Community Analysis of Epiphytic Diatoms From Selected Species of Macroalgae Collected Along the Texas Coast of the Gulf of Mexico

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ABSTRACT

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The epiphytic diatom community represents one of the least well known benthic diatom assemblages, especially in terms of species composition and seasonal variation. The present study investigated the epiphytic community structure associated with selected species of macroalgae along the Texas coast of the Gulf of Mexico using community composition statistics, multivariate analyses, and scanning electron microscopy. This study represents the first investigation of epiphytic diatoms from this area, as well as the first seasonal study of epiphytes over a two year period in the western hemisphere. Because it was a baseline study of this flora, questions as to which species were present, how they varied seasonally, and what variations could be correlated with environmental changes or with the host plant itself were addressed.

Samples of host plants were collected at two month intervals from granite jetties at Galveston, Port Aransas, and Port Isabel, Texas. A wash, tip, and base preparation from each host plant was processed for

statistical analyses. Community composition statistics revealed that the diatom assemblages washing off the host plants were statistically different from those attached to the host plant during the fall and spring. During the winter, the diatom assemblages associated with the host plant were more alike. The variation between the different species of host plants was greater than the variation between replicas of the same host plant, especially at Galveston and Port Aransas. There was a subtle seasonal change with ten taxa comprising 50-60% of the flora in the spring. The community gradually changed so that only three taxa were dominant in the winter. Multivariate analysis demonstrated that there was a continuum in the diatom community down the coast southward from Galveston to Port Isabel that could be weakly correlated with increasing salinity.

A distinct change in abundance of epiphytes could be demonstrated among the host plants as branching increased. Abundance and diversity also increased distally from the tip of the host plant. The increased diversity of the wash often help mask the host-related differences in the attached assemblage. The microdistribution of the epiphytes as they relate to both host plant shape and increasing distance from the actively growing meristem was documented with the use of scanning electron microscopy.

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INTRODUCTION

Diatoms comprise one of the more important microalgal groups contributing much in terms of species richness and primary production in many varied habitats. Some habitats, such as the marine and freshwater plankton and freshwater benthos, where diatoms are known to be abundant, have been extensively investigated (Guillard and Kilham, 1977; Patrick, 1977). Benthic marine habitats, although well defined spatially, i.e. epipelic (on silt or sand), epipsammic (on sand), epilithic (on rocks), epiphytic (on plants), and epizooic (on animals), are not, by comparison, as well known in terms of species composition and seasonal variation (Round, 1971; McIntire and Moore, 1977).

Among these benthic communities, the epiphytic one poses several interesting questions because the diatoms must interact with the host itself, as well as respond to subtle or dramatic changes within the physical realm of their environment. Diatoms living attached to a host plant (epiphytic) or in the mucilaginous waters surrounding it (metaphytic, Behre, 1943; Round, 1980) must interact with biologically active compounds being secreted by the host plant that may enhance or deter the growth of these cells.

Auxin-like (growth enhancing) compounds have been documented from macroalgae (Augier, 1978), but their effects on epiphytic growth have yet to be investigated. "Antibiosis," defined as the antagonistic

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association between one organism and a metabolic product of another, is well documented in land plants because specific compounds can be identified as repellents or attractants for predators (Sieburth, 1968). These compounds are classified as secondary compounds rather than primary compounds, which are those directly involved in the plant's metabolism. In the marine environment the existence of secondary plant compounds has been described, but because they are not, in most cases, a prime controlling factor in biotic interactions, many marine ecologists are reluctant to recognize "that they do play an influencing role in the dominance, suppression, and succession of at least some marine microorganisms" (Sieburth, 1968, p. 64).

Macroalgae and aquatic flowering plants are known to release several types of biologically active compounds. Sieburth (1968) has grouped these compounds into the following major categories: 1) allyl sulfides--whose degradation products, i.e. acrylic acid, are known antibiotics, 2) polyphenols (tannins)--which are commonly produced in brown algae and are known repellents for predators because they have an astrigent taste and protein precipitating properties, 3) terpenes--which are also repellents, 4) chlorophyllides--which are chlorophyll degradation products and which would be released during senescence and cell lysis. The production of these compounds can vary seasonally, between host plant species, and within the host itself (Sieburth, 1968; Hornsey and Hide, 1974, 1976a,b), and thus may modify, accordingly, the epiphytic flora of the host plant.

Hornsey and Hide (1974, 1976a) tested 151 species of macroalgae for the production of antibiotics against five species of bacteria at

three month intervals for one year. Antibacterial activity occurred in all three major macroalgal classes (Chlorophyceae, Rhodophyceae, Phaeophyceae). Although many species exhibited little or no activity, three main patterns of activity emerged from this survey. Certain macroalgae, especially of the Family Rhodomelaceae, Division Rhodophyta, displayed uniform antibacterial activity throughout the year. Other groups have marked periods of inactivity, especially during the winter, e.g. Laminaria, or marked periods of activity, especially during the spring when the maximum growth period occurred, e.g. Codium. In some cases, the presence or absence of antimicrobial activity appeared to be of some taxonomic significance (e.g. Family Rhodomelaceae was active; while the Family Fucaceae was inactive). In others, closely related species, even within the same genus, displayed opposing attributes. Also, within the thallus, production of antibiotics varied (Hornsey and Hide, 1976b). In Laminaria, activity increased away from the meristem; while in Codium, activity was highest at the meristem. Ulva displayed similar activity throughout the plant. Sporelings of Chondrus crispus (L.) Stachk. with very active meristems have been shown to inhibit benthic diatom growth by production of antibiotics which resulted in a clear inhibition zone around cultured germlings of the macroalga (Khfaji and Boney, 1979).

The tannic acid found in the physode vesicles of Phaeophytes has been tested for immobilization of epifauna and found to be effective against hydroids, bacteria, flatworms, roundworms, copepods, and to some extent, polychaeta (Sieburth and Conover, 1965). Tannic acid extracts used as antifoulant paint prevented settling of barnacles and

algae but were not as effective as commercial products.

The survival and reproductive rates of Vorticella cultures were monitored following exposure to the exudates from these macroalgae: Cladophora, Polysiphonia, Ascophyllum, Fucus, and Scytosiphon (Langliss, 1975). Highest survival and reproductive rates were found in the cultures exposed to exudates from Cladophora and Polysiphonia. The exudates were chemically analyzed for dissolved organic matter (DOM), polyphenols, and carbohydrates. An analysis of variance revealed that DOM caused the most variation in response of the protist. The release of these compounds could be important in controlling community structure and nutrient recycling in individual tide pools.

Diatoms attached directly to the plant respond to these chemicals in varying manners. The most easily detected response is the absence of epiphytes. If epiphytic growth is present, then the magnitude of the populations and the means of attachment to the host plant also indicate the epiphyte's tolerance of these chemicals and/or if the host plant is producing antagonistic products (Hendey, 1951; Sieburth, 1968).

Some cells, more tolerant of these products, are attached directly to the host plant surface, while others are slightly removed from the surface by a mucilage pad or stipe and assume a perpendicular attachment. Some cells can assume a flat attachment only after an initial mucilage layer is deposited. Still others are enclosed within mucilage tubes, which afford maximum protection. Sieburth (1968) and Conover and Sieburth (1963) documented a succession in the epibiota on

Fucus and Sargassum from the meristem toward the base of the plants. This succession involved not only a change from perpendicular to flat epiphyte attachment after an initial mucilage layer was formed but also a gradual increase in epiphyte diversity. A decrease in antibiotic activity could be correlated with distance from the apex. The monospecific growth of Cocconeis scutellum Ehr. near the meristem of seagrasses has been noted by several workers (Main and McIntire, 1974; Sieburth and Tomas, 1973; Sieburth et al.,1974; Medlin, pers. obs). Excessive fouling by other organisms occurs in older regions only after a crust of Cocconeis has formed. Main and McIntire were able to detect statistically a preference by Cocconeis for the seagrass substrate. This sequence of fouling events suggests the possibility that C. scutellum could be more tolerant of inhibitory compounds, such as tannins. Certainly its means of attachment, flat, almost embedded in the epidermis of the seagrass, would indicate a close interaction between the host plant and epiphyte.

