winter. A possible explanation for this could be the close proximity to the sediment resulting in a large build-up of mud-inhabiting diatoms on the stems.

IV. COMMUNITY STRUCTURE

To facilitate determination of community structure, the stems were divided into three vertical height classes: 0-10 cm, 10-20 cm, and 20-30 cm. Algal densities show a horizontal and vertical gradation with the greatest density found at the water's edge at the 0-10 cm level and the smallest number found inland at the 20-30 cm level (see Figures 10-11). The larger filamentous algae, Bostrychia, Polysiphonia, Ectocarpus, and Enteromorpha, constitute the bulk of the attached algal biomass. The larger algae were restricted to the water's edge community. Blue-green algae were found on few occasions and without uniform distribution. Generally the blue-green algal distribution was dependent on sedimentation of the stems. In terms of total numbers of individuals and numbers of species, the diatoms were the most common single group.

A list of the more common epiphytic algal species found in the Barataria Bay area is shown in Table 4.

Much of the species composition for the filamentous algae has been discussed in the earlier section on seasonal distribution of filamentous epiphytes. The summer flora was dominated by Bostrychia radicans and Polysiphonia havanensis. Of these two Bostrychia was the more abundant. During the May-June decline the green alga Chaetomorpha aerea became a conspicuous component of the epiphytic community and remained so throughout almost all of the summer. During
### Table 4

**Some of the More Common Epiphytic Algae and Time of Most Common Appearance**

<table>
<thead>
<tr>
<th>Macrophytes</th>
<th>Diatoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bostrychia rivularia</td>
<td>Anchnanthes brevipes</td>
</tr>
<tr>
<td>Cladophora gracilis</td>
<td>Amphiprora sp.</td>
</tr>
<tr>
<td>Ectocarpus sp.</td>
<td>Amphora spp.</td>
</tr>
<tr>
<td>E. siliculosus</td>
<td>Amphora cymbifera</td>
</tr>
<tr>
<td>Enteromorpha flexuosa</td>
<td>Amphora granulata</td>
</tr>
<tr>
<td>Polysiphonia havanensis</td>
<td>Amphora ventricosa</td>
</tr>
<tr>
<td>Rhizoclonium riparium</td>
<td>Bacillaria paradoxa</td>
</tr>
<tr>
<td></td>
<td>Caloneis liber</td>
</tr>
<tr>
<td>Cyanophyta</td>
<td>Cocconeis sp.</td>
</tr>
<tr>
<td></td>
<td>C. placentula</td>
</tr>
<tr>
<td>Oscillatoria</td>
<td>C. scutellum</td>
</tr>
<tr>
<td>Lyngbya</td>
<td>Coscinodiscus spp. (3)</td>
</tr>
<tr>
<td>Spirulina</td>
<td>Cyclotella spp. (3)</td>
</tr>
<tr>
<td></td>
<td>Cylindrotheca closterium</td>
</tr>
<tr>
<td></td>
<td>C. fusiforma</td>
</tr>
<tr>
<td></td>
<td>Denticula spp.</td>
</tr>
<tr>
<td></td>
<td>Diploneis sp.</td>
</tr>
<tr>
<td></td>
<td>C. interrupta</td>
</tr>
<tr>
<td></td>
<td>D. smithii</td>
</tr>
<tr>
<td></td>
<td>Grammatophora marina</td>
</tr>
<tr>
<td></td>
<td>Gyrosigma spp. (4)</td>
</tr>
<tr>
<td></td>
<td>Mastogloia spp.</td>
</tr>
<tr>
<td></td>
<td>Melosira sp.</td>
</tr>
<tr>
<td></td>
<td>Navicula spp.</td>
</tr>
<tr>
<td></td>
<td>N. calida</td>
</tr>
<tr>
<td></td>
<td>N. rostellata</td>
</tr>
<tr>
<td></td>
<td>N. trompii</td>
</tr>
<tr>
<td></td>
<td>Nitzschia spp.</td>
</tr>
<tr>
<td></td>
<td>N. acuminata</td>
</tr>
<tr>
<td></td>
<td>N. constricta</td>
</tr>
<tr>
<td></td>
<td>N. grosssestriata</td>
</tr>
<tr>
<td></td>
<td>Opephora schwartzii</td>
</tr>
<tr>
<td></td>
<td>Pleurosigma spp.</td>
</tr>
<tr>
<td></td>
<td>Rholpalodia gibberula</td>
</tr>
<tr>
<td></td>
<td>Surirella fastuosa</td>
</tr>
<tr>
<td></td>
<td>Synedra sp.</td>
</tr>
</tbody>
</table>