Diatoms attached to Potomogeton increased their numbers from the apex until a maximum two to three times higher was reached 10 cm back from the meristem (Siver, 1980). Remaining portions of the plant were less heavily epiphytized. During the winter, when apical growth declined, there was a uniform distribution of epiphytes along the entire axis. Thus, inhibition of epiphyte settling was correlated with active growth of the macrophyte and was localized near the meristem. Because this macrophyte grows horizontally along the bottom, vertical differences in light intensity, temperature, and nutrients along the axis are assumed to be minimal and would not cause

the zonation seen in epiphyte density. Decay of epidermal cells preceded diatom colonization of Potomogeton.

Achnanthes spp. are often the dominant members of the fouling community established on ship hulls (Evans, 1981). These species are attached by a long mucilage stipe above the treated surface and seem to be more tolerant of the leaching antifouling chemicals than other epiphytes. Achnanthes spp. can vary stipe length in response to increasing concentrations of biotoxins (Callow and Evans, 1981). Amphora, which has also been noted as a dominant fouling species, attaches itself directly to the ship's hull, but is protected from from the leaching antifoulants in two ways (Daniel, Chamberlain, and Jones, 1980). Species of this genus completely encapsulate themselves by secreting copious amounts of mucilage and then, intracellularly, sequester copper-containing granules within cell vacuoles for protection against toxicity. Epiphytes on macrophytic surfaces could presumably respond similarly to host plant secondary compounds.

These "antibiotic" compounds being secreted by the host plant may also affect its palatability, which in turn will affect the grazing of small invertebrates (Bold and Wynne, 1978). Littorina littorea (L.) will graze Enteromorpha in preference to the more cartilaginous Chondrus crispus to such an extent that intense snail grazing will eliminate the ephemeral small algae like Enteromorpha from small tide pools and allow the inedible Chondrus to dominate (Lubchenco, 1978). Epiphytes on Chondrus are not plentiful or are non-existant (Aleem, 1969). The rapid replacement of the ephemeral algae would not allow enough time for heavy epiphytic colonization.

In controlled feeding experiments, caddis larvae, Potomophylax cingulatus (Steph.), preferred portions of terrestrial over aquatic macrophytes (Otto and Svenson, 1980). Caddis larvae are known to be non-selective feeders, and the decline in consumption rate of aquatic macrophytes was linked to the production of plant secondary compounds that inhibited aquatic herbivores. Prolonged exposure of the vegetative portions of aquatic plants to herbivores as compared to that of their terrestrial counterparts could be a factor in evolving these grazer repellants.

The actual noises created by grazing herbivores have been monitored with underwater microphones (Kitting, 1979, 1980). The feeding sounds not only differentiate the texture of the algae, but also indicate when the herbivore is "licking" the plant surface (i.e. feeding on epiphytes), biting into the alga, or avoiding a surface or an alga. Interpretation of these sounds has provided more evidence that herbivores select their food, as well as select the appropriate mixture to maintain a diet suited to their metabolic needs and to optimize their reproductive rate.

Grazing can alter the species composition of the epiphytic community through frequent and/or selective perturbation (Castenholz, 1961; Nicotri, 1977; Medlin, 1981). Controlled caged and uncaged experiments on rock surfaces and tide pools along the southern Oregon coast revealed that limpets can effectively eliminate the diatom cover during the summer months by heavy grazing activity (Castenholz, 1961). Three littorines/dm^2 was sufficient density to keep the area nearly free of diatoms for two weeks. Thus, these grazers were directly

responsible for keeping the diatom population low during the summer when all other conditions were conducive for heavy diatom growth. Selective grazing of diatom communities by limpets and littorines has also been investigated (Nicotri, 1977; Medlin, 1981). These studies provided evidence that chain forming species, stalked species, and loosely attached species of diatoms were more easily grazed by these herbivores. Low-lying forms or those stalked forms with tighter adhesion were left behind, thus altering the community. Opportunistic species recolonized the grazed areas quickly to add further changes to the community structure.

Subtle and/or dramatic differences in epiphyte coverage between different host plants has been documented by studies from various parts of the world (Table I). In the Ouse Estuary, Sussex, U.K., Rhodophytes and Enteromorpha supported the heaviest epiphytic growth (Hopkins, 1964). Differences in epiphytic settlement were also noted within parts of the same plant. For example, Synedra and Licmophora spp. were prevalent on older parts of Ceramium, while younger parts hosted stands of Melosira moniliformis (O. F. Mull.) Ag. Ronnberg and Lax (1980) found Licmophora, Rhoicosphenia, Gomphonema, and Diatoma concentrated at the apex of Cladophora glomerata (L.) Kütz. Epithemia dominated the middle of the alga and Cocconeis at the base. Aquatic macrophytes examined by Godward (1934) were epiphytized by Epithemia, while dead portions were colonized by Gomphonema. In two Norwegian estuaries, filamentous algae were found to be better hosts than the foliose and membraneous thalli of Enteromorpha, Fucus, and Porphyra (Holt, 1980). In two British coastal sites, Aleem (1950, 1969) found

Table I. Selected Epiphytic Diatom studies from Various Parts of the World.

Source	Type of Host Plant	Location
Skvortzow, 1929	Laminaria (P)	Siberian Shore, Japanese Sea
Carter, 1932, 1933a,b	Vaucheria (X),	Canvey Marsh, UK
Ghazzawi, 1933	mixed macrophytes Chlorophytes	Liverpool & Isle of Mann, U.K.
Aleem, 1949	mixed macrophytes	Swanage, UK
Møller, 1950	mixed macrophytes	Praestø, Fjord, Finland
Hustedt & Aleem, 1951	Vaucheria (X)	Salstone, Plymouth, UK
Crosby & Wood, 1959	Zostera, Posidonia Ruppia (A)	Australia & New Zealand
Takano, 1961	Geliaceae (R)	Japan
Takano, 1962	mixed macrophytes	Japan
Hopkins, 1964	mixed macrophytes	Ouse Estuary, Sussex UK
Hargraves, 1965	Zostera, Laminaria Laminaria (P)	Rhode Island, USA
Edsbagge, 1966	mixed macrophytes	Swedish west coast
Aleem, 1969	mixed macrophytes	Cullercoats,UK
Reyes-Vasquez, 1970	Thalassia (A)	Biscayne Bay, Fl. USA
Carpenter, 1970	Sargassum (P)	Sargasso Sea
Giffen, 1970, 1971, 1973	mixed macrophytes	South Africa
Rautiainen & Ravanko, 1972	mixed macrophytes	Seili Island, Finland
Main and McIntire, 1974	mixed macrophytes	Yaquina Estuary, Ore. USA
Taasen, 1974	Dumontia (P)	Espergrend, Norway
Lee et al., 1975	Enteromorpha (C)	Long Island Marsh, N.Y. USA
Ramm, 1977	mixed macrophytes	Kiel Bight (West Baltic)
Hendey, 1977	Ceramium (R)	Corwall, UK
Sullivan, 1977	Ruppia (A)	Great Bay salt marsh, N.J.
Cattaneo, 1978	Potomogeton (A)	Lake Menaphremagog, Canada
Koppen & Crow, 1978	mixed macrophytes	Kachemak Bay, Alaska USA
Li, 1978	Ulva, Enteromorpha (C) Ectocarpus, Sargassum (P)	Pascadores, Taiwan
Siver, 1978, 1980	Potomogeton (A)	Wheelwright Pond, N.J., USA
Jacobs & Noten, 1980	Zostera (A)	Netherlands
Sullivan, 1980	Halodule, Thalassia Cymodocea (A)	Mississippi Sound, USA

(A) = Anthophyta, (C) = Chlorophyta, (R) = Rhodophyta (P) = Phaeophyta, (X) = Xanthophyta

the Rhodophytes and Chlorophytes were better phytal substrates than Phaeophytes. Among these groups, again, the filamentous forms were also more heavily colonized than the cartilaginous, foliose, or coralline hosts.

In contrast to these observations, Edsbagge (1965, 1966, 1968a,b,c) recorded from the Swedish west coast more epiphytes on Rhodophytes and Phaeophytes than on Chlorophytes but could not detect any differences between thallus shapes with respect to epiphyte settlement. However in his study Ulva, Enteromorpha, and Bangia were poor host substrates. In two Canvey, U.K. salt marshes, diatom communities that occurred among stands of Vaucheria, Chlorophytes, and other Cyanophytes were also found to be essentially identical (Carter, 1932; 1933a,b).

Statistically significant differences in the density of epiphyte colonization, as well as host-epiphyte specificity, was documented by Prowse (1959). He allowed "clean" specimens of Utricularia, Naias, and Enhydrias to be colonized by natural diatom communities in a fish pond. Colonization was significantly heavier on Utricularia than on the two other macrophytes. Each host plant had a dominant epiphyte, e.g. Gomphonema on Utricularia, Eunotia on Naias, Oedogonium on Enhydrias. In all but two of thirteen sites selected on the rocky shores of the Finnish archipelago, distinct diatom zonation could be statistically associated with differing macroalgal vegetation belts (Rautiainen and Ravanko, 1972). The numbers of diatom species increased seaward. Cocconeis spp. were characteristic of Cladophora (high intertidal) and Potomogeton (low intertidal). Rosen et

al.(1981) observed differential epiphytism between Cladophora glomerata and Bangia atropurpurea (Roth.) Ag. There were 1000 times more epiphytes on Cladophora than on Bangia.

The only published examples of obligate host specificity are those diatoms that are endophytes. Navicula endophytica Hasle, Navicula fucicola Taas., and Navicula dumontiae Baard. et Taas. are restricted to their respective host plants because they live inside the macrophyte thallus (Baardseth and Taasen, 1973; Taasen, 1975).

Main and McIntire (1974) demonstrated that the structure of the diatom community on adjacent host plants of the same species often differed as much as the community structure from host macrophytes of different species in a temperate climate. The differences in species composition between host macrophytes were more pronounced during the winter, but these differences were attributed to the large differences in vertical and horizontal distribution of the host plants rather than host specificity. No significant differences could be found between the epiphytic communities on Halodule beaudettei (Den Hart.) Den Hart., Cymodocea filiforme (Kütz.) Corr., or Thalassia testudinum Konig sampled during the summer from Mississippi Sound (Sullivan, 1980). Earlier, Sullivan (1977) also noted similar epiphytic communities on the leaves and internodes of Ruppia maritima (L.). Diversity of the community was high but dropped after host vegetative growth ceased, perhaps, because the epiphytes were no longer being sustained by the nutrients, which seagrasses are known to leak through their leaves (McRoy and Goering, 1974). Thus, examples of host-epiphyte specificity are often contradictory, and the question is far

from being settled.

In addition to the host plant-epiphyte interaction, physical factors play a role in determining species composition and seasonal variation. The velocity of the water around the host plant will determine initial settling rates of colonizing cells (Stevensen, 1981). Overall shape of the host plant will interact with these microcurrents to influence settling. Any projection from the surface of the host plant will reduce the currents so that settling rates are increased. Fluid dynamics will also predict the chance that any immigrated cell, once settled, will be scoured.

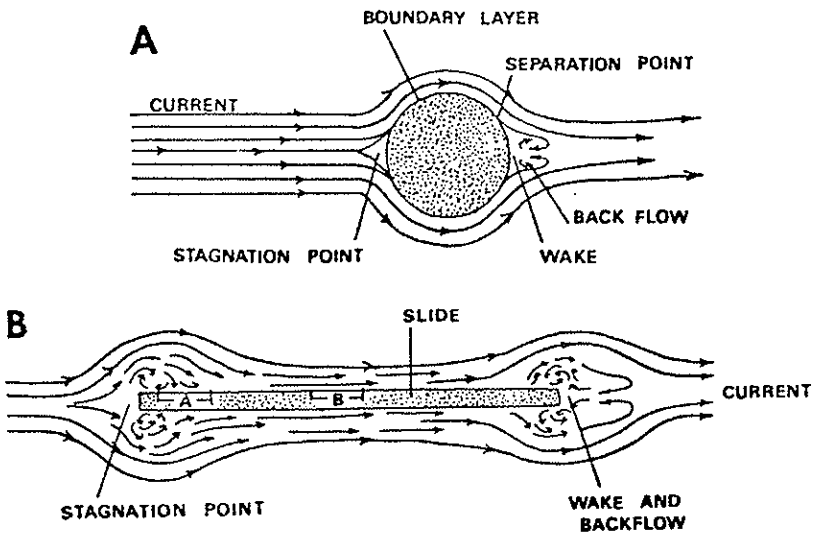


Figure 1. Diagrams of movement of a viscous liquid around a cylinder (A) and around a glass slide (B). Taken from Munteanu and Maly (1981).

A model based on water flow has been proposed by Munteanu and Maly (1981) (Fig. 1) to explain preferential settlement of diatoms on

glass slides oriented parallel to the current. These slides were more heavily colonized on the upstream side, while perpendicularly oriented slides were uniformly colonized. Increased turbulence at the leading edge of the slide increases the probability of collision of a particle with a surface (i.e. settlement). Laminar flow across the middle of the slide would tend to scour the slide (Fig. 1). This model could easily be applied to macroalgal thallus shapes. As the host plant shape varies, i.e. more branches, etc., the possibility of breaking up laminar flow increases, and thus settlement would increase.

The preference for epiphyte attachment to the edge of macrophyte host plants has been well established (Van den Ben, 1969; Cattaneo, 1978; Siver, 1980). Van den Ben (1969) documented a definite spatial arrangement and sequential colonization of the epiphytic community on Posidonia oceanica (L.) Delile. Not only were the meristematic regions clean of epiphytes, but also a clear preference for edges was demonstrated. The middle of the blade was either clean or colonized by bryozoans and hydroids. Nutrient renewal was one of the first suggestions as to the possible advantage for this phenomenon (Cattaneo, 1978). However, when all diatoms showed a preference for the edge on both natural and artificial leaves in his study, the pattern had to be attributed to physical rather than biological mechanisms. Yet, biological interaction must not be totally discounted because Eunotia spp. significantly preferred the underside of natural leaves but exhibited no preference on artificial leaves. Cocconeis placentula v. euglypta Ehr. was more concentrated the upper surface of artificial leaves but was equally distributed on natural

leaves.

Van den Ende and Haage (1963) noted that in sheltered areas, epiphytes preferred the edges of Zostera, while in stronger current areas the lamina of the blade was the preferred settling site. Epiphytic diatoms on Cladophora glomerata reached their highest numbers on filaments exposed to heavy wave action and swells from ferry traffic than on those in sheltered areas (Ronnberg and Lax, 1980). In areas of maximum wave action Rhoicosphenia abbreviata (Ag.) Lange-Bert. (= curvata) dominated the entire growing season. As sites became more protected, other species co-dominated the community.

Potomogeton has marginal cells with spine-like extensions. Siver (1980) speculated that, perhaps, these extensions changed water flow so that settlement was induced. C. placentula v. euglypta and Eunotia incisa Wm. Sm. ex Greg. were the pioneer stages, which were later replaced by Achnanthes minutissima Kütz. and Anomoeneis vitrea (Grun.) Ross (Siver, 1978). Siver (1980) attributed the early settlement of Cocconeis and Eunotia to their superior attachment mechanisms and ability to attach without a layer of mucilage present.