Sp = Spring  
Su = Summer  
F = Fall  
W = Winter  
A = All seasons  
w = Water's edge  
i = Inland  
a = All locations
the winter two algal genera, *Ectocarpus* and *Enteromorpha*, were very common inhabitants of the epiphytic community. At least two species of *Ectocarpus* (*E. intermedius* and *E. siliculosus*) were common components of the winter flora. The winter forms, although also found attached to *Spartina* stems, were more common on the mud flats and stream banks. Estimations of relative abundance indicated that less than 1% of the total winter flora was found as epiphytes.

The seasonality and factors affecting the seasonality of these filamentous algae have been discussed earlier (see Seasonality of filamentous epiphytes).

The blue-green algae were surprisingly sparse in the epiphytic community. Their greatest abundance was in the mud under the *Spartina* stems. Three genera (*Oscillatoria*, *Lyngbya*, and *Spirulina*) were the most common blue-green algae found in the epiphytic community. *Oscillatoria* and *Lyngbya* were most commonly found in the mud under the *Spartina*, occasionally migrating up the lower portions of the stems. *Spirulina*, on the other hand, was often found in thick sheets on heavily sedimented stems. *Spirulina* was more common at the water's edge, while *Oscillatoria* and *Lyngbya* were more common inland.

Diatoms were the other major component of the epiphytic algal community. Table 4 lists the dominant diatoms found. In those cases where specific identification was not possible or the number of species was very small, the diatoms were classified under the generic name. A more detailed presentation of algal location and seasonality is available in the appendix.

At any one time three to five genera comprised 75% or more of the total diatom number. The dominant genera were *Amphora*,
Cocconeis, Denticula, Navicula, and Nitzschia. The genera Cocconeis and Denticula were represented by a relatively few species; whereas Amphora, Navicula, and Nitzschia each contained large numbers of species. While other diatoms were common within this environment, the interpretation of general trends and gross characterizations of the epiphytic diatom community is possible from a study of the members of these five genera.

The genus Denticula with two species (D. subtilis and an unidentified form) comprised the largest and most stable group over the year. The genus was found at all three height-classes and at both locations. During the winter Denticula was commonly found in great abundance on the lower portions of the stems. With the onset of the seasonally rising tides in the spring and summer, Denticula began to "migrate" to higher positions on the stems. When water was high, Denticula distribution relative to all diatoms was like an inverted pyramid. This percentage increase was the result of a reduction in the number of other diatoms rather than an increase in the number of Denticula. Because of this distribution pattern indicated that Denticula would be classified as a splash zone inhabitator due to its ability to tolerate periods of desiccation.

The genus Cocconeis was a common inhabitant of the littoral zone (Round, 1971). Unlike Denticula, Cocconeis showed distinct seasonal trends with greater abundance occurring during the spring and summer. It was common to find Cocconeis spp. densely coating Bostrychia and Polysiphonia during the summer. Cocconeis spp., on occasion, have been found so densely colonizing Chaetomorpha sp. that the green alga filaments were dark brown. The rising water in the

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early spring marked the initial appearances of *Cocconeis* spp., which remained until the late fall drop in water level. During the May-June decline of the filamentous algal standing crop (which has been attributed to the drop in water level), there was a similar drop in the number of *Cocconeis* spp. This inconsistency was further reinforced by the fact that *Cocconeis* tended to colonize heavily the filamentous red algae. This diatom was generally restricted to the lower portions of the water's edge stems.

The genera *Cocconeis* and *Denticula* could be used as markers of water level. *Denticula* was basically a supralittoral organism which was found year-round and which dominated those portions of the stems that were slightly above the average water level. *Cocconeis* did not appear in the epiphytic community until the onset of regular marsh flooding. The appearance of *Cocconeis* coincided with the changes in water level, or an upward shifting of the littoral zone. Thus, with these two genera, it was possible to follow the seasonal shifting of the littoral zone as reflected in the vertical migrations of the diatoms.