On Elodea, diatoms were especially found at cell junctions where there was a slight groove (Godward, 1934). Presumably, these cells were more protected in this position. The same phenomenon could be duplicated by etching glass slides. As would be expected the size of the epiphyte was relative to the width of the groove.

Seasonal variation in the epiphytic community has been related to changing abiotic factors. In fact, seasonality may outweigh succession toward a climax community as an overriding factor in

determining microalgal community structure (Hoagland et al., 1982). Water temperature and light intensity were the limiting factors controlling seasonal change in the epiphytic community of the Ouse estuary (Hopkins, 1964). The cells' ability to survive depended on water retention capabilities. Achnanthes spp. were considered to be more tolerant of desiccation and higher water temperatures than were other species. Godward (1934) found that most epiphtytic diatoms tolerated low light. In a growth experiment involving varying light intensities, Cocconeis placentula exhibited a clear preference for low light. From the Swedish west coast, Edsbagge (1966) reported Achnanthes brevipes Ag. and Licmophora spp. to be light-loving species. He found no real seasonal variation except for Striatella unipunctata (Kütz.) Grun., which had a winter maximum. In general, the epiphytic community varied continously but reached maximum numbers in autumn after growth of the macrophytic host plant declined.

Edsbagge (1965) established a definite vertical distribution of diatoms based on their response to environmental factors, especially salinity. Because of the overlying low salinity waters from the Baltic Sea along the Swedish west coast, true marine species were only found at the deepest depths. This vertical distribution was similar to that found in the Baltic by Simonsen (1962), except for the missing marine species in the deeper waters of the Baltic. The zonation of the upper littoral epiphytic community also corresponded well that seen along the British coast by Aleem (1949), but the sublittoral community of the Swedish west coast was found in the lower littoral zone along the English coast.

The epiphytic community can be quite complex. The host plant can depress the overall effect of epiphytic growth either by secreting antibiotic compounds, by sloughing epidermal cells, or by accelerating its own growth to offset epiphytic growth (Sand-Jensen, 1977; Sieburth and Tootle, 1981). If the host plant is nitrogen limited, then its mucilage layer dissolves away, and the dissolution retards epiphyte settlement (Fitzgerald, 1969). The host plant may enhance epiphytic growth with the transfer of nitrogen and carbon compounds from the host plant to the epiphytes (Harlin, 1973; McRoy and Goering, 1974).

Estimates of primary productivity by the epiphytic community range from one-fourth to more than that produced by the host plant (Penhale and Smith, 1977; Capone et al., 1979) at rates of 26.8 g $C/m^2/yr$ (Hooper and Robinson, 1976) to 48 g $C/m^2/yr$ (Borum and Wium-Anderson, 1980) which are comparable to offshore phytoplankton productivity.

Epiphytes offer some protection to their host plant by trapping water to retard desiccation. Dissolved organic carbon (DOC) released by the seagrass Zostera marina (L.) was monitored from "clean" as well as "colonized" plants (Penhale and Smith, 1977). The decrease in released DOC observed in colonized plants was attributed to the uptake of DOC by the epiphytes. Following desiccation, colonized plants excreted one/ninth the DOC secreted by clean plants, and this was attributed to the protection of the host plant by the epiphytes.

Epiphytes can be potentially harmful to the host plant and can reduce their photosynthetic rate up to 30% by acting as a barrier to carbon dioxide and by reducing light intensity reaching the macrophyte (Sand-Jensen, 1977).

When epiphytes proliferate, they supply food for various kinds of herbivores (Crosby and Wood, 1959; Prowse, 1959; Nienhaus and van Ierland, 1978; Morton, 1980; Rosen et al., 1981; Kitting, 1980) and play an significant role in shallow macrophyte-dominated aquatic ecosystems because the epiphytes, not the macrophytes, serve as a direct food supply for grazing invertebrates (Borum and Wium-Anderson, 1980).

Thus, the epiphytic diatom community offers an excellent system to study attachment mechanisms of epiphytes and community changes in response to biological and physical factors. The general objective of this study was to generate and examine hypotheses regarding mechanisms that account for spatial and temporal patterns in the epiphytic diatom flora along the Texas coast of the Gulf of Mexico. More specifically, seasonal floristic patterns were examined over a two year period. Spatial differences in the diatom flora were examined relative to host plant shape, position of the host plant in the intertidal zone (i.e. degree of exposure), water temperature, and salinity.

Description of Study Area

The Texas coast of the Gulf of Mexico is characterized by a series of barrier islands, which front extensive drainage basins. Six such basins can be identified along the Texas coast: Galveston, Matagorda-Brazos, San Antonio, Copano-Aransas, Corpus Christi, and Laguna Madre (Shew et al., 1981). Of these six basins, three were

chosen as collecting sites for this study. These three sites (Galveston, Copano-Aransas, and Laguna Madre) are located in the upper, mid, and lower regions of the Texas barrier island system and represent a transition from a humid climate (Galveston Bay system) to a semi-arid climate (Laguna Madre system) with the Copano-Aransas system as a median point.

Geology

The surface sediments of all three bay systems were deposited during the Quarternary period (Fisher et al., 1972 cited in Shew et al., 1981) and have formed from the late Pleistocene to present. Sediments are carried into each basin through its associated rivers with Galveston Bay having the largest sediment load and Copano-Aransas and Laguna Madre ranking 5th and 6th respectively out of all the Texas basins. In addition to the riverine imput into each basin, sediments from the Mississippi River are carried along the Texas coast southward, but the effect of these sediments diminishes southward. There are no natural rocky substrates along this coastline; however granite jetties and groins have been constructed at natural passes between several of these barrier islands to maintain open, dredged roads into the basins for shipping. There are jetties constructed seaward at each of the three study sites, and these rocks provide the major solid substrate other than pilings and oyster reefs for macroalgal attachment.

Precipitation

The amount of precipitation along the Texas coast decreases southward. The Galveston Bay system, specifically Galveston Island, receives 1072 mm/year average rainfall with increasing abundance during the late summer, while the inland areas of the system have a bimodal distribution. The Copano-Aransas system also has a bimodal distribution, one in late spring and another in early fall, and averages 835 mm annual precipitation. The study site at the lower Laguna Madre receives the least amount of precipitation, averaging 638 mm per year. The single late summer peak in rainfall at this site is unusual for the entire Gulf coast, occurring only along the south Texas and south Florida coast (Shew et al., 1981).

Air Temperatures

Galveston is the coolest of the three study sites with a mean annual air temperature of 21.0°C. This is reflected in a growing season that averages 265 days. The mean annual air temperature in the Copano-Aransas area is nearly the same (21.5°C), but the growing season increases to an average of 310 days because of the milder winter temperatures along the coast. In the lower Laguna Madre, temperatures are generally warmer throughout the year with an annual average of 23.2°C. The growing season in the Rio Grande delta increases to an average of 330 days accordingly (Shew et al., 1981).

A theoretical climatic water budget can be estimated from rainfall and temperature data to provide a fair representation of water demand by the natural environment (Thornwaite and Mather, 1955

cited in Shew et al., 1981). Along the three study sites, the amount of evapotranspiration has been calculated for a ten year period from 1969-1978 to be a net surplus of 169 mm average on Galveston Island, a 330 mm net deficit in the Copano-Aransas Bay area, and a 700 mm net deficit in the Port Isabel area. This measure helps to explain the transition from a humid climate in Galveston to that of a semi -arid one in Port Isabel.

Wind Patterns

All three study sites are influenced by three distinct wind regimes: southeasterly to southerly, northerly, and the highly variable wind patterns associated with tropical disturbances (Shew et al., 1981). The influence of wind intensity is greatest along the lower Texas coast where the prevaling and predominant winds are from the southeast and form extensive dune fields.