It is not possible to draw many general conclusions at the generic level due to the large number of species of the other three dominant diatom genera. According to abundance level, they would be ranked *Nitzschia*, *Navicula*, and *Amphora*.

Size was an important factor, with the genus *Nitzschia* containing a large number of individuals measuring 8-12 μ in length. *Amphora* also contained a number of 10 μ and larger individuals. Although the method used to estimate diatom number was not so refined as intensive counts, there did appear to be a trend consistent with
that reported by Williams (1962). He stated that seasonal cycling of diatom number appeared to be more closely associated with changes in the number of the smaller organisms than with changes in the number of larger individuals.

Heterotrophy and/or photoheterotrophy should be considered as a possible mode of survival by the epiphytic diatoms. Lewin and Lewin (1960) confirmed 25 different heterotrophic diatoms isolated from the marine littoral zone. At least ten of these diatoms were found as epiphytes in the Barataria Bay area of Louisiana (see appendix). In addition, the findings of Bunt (1969), that a species of Cocconeis is capable of photoheterotrophic survival, indicated the possibility that many of the diatoms in this epiphytic community were consumers rather than producers.

In summary, the epiphytic algal community was dominated by the filamentous algae at the water's edge and by the diatoms at the inland site. The filamentous algae are composed of four to five genera and seven species. The diatoms are presented by 26 genera and 56 species.
SUMMARY AND CONCLUSIONS

In order to determine the contribution of the epiphytic algal community to the overall energy flow patterns in the Barataria Bay system, primary productivity, community respiration and algal community structure were determined over a period of a year. The epiphytic community was investigated in two locations: the water's edge community and 1.5 meters inland. The rationale for this division was based on the initial observation that filamentous epiphytic algae were always absent from the inland location. The water's edge community was defined as the band of *Spartina* closest to the water. At times this band of *Spartina* was partially covered by the water, and, at other times during the year, the bases of the *Spartina* stems remained exposed for several days.

The dynamic nature of the epiphytic community was seen by changes in algal biomass and species composition. These changes were the result of interactions between water level, temperature, salinity, nutrient levels and the state of the host plant. Seasonality of primary production at the water's edge was most dramatically related to changes in the summer algal flora. During periods of the year when no macroscopic algae were prominent on the *Spartina* stems, low but detectable rates of production were found. The very high respiratory rates for the water's edge community was due partially to the large number of amphipods, worms, protozoans and microbes. The highly branched nature of the densely colonized *Bostrychia* and *Polysiphonia* caused self-shading and increased respiration. High
respiration and low production for the inland community was due to the shading by dense growths of *Spartina*, high microbial populations, and the heterotrophic nature of some of the algal inhabitants of the epiphytic community.

A diagram for the energy flow for the water's edge epiphytic community is shown in Figure 12 which shows the principal energy sources, gross production, respiration, and net export from the community. The double-headed arrows show a feedback between components of the community and their environment.

Energy for the water's edge community is derived from three sources: radiant energy from the sun, organic energy from the stems, and components of the water column. In addition, other materials the epiphytic community may derive from its host plant or environment are shown. Radiant energy is the only energy used solely by the attached algae. Some forms of energy available in the stems and water (e.g., organic nutrients) are used by all components of the epiphytic community. The consumers also interact with each other and with the attached algae by means of \( \text{CO}_2 \) production, organic and inorganic nutrient production, or regeneration.

Energy entering the epiphytic community was channeled in part to the consumer by the photosynthetic process of the epiphytic algae. Some of the energy in the form of the organic nutrients was utilized directly by the primary consumers.

Although there was no accurate assessment of the amount of exogenous material used by the consuming epiphytic population, the results suggest that, on an annual basis, no net input of exogenous material was necessary for the maintenance of the water's edge...
Figure 12. Diagrammatic representation of possible energy flow for the water's edge epiphytic community; showing gross production, respiratory loss, and export from the community.
epiphytic community.

Gross production and respiration for the water's edge community were 10.39 g C/m²/year and 87.8 g C/m²/year, leaving about 16.06 g C/m²/year available for export. Since this export figure was determined by measurements conducted on wet tissue, the actual export may be significantly less. If the manometrically determined photosynthetic and respiratory rates of wet and dry Bostrychia are realistic the annual export would be reduced by half.

A diagram for general energy flow for the inland community is shown in Figure 13. As in the case of the water's edge community, energy and nutrients were derived from three sources: sun, stems and water. However, because the inland community was less frequently flooded than the water's edge community, the water was a less significant source inland than it was at the water's edge.

Also, as in the case of the water's edge community, the attached algae mediated some of the energy flow. However, attached algae provided less than one-third the energy required to maintain the inland community. Additional organic input of 63.4 g C/m² was required annually to maintain the inland community. The major source of this energy must have come from the Spartina itself.

The epiphytic community in the Barataria Bay area of Louisiana was divided into two types: (1) producing, and (2) consuming. The producing community was restricted to a zone approximately 30 cm wide at the water's edge of the lakes and streams. Productivity, within this community, was a function of the density and duration of the filamentous algae. Two distinct types of filamentous algal communities were found: the summer forms (Bostrychia and Polysiphonia) and
Figure 13. Diagrammatic representation of possible energy flow for the inland epiphytic community; showing gross production, respiration loss, and import into the community.
the winter forms (*Ectocarpus* and *Enteromorpha*). The summer forms
generally lasted from March to October. Fluctuations in the standing
crop of the summer forms were reflected in changes in the productivity
of the epiphytic community.

The consuming population was inland of the water's edge. Shading by dense growth of *Spartina* on all four sides, the lack of
significant filamentous algal populations and the fact that some of
the diatoms found in this environment are known heterotrophs—all
contributed to the consumptive nature of this community.

The high respiratory rates within the producing community were
thought to be the result of heavy amphipod, worm, protozoan and
microbial populations. The inland respiration was attributed to
microbes, some worms, and protozoans. On an equal surface area of
the marsh, the inland area had a higher respiration rate than the
water's edge area. However, when converted to a per stem basis, the
water's edge community consumed almost twice as much (0.40 to 0.25 g
C/stem/year) as the inland community. This difference could be due
to the dense filamentous growth and the large amphipod population
found among the algal filaments.

Therefore, it was the seasonality and density of the filamentous
algal forms which dictated the direction and magnitude of epiphytic
primary production in this ecosystem.
LITERATURE CITED


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Ho, C. and J. Lane. Seasonal change in interstitial water composition in Barataria Bay (Louisiana) sediment. (in preparation).


Mann, K. H. 1970. Seaweed productivity compared with plankton productivity in a coastal embayment of forty square miles. Abstract of paper submitted for the 33rd Annual Meeting American Society


Van Heurck, H. F. 1896. A treatise on the Diatomaceae, containing introductory remarks on the structure, life, history, collection, cultivation and preparation of diatoms, and a description and figure of every species found in the North Sea and countries bordering it, including Great Britain, Belgium, etc. Translated by W. E. Baxter. London, William Wesley and Son, xx + 558 pp. + 35 pls.


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APPENDIX

Algal species found on *Spartina alterniflora* in the Barataria Bay area of Louisiana are listed alphabetically by groups, and includes the reference used in their identification, with location and season of greatest abundance.

MACROPHYTES.

**Bostrychia rivularia** Harvey

Water's edge: spring, summer, fall--very common.


**Cladophora gracilis** (Griffiths) Kutzing

Water's edge: early summer--not common.

Humm and Caylor (1957) Pl. 5 fig. 2-3.

**Ectocarpus sp.**

Water's edge: winter--very common (more commonly found on mud flats).

**E. siliculosus** (Dillwyn) Lyngbye

Water's edge: winter--common.


**Enteromorpha flexuosa** L. Agardh

Water's edge: winter--common (more commonly found on mud flats).

Humm and Caylor (1957) Pl. 5 fig. 4.

**E. intestinalis**

Water's edge: winter--common (more commonly found on mud flats).
Polysiphonia havanensis Montagne

Water's edge: spring, summer, fall—common.


Rhizoclonium sp.

Water's edge: early summer—not common.