Tides

Tides along the Texas coast are mixed diurnal with a small tidal range. At Galveston, tidal range is 11 cm, at Copano-Aransas 25 cm, and at lower Laguna Madre 15 cm. Seasonal changes in tidal amplitude produce a winter minimum and a fall maximum, and are subject to local climatic changes, especially to the passage of major weather systems.

Salinity

The salinity regimes of each basin are determined by the interaction of tidal and freshwater flow combined with circulation

patterns, as well as local precipitation and evaporation rates. Mean salinity from 1965-1975 was 17.3 o/oo within the Galveston Bay complex, 16.4 o/oo for the Copano-Aransas Bay, and exceeded that of seawater in the lower Laguna Madre.

Water Temperatures

Water temperatures of each basin closely follow air temperatures primarily because of the shallowness of the waters. Water temperature ranges in the Galveston Bay complex from 12 to 29°C, in the Copano-Aransas Bay from 10 to 30°C, and in the lower Laguna Madre from 9.9 to 31°C.

MATERIALS AND METHODS

Sampling Strategy

Field samples were collected at two month intervals from September 1977 to July 1979 from selected species of macroalgal host plants growing attached to granite jetties extending seaward at Galveston, Port Aransas, and Port Isabel, Texas (Fig. 2). During the first year, host plants were selected based on differences in host plant shape, position of the host plant in the intertidal zone, and availability of the host plant at all three sites (Table II). Several host plants could be collected year-round, but most other macroalgae sampled throughout the year on the jetties were replaced during March by a Petalonia-Porphyra community. During the second year the number of host plants was reduced and collected in triplicate to determine within host variation of the epiphytic diatom composition (Table III). Selection of these species was based on their year-round collectability. Replicates were taken approximately 30 meters apart at all locations. All samples were refrigerated until processed.

Water temperature and salinity measurements were taken at each site. Surface salinity was determined with an AO refractometer. Temperature and salinity measurements taken by the National Ocean Survey/NOAA were also used to obtain changes in water temperature and salinity for the two week period prior to the collection date.

All samples were processed in a similar manner. Each host plant was halved and examined separately to determine if diatom species composition differed from tip to base of the macrophyte. Tips and

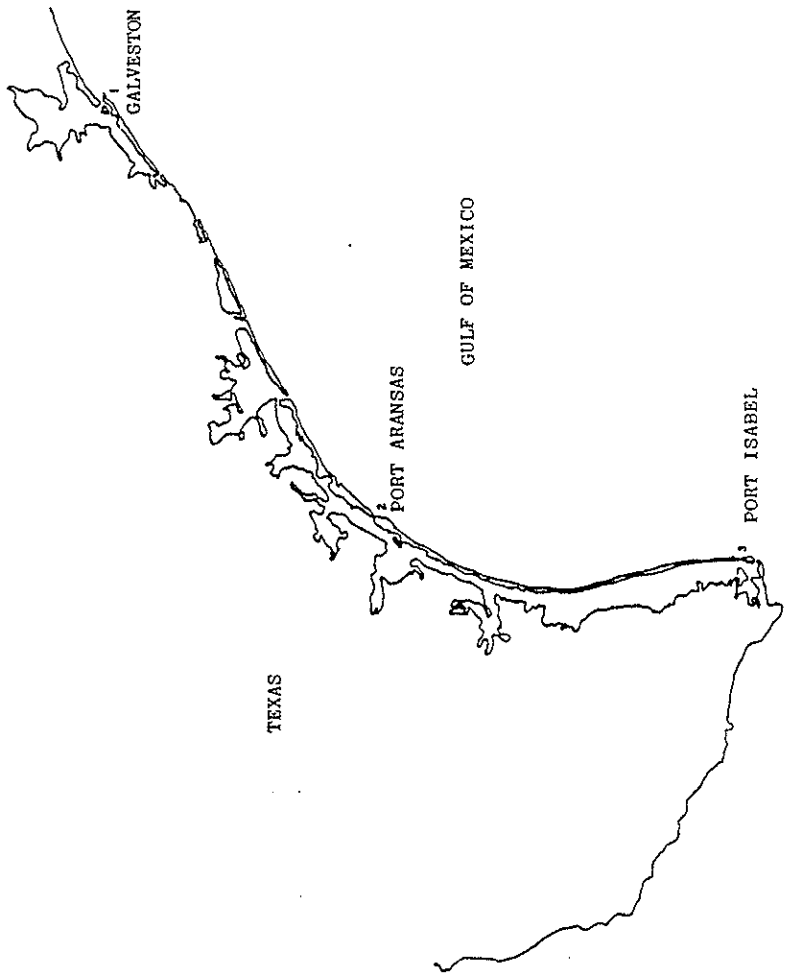


Figure 2. Location of collecting sites along the Texas coast of the Gulf of Mexico.

Table II. Horizontal and Vertical Distribution of Macroalgal Host Plants Collected during the First Study Year.

GALVESTON

	SPRING-FALL	WINTER
SPLASH ZONE	Chaetomorpha linum (Muell.) KÜtz. (Summer only)	Bangia fuscopurpurea (Dill.) Lyng.
HIGH INTERTIDAL	Enteromorpha lingulata (Roth) Grev.	Enteromorpha lingulata
MID INTERTIDAL	Bryocladia cuspidata (J. Ag.) De Toni Cladophora dalmatica KÜtz. Gelidium crinale (Turn.) Lam.	Bryocladia cuspidata Cladophora dalmatica Gelidium crinale Petalonia fascia (O.F. Muell.) Kuntze
LOWER INTERTIDAL	Ceramium strictum (KÜtz.) Harvey (Summer only)	

PORT ARANSAS AND PORT ISABEL

	SPRING-FALL	WINTER (PA)	Winter (PI)
SPLASH ZONE	Chaetomorpha linum	B. fuscopurpurea	B. fuscopurpurea
HIGH INTERTIDAL	Enteromorpha lingulata Centroceras clavulatum (C. Ag.) Mont.	E. lingulata	E. lingulata
MID INTERTIDAL	Bryocladia cuspidata Cladophora spp. Gelidum crinale Hypnea musciformis (Wulf.) Lam.	B. cuspidata Cladophora spp. G. crinale Porphyra leucosticta Thur. Petalonia fascia	B. cuspidata Cladophora spp. G. crinale H. musciformis P. leucosticta P. fascia
LOWER INTERTIDAL OR SUBTIDAL	Haliptylon subulata (Ellis et Sol.) John. Dictyota dichotoma (Hud.) Lam. Padina vickersiae Hoyt		H. subulata Polysiphonia denudata (Dill.) KÜtz.
	Rhodymenia pseudoplamata (Lam.) Silva	R. pseudoplamata	R. pseudoplamata

Table III. Horizontal and Vertical Distribution of Macroalgal Host Plants Collected during the Second Study Year.

Galveston

	Spring-Fall	Winter
High Intertidal	Cladophora dalmatica	Cladophora dalmatica
Mid Intertidal	Gelidium crinale Bryocladia cuspidata	Gelidium crinale Bryocladia cuspidata

Port Aransas and Port Isabel

	Summer-Fall	Winter-Spring
High Intertidal	Centroceras clavulatum	Cladophora dalmatica or Cladophora vagabunda
Mid Intertidal	Gelidium crinale Bryocladia cuspidata	Gelidium crinale Bryocladia cuspidata

bases of the host plants were placed in separate containers and manually agitated for 30 seconds to remove the metaphyton from the epiphyton. Tips and bases of the host plants and their respective washings were cleaned of organic matter by boiling in nitric acid or by treating the sample with permanganate and hydrochloric acid (Simonsen, 1974). Permanent slides were made; five hundred valves were counted from the tip and base preparation of each alga. Two hundred fifty valves were counted from each wash, and the totals were pooled to obtain a single wash sample for the entire plant. Counts were made from those algae collected during the first year that were also continuously sampled during the second year.