BLUE-GREEN ALGAE

Oscillatoria sp.

Water's edge: year round—sporadically; inland: year round—
sporadically (most abundant in the mud under the Spartina stems).

Lyngbya sp.

Same as Oscillatoria.

Spirulina sp.

Water's edge: year round—sporadically; inland: year round—
sporadically (found in sheets on sedimented stems).

DIATOMS

Achnanthes brevipes Agardh.

Water's edge: winter—rare.

Hendey (1964) Pl. 28, fig. 7-8.

Actinoptychus senarius Ehrenberg

Inland: winter—rare.

Hendey (1964) Pl. 23, fig. 1-2.

Amphiprora sp.

Water's edge: year round—rare; inland: year round—rare.

Amphora spp.

Water's edge: year round—very common; inland: year round—very
common.
**A. augusta** (Greg.) Cl.

Water's edge: winter--rare; inland: winter--rare.

Hustedt (1955) Pl. 16, fig. 26.

**A. aspera** Petit

Water's edge: fall, winter--rare.

Hustedt (1955) Pl. 13, fig. 6.

**A. cymbifera**, Greg.

Water's edge: year round--common; spring--common.

Van Heurk (1896) Pl. 24, fig. 6, 7, 8.

**A. granulata** Greg.

Water's edge: year round--very common; inland: spring, summer, fall--common.

Hustedt (1955) Pl. 14, fig. 8-10, 21, 27.

**A. rostrata** W. Sm.

Water's edge: winter--rare; inland: winter--rare.

Van Heurk Pl. 24, fig. 679.

**A. ventricosa** Gregory

Water's edge: fall, winter--common; inland: fall, winter--common.

Hendey (1964) Pl. 38, fig. 12.

**Bacillaria paradoxa** (Gmel.) Grun.

Water's edge: year round--not common; inland (in colonies):

year round--not common.

Van Heurk (1896) Pl. 15, fig. 518.

**Caloneis liber** (Wm. Smith) Cleve.

Water's edge: winter--rare.

Hendey (1964) Pl. 29, fig. 2.
**Camphyllodiscus sp.**

Water's edge: year round--not common; inland: year round--not common.

**Cocconeis sp.**

Water's edge: spring, summer, fall--common.

**C. placentula Ehr.**

Water's edge: spring, summer, fall--very common (usually associated with the filamentous red algae).

Van Heurk (1896) Pl. 8, fig. 341.

**C. scutellum Ehrenberg**

Water's edge: winter--rare; spring, summer, fall--very common (often associated with the filamentous red algae).

Hendey (1964) Pl. 27, fig. 8.

**Coscinodiscus spp.**

*C. lineatus* and *C. nitidua* and an unidentified species of this genus were found sporadically in the epiphytic community. Their presence is considered to be more accidental than real.

**Cyclotella spp.**

At least three different types of this genus were found with the greatest abundance occurring during the summer. Specific identification is very uncertain.

**Cylindrotheca closterium** (Ehrenb) Reimann and Lewin.

Water's edge: year round--common (an occasional epiphyte also found in plankton and on mud banks).

Reimann and Lewin (1964).

**C. fusiforma** Reimann and Lewin

Water's edge: year round--common (an occasional epiphyte also
found in plankton and on mud banks).

Reimann and Lewin (1964).

**Denticula subtilis** Grun.

Water's edge: year round--very common; inland: year round--very common.

Hustedt (1955) Pl. 9, fig. 26-28.

**Denticula sp.**

Same as *D. subtilis* (very similar to *D. subtilis* except approximately 25-30 u long).

**Diploneis sp.**

Inland: year round--relatively rare.

**D. interrupta** (Kutzing), Cleve

Water's edge: year round--not common; inland: year round--not common.

**D. smithii** (de Berbisson) Wm. Smith

Water's edge: winter, spring--rare; inland: winter, spring--rare.

Hendey (1964) Pl. 32, fig. 10.

**Grammatophora marina** (Lyngb.) Kutz.

Water's edge: summer, fall--common (often attached to the summer algae).

Van Heurk (1896) Pl. 11, fig. 479.

**Gyrosigma spp.**

*G. hummii, G. obscurum, G. simile, and an unidentified species* were found occasionally on the *Spartina* stems. The members of this genus were commonly found in mud under *Spartina* stems.

**Isthmia enervis** Ehrenberg

Water's edge: early summer--rare (found in association with the
red algae).

Hendey (1964) Pl. 25, fig. 2.

**Mastogloia sp.**

Water's edge: late summer—common.

**Melosiara sp.**

Water's edge: summer, early winter (common on the filamentous red algae).

**Navicula spp.**

Two to three different individuals in the range of 10-20 µ long very common year round at both locations.

**Navicula spp.**

Three to four individuals 25 µ plus long common year round.

**N. calida** Hendey

Water's edge: late summer, fall—not common.

Hendey (1964) Pl. 43, fig. 10-11.

**N. cryptocephala** Kutz.

Inland: winter—not common.

Van Heurk (1896) Pl. 13, fig. 122.

**N. delicatula** Cleve.

Water's edge: early spring—not common.

Hustedt (1961) page 33, fig. 1191.

**N. lyra** Ehrenberg

Inland: winter—rare.

Hendey (1964) Pl. 33, fig. 2.

**N. rostellata** Kutzing

Water's edge: spring—not common.

Hendey (1964) Pl. 30, fig. 11.
**N. trompiki** Cleve.

Water's edge: spring--common; inland: spring--not common.

Hustedt (1961) page 41, fig. 1195.

**Nitzschia sp** 10 u

Two to four different individuals having a size range 8-10 microns, they are very common at the water's edge in the winter and common in the summer. Inland they are common year round.

**Nitzschia sp.**

Four to five different individuals considerably larger than the above mentioned group. Very common at the water's edge and inland year round.

**N. acuminata** (Wm. Sm.) Grun.

Inland: on the higher portions of the stems, rare

Van Heurk (1896) Pl. 15, fig. 506.

**N. consticta** (Greg.) Grun.

Water's edge: fall, winter--rare; inland: fall, winter--rare.

Van Heurk (1896) Pl. 15, fig. 501.

**N. grossestriata** Hustedt

Water's edge: fall, winter--common; inland: winter--common.

Hustedt (1955) Pl. 16, fig. 8-10.

**N. tryblionella** Hantzsch.

Water's edge: winter--not common; inland: winter--not common.

Van Heurk (1896) Pl. 15, fig. 493.

**Opephora schwartzii** (Grun.) Petit.

Water's edge: winter--rare.

Patrick and Reimer (1966) Pl. 3, fig. 1.
Pleurosigma salinarum Gun.

Inland: spring--rare (common in the mud under the Spartina).

Patrick and Reimer (1966) Pl. 27, fig. 2a-c.

P. strigosum Wm. Sm.

Inland: spring--rare (common on the mud under the Spartina).

Patrick and Reimer (1966) Pl. 28, fig. 2a-c.

Rhopalodia gibberula (Ehrenberg)

Water's edge: winter--not common

VanLandingham (1966) Pl. 3, fig. 52-53.

Surirella fastuosa (Ehrenberg) Kutzing

Inland: winter--rare (commonly found on mud).

Hundey (1964) Pl. 40, fig. 4.

Synedra sp.

Water's edge: year round--common; inland: fall, winter--not common.

Trachyneis aspera (Ehrenberg.) Cleve

Water's edge: spring--rare.

Hendey (1964) Pl. 29, fig. 13.
VITA

Wilmer C. Stowe was born in Lake Charles, Louisiana on January 7, 1941. He attended public school and was graduated from Lake Charles High School in June, 1960. He entered Louisiana Polytechnic Institute in September, 1960, and completed the requirements for the B. S. degree in Microbiology in January, 1965. He received the M. S. degree in Microbiology from Louisiana Polytechnic Institute in August, 1966. He was employed as an Instructor of Biology at Pan American College in Edinburg, Texas from September, 1966 to August, 1968. He married the former Priscilla A. Torregrossa on December 27, 1966, and is the father of a two year old son. He is presently a candidate for the Ph.D. degree in Botany at Louisiana State University.
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Major Field: Botany

Title of Thesis: Community Structure and Production of Epiphytic Algae in the Barataria Bay Area of Louisiana.

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Date of Examination:

July 14, 1972