Each diatom species encountered during the counting was photographed using a Zeiss standard K microscope equipped with phase contrast and Nomarski interference phase optics, identified to species or variety, or assigned a reference number.

Although the above treatments were done on fresh samples kept refrigerated, portions of host plants were preserved in unbuffered formalin in seawater, dehydrated through a graded alcohol series, and critical pointed dried (Marchant, 1973). Tips and bases of the host plant were separated and coated with approximately 200 A of gold-palladium using a Technics Hummer-1 and examined with a JEOLCO SEM-25 at the Electron Microscopy Center at Texas A&M University at an accelerating voltage of 12.5 or 15 KeV. All specimens were viewed at both 10 and 48 mm working distance, and unless otherwise stated, 0° tilt. Samples of cleaned material were also examined with the SEM to facilitate species identification.

Community Composition Parameters

After the samples were analyzed taxonomically, the following community composition parameters were calculated:

1) Diversity Index = $H''_j = -\sum_{i=1}^{S} P_i \log_2 P_i$

where P_i is the proportion of the $_i$th species in the $_j$th sample, and S is the total number of species in the sample. H" is a biased estimator of the community composition parameter H' (Pielou, 1975), but the bias is negligible at sample sizes of 500 counts (McIntire and Overton, 1971).

Based on the observed number of species in each sample, a conditional maximum and minimum diversity for that sample can be calculated from the expressions:

2) $H''_{max|S} = \log_2 S$

3) $H''_{min|S} = -\left[\frac{S-1}{N} \log_2 \frac{1}{N} + \frac{N-S+1}{N} \log_2 \frac{N-S+1}{N} \right]$

where S and N are the number of species and individuals in that sample, respectively (McIntire and Overton, 1971). These values were used to calculate a redundancy index (REDI):

$$4)\quad REDI = \frac{H''_{max|S} - H''_{j}}{H''_{max|S} - H''_{min|S}}$$

where REDI is a measure of the relative degree of dominance in a sample (McIntire and Overton, 1971). Values from this statistic can range from 0, if all species are equally common, to 1, if all species but one are represented by one individual.

Simpson's diversity index was also calculated to provide a comparison to the Information Index. Simpson's index gives greater weight to the dominant taxa than the Information Index.

$$5)\quad SDI_j = 1 - \sum_{i=1}^{S} p_i^2$$

where P_i is the proportion of the $_i$th species in the $_j$th sample, and S is the total number of species in the sample.

Resemblance measures detect the degree of similarity between any two samples. Similarity will be measured by two indices:

$$6)\quad SIMI_{1,2} = \frac{\sum_{i=1}^{S} P_{i1} P_{i2}}{\sqrt{\sum_{i=1}^{S} P_{i1}^2 \cdot \sum_{i=1}^{S} P_{i2}^2}}$$

where P_{i_1} and P_{i_2} are the proportions of each taxon in samples 1 and 2 (Stander, 1970). SIMI values range from 0, when samples have no taxa in common, to 1, when samples have same taxa and relative abundance.

$$7)\quad DIFF = \exp\left[H_T - \bar{H}''\right]$$

where H_T is the diversity if the two samples to be compared are pooled as one, and $\bar{H}''$ is the average of diversity of the two samples to be compared (MacArthur, 1965). DIFF values range from 1, when samples have same taxa and relative abundance, to 2, when samples have no taxa in common. These two statistics weight the taxa differently. SIMI gives more weight to the abundant taxa, while DIFF gives more weight to the rare taxa. These statistics were used to compare tips and bases of the same host plant to determine vertical zonation within the host plant, to compare the washings to the attached species, thus separating the metaphyton from the epiphyton, to compare replicate host plants for within host differences, and to compare pooled host plants from each site.

The niche breadth (Bj) of each taxon was measured from the expression:

$$8)\quad B_j = \exp\left[\sum_{i=1}^{K} \frac{P_{ij}}{R_j} \log_e \frac{P_{ij}}{R_j}\right]$$

$$\text{where } R_j = \sum_{i=1}^{K} P_{ij}$$

where P_{ij} is the proportion of each taxon (j) at a site (i) and R_j is the sum of the P_i for the $_j$th taxon at all sites (K) (McIntire and Overton, 1971). The value of Bj is an indication of the ability of a taxon to do equally well at all sites (i.e. host plants) and is not

necessarily related to its total relative abundance in all samples. Values of Bj range from 1 if a taxon is found at only one site or on one host plant, to K if it is equally common at K sites or K host plants. High Bj values would be predicted for species that do not discriminate between host plants, while low values would indicate the possibility of host specificity.

The diversity and redundancy measures were calculated using the AIDONE program at Oregon State University, while similarity, difference, and niche breadth measures were obtained with the AIDN or AIDNX program. Because of the constraints of the AIDN or AIDNX program regarding maximum number of blocks (i.e. samples) to be compared, the samples were pooled as follows:

1) To compare treatments (wash, tip, and base) within host plants, each site for each year was examined separately.

2) To determine within host plant variation, the treatments of each host plant collected during the second year were pooled to represent a composite count for the entire host plant. Replicate host plants were then compared.

3) To determine within year variation, the samples collected at the three sites the first year were compared together, while those collected the second year were compared together. In each case, the three treatments representing a single host plant were pooled to form a composite count for the entire host plant, and host plants were compared.

4) To determine between year variation, all samples collected at the three sites the first year were compared only to

those samples representing the second replicate collected at the three sites during the second year. The site where the second replicates were taken most closely corresponded to the site where the host plants were sampled the first year. Also, during the second year Bryocladia cuspidata was not collected at the site where the first replicates were taken in Galveston for May 1979. Fewer than 150 cells were present in the wash for the first replicate of Bryocladia cuspidata collected Sept 1978 from Port Isabel.

An analysis of variance in conjunction with a Duncan's multiple range test was performed to test the differences between the means of the SIMI values when the data were pooled by treatment and by plant.

Multivariate Analyses

Multivariate analyses are mathemathical tools that attempt to reduce the variation in community composition and in species relative abundance into identifiable patterns and to relate these patterns to environmental variables. By reducing the dimensionality of the community, biological interpretation of the ordination (i.e. arrangement of sites or species to environmental gradients) is often possible (Gauch et al., 1977).

Three types of ordination analyses commonly used in ecological studies today are: 1) polar ordination (PO), 2) principal components analysis (PCA), and 3) reciprocal averaging (RA) (Gauch et al., 1977). Advantages and disadvantages are noted below.

Polar ordination orders sites (species) by assigning two end points and placing all other observations relative to their degree of

dissimilarity to the end points. This ordination analysis is the least vulnerable to the natural curvilinear distribution of species along environmental gradients and is not usually subjected to involution and to distortion by clusters of samples and outliers. The major limitation to this analysis is its subjective end point choice.

Principal components analysis views sites (species) as points in a multidimensional space whose positions can be projected onto an axis. The PCA algorithm generates new axes, orthogonal from the previous ones, from linear combinations of the original variables (Gauch, 1982). Each new axis will maximize the variance within the group of variables. PCA unpredictably distorts clusters of samples and can distort large communities into complex surfaces because it is not mathematically appropriate for ordination of the curvilinear and non-monotonic relationships common to community gradients (Gauch et al., 1977).

Reciprocal Averaging is a weighted average ordination achieved by successive approximations (Gauch et al., 1977). Species are weighted by positions along an initial gradient, and these weights are used to ordinate samples. The weighted sample scores are then used to calculate new weighted species ordinations. This procedure is repeated back and forth until an optimal ordination is reached. This analysis is not as prone to distortion as PCA, yet has the advantage of objectively selecting end points, which is not available with PO. RA commonly distorts the major axis of sample variation into an arch in the second axis of ordination, but is the technique of choice for indirect ordination to reveal a first, major direction of sample

variation in response to environmental gradients.

RESULTS

Analyses of Environmental Data

Water temperatures for the sampling period ranged from 7.7°C to 31°C at Galveston, from 7.7°C to 30°C at Port Aransas, and from 11.5°C to 28.8°C at Port Isabel (Fig. 3). Because of the wide water temperature range characteristic of this region, the Texas coast supports a warm temperate macroalgal flora. For most of the year, while water temperatures are high, a tropical flora of Carribbean affinity dominates. As temperatures drop during the winter, the tropical floras become senescent and are replaced by cool temperate forms of North Atlantic affinity (Edwards and Kapraun, 1973).

Salinity values for the sampling period ranged from 19 to 35 o/oo at Galveston, from 22 o/oo to 38 o/oo at Port Aransas, and from 28 o/oo to 38 o/oo at Port Isabel (Fig. 4). This distinct reduction in the annual salinity range at the three collection sites can be related to the amount of freshwater input characteristic of each basin. The water at Port Isabel can be hypersaline for several months during the summer.

Comparison of Host Plant Shapes

During the first year, macroalgae representing various taxonomic groups, thallus shapes, and locations in the intertidal zone were collected (Table II, see pg. 24). Although cell counts were made only from selected species of host plants, qualitative observations from all those plants collected are useful to determine a relative

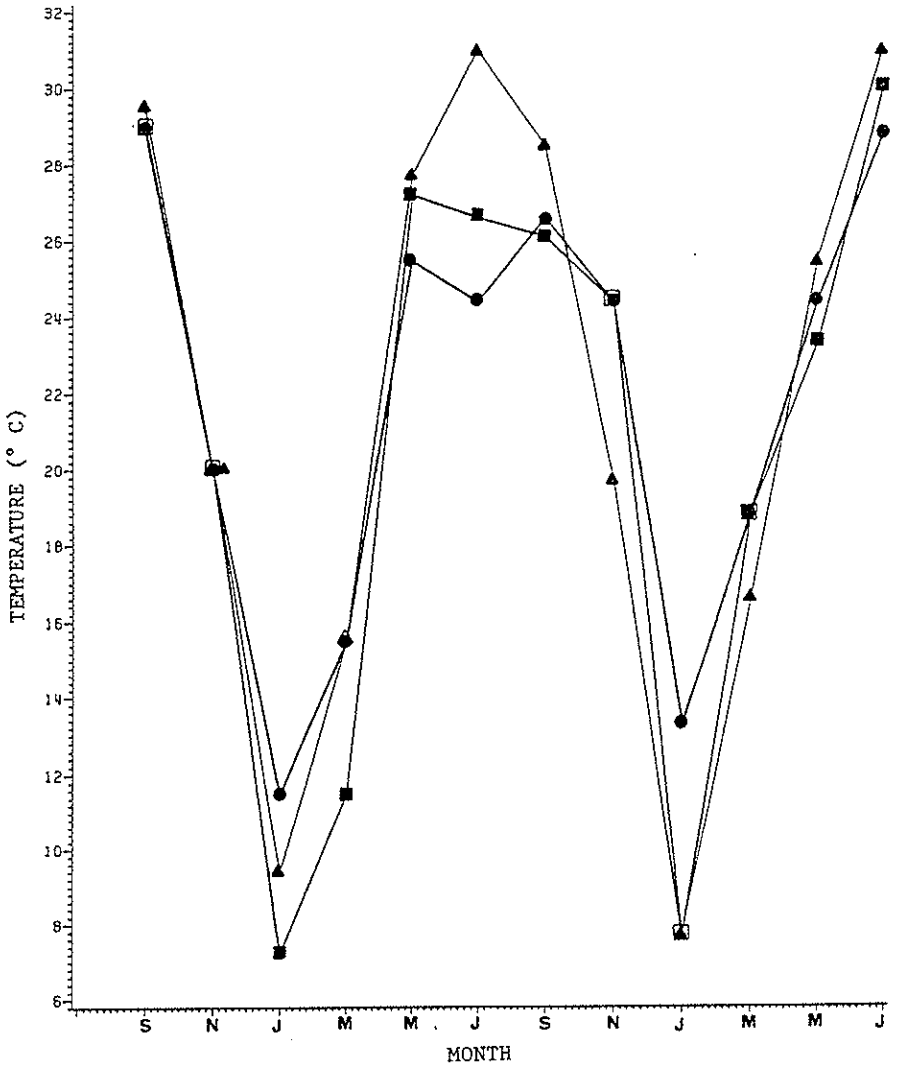


Figure 3. Water temperatures at Galveston (▲), Port Aransas (■), and Port Isabel (●) for the two year study period.

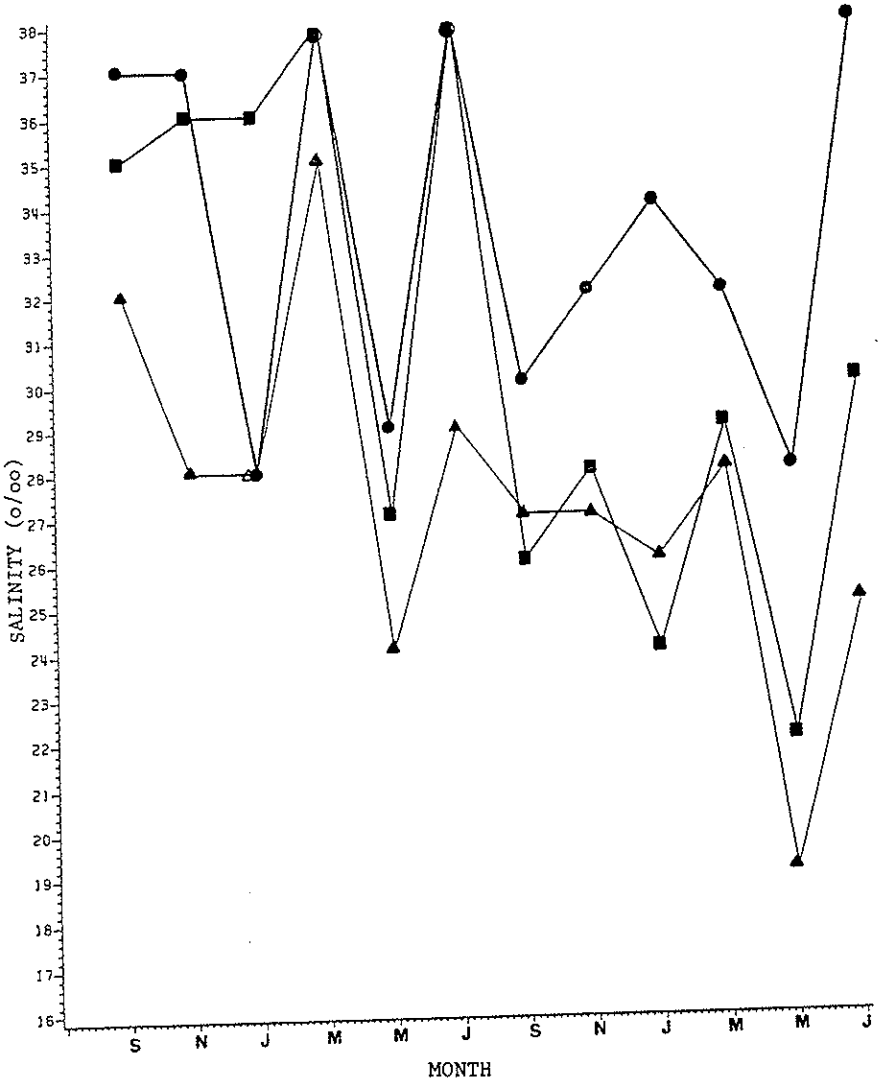


Figure 4. Salinity at Galveston (▲), Port Aransas (■), and Port Isabel (●) for the two year study period.

variation within the epiphytic community.

At the high intertidal-splash zone level, I collected at Galveston (Fall, 1977 and Spring 1978), the filamentous algae, Cladophora dalmatica, Chaetomorpha linum (Chlorophyceae) and the foliose alga, Enteromorpha lingulata (Chlorophyceae). In addition, at Port Aransas and Port Isabel, I collected a pseudofilamentous alga, Centroceras clavulatum (Rhodophyceae), and other species of Cladophora. No filamentous algae belonging to the Phaeophyceae were collected, although they were present, primarily in the winter (Edwards, 1970).

The distribution and abundance of the diatoms on these host plants varied considerably. Chaetomorpha, in the splash zone, occupied a position where it was subject to the strongest light intensity and the longest periods of desiccation. Diatoms were present on the plant and increased in numbers and in diversity toward the base. Cocconeis scutellum was a dominant colonizer in the spring, and it was replaced by a more diverse assemblage during the summer. Cladophora spp., collected from the high intertidal, are highly branched plants, and the diatoms seemed to prefer settling within the forks or on the inner surface of the many branches of these macroalgae. Also, these host plants received more impact from waves than those plants in the splash zone, which may account for the increased settlement within the protected areas on the plant. There were often only two or three dominant species present on the tips, while the diversity and relative abundance of the diatom community increased toward the base. Cocconeis spp. were noticeably missing or

reduced in numbers on Cladophora, while nearby hydroids (even those attached to Cladophora) would be covered with them. Freshwater species of Cladophora are commonly epiphytized by Cocconeis (Rosen et al., 1982; Patrick, 1977). Enteromorpha lingulata was usually barren of epiphytes. Occasionally, isolated cells were found on this host plant. However, during the winter, it, too, could be colonized, primarily at the base of the host plant. Clusters of cells were usually widely spaced. Often the holdfast area and the branches in the immediate vicinity would become intertwined with tube dwelling Navicula.

Centroceras clavulatum, collected only from Port Aransas and Port Isabel, was colonized in a repeatable spatial pattern with increasing diversity and relative abundance of the diatoms toward the macroalgal base. Because this pattern was unique, it was studied in greater detail using SEM and will be discussed in another section.

During the winter of 1977 another filamentous alga, Bangia fuscopurpurea (Rhodophyceae) was collected from the splash zone. Few epiphytes were ever found on this alga, an observation previously reported for Bangia in the Great Lakes (Rosen et al., 1982).

From the mid-intertidal zone, algae representing several host plant shapes, all from the Class Rhodophyceae, were collected (Table II, see pg. 24). Bryocladia cuspidata (cylindrical shape with many branchlets) proved to be the most heavily epiphytized host plant, often being completely engulfed with a deep golden brown layer of diatoms. The epiphytic community on Bryocladia was most prolific toward the tips; the diatom species present on the branchlets often

differed from those on the main axis. The spiral arrangement of the branchlets along the main axis offered a trap for settling silt particles and other living cells. Navicula spp., which are more commonly associated with the sediments, and small Thalassiosira spp., which are planktonic, were seen among the branches. These species are not directly attached to the host plant and therefore would have to be considered part of the metaphytic community. Oscillatoria was a common epiphyte on Bryocladia in Port Aransas during the spring of 1978 and 1979, where it also grew in a distinct vegetation belt along the upper intertidal zone (Medlin, submitted). The unique spatial arrangement of the epiphytes on Bryocladia was also studied in detail using SEM.

Hypnea musciformis (cylindrical plant with widely spaced, recurved branches) occurred in late spring and was usually free of epiphytes except near the holdfast. Throughout the summer, epiphyte coverage increased, with settlement of stalked forms primarily clumped within forks or along the inner side of a branch or in injured (? grazed) areas. Cocconeis dominated the more exposed areas of the thallus. When Hypnea completed its growing season (late winter in Port Aransas or early spring in Port Isabel), the entire thallus could be overgrown with epiphytes.

Gelidium crinale (cylindrical to flattened plant with few pinnate branches) was most commonly epiphytized by Cocconeis spp. Rhoicosphenia genuflexa and Grammatophora oceanica were concentrated within forks and wound areas on the thallus. Bryozoans were also plentiful on this alga. Often the entire surface was covered with a

unicelluar blue-green or green epiphyte. Because epiphyte settlement on this alga offered such a contrast to that on Bryocladia and Centroceras, a study of settlement patterns was also done with SEM.

Both Petalonia fascia (foliose Phaeophycean occurring in winter) and Porphyra leucosticta (foliose Rhodophycean also occurring in winter) were sparingly colonized. The holdfast area of Petalonia could be moderately colonized with diatoms.

Foliose host plants were primarily collected from the lower intertidal or subtidal zone. Rhodymenia pseudopalmata (Rhodophyceae), Dictyota dichotoma, and Padina vickersiae (Phaeophyceae), each displayed similar settlement patterns. Early spring growth retarded diatom settlement near the tips where the meristem was located but not at the base. With time more of the plant was colonized, especially on Padina and Rhodymenia. Cocconeis spp. were common near the tips. Other epiphytes (macroalgal, microalgal and hydoids) were prevalent nearer the holdfast as the macroalga aged. Many naviculoid diatoms, as well as Nitzschia and Amphora species were embedded in mucilage near the plant base or attached directly by the cell apex; Rh. genuflexa was attached without a stipe. Often stalked or stiped cells were more common around the plant margins (especially on Rhodymenia). Sometimes stalked or stiped diatoms could be found only on filamentous algae or hydroids, themselves epiphytic on the larger host plant, while being noticeably absent or reduced in numbers on the foliose plant. Both Padina and Dictyota form reproductive structures known as sori, which are small bumps or warts on the surface of the macroalga occurring during the summer. Small naviculoid cells,

presumably Navicula diserta, were often clustered around the base of these reproductive structures.

Haliptylon subulata (cylindrical or flattened plant with fan-shaped branches) was also collected subtidally from Port Aransas and Port Isabel. As the only calcified alga collected, epiphyte settlement appeared to be related to those areas of calcification. For example, a wide variety of diatoms occurred between the nodes and within the branches of this macroalga where host tissue was not calcified. On the calcified nodes, Cocconeis spp. dominated; Grammatophora, attaching by a mucilage pad, occurred randomly over the host plant. Epiphyte coverage decreased toward the base; however during late winter-early spring the entire plant could be covered with epiphytes as the growing season of the host plant terminated.

During the winter at Port Isabel, the filamentous alga, Polysiphonia denudata, occurred subtidally but was essentially free of epiphytes.

Community Composition Parameters

The epiphytic diatom community sampled over the two year period from September 1977 to July 1979 contained a total of 351 taxa (species and varieties of species representing 68 genera) (Appendix A). The majority of these taxon accounted for less than 20% of the cells present and were usually represented by 5 or fewer individuals in any one sample. The most commonly encountered taxa for the two year sampling period (year 1, year 2) were: Rhoicosphenia genuflexa (20%,27%), Navicula diserta (11%,10%), Cocconeis scutellum (9%,6%),

Grammatophora oceanica (6%,8%), Navicula stompsii (4%,5%), Nitzschia frustulum (4%,4%), Synedra fasciculata v. truncata (3%,5%), Thalassiosira cf. profunda (5%,3%), Licmophora abbreviata (7%,1%), Cymatosira belgica (4%,2%), Navicula pseudocomoides (2%,3%), Amphora acutiuscula (2%,2%), lineate Thalassiosira sp. (1%,2%).

These taxa are illustrated in Fig. 5 and 6.. Thalassiosira cf. profunda is a small centric, diameter 7-8 μm with 4-5 marginal strutted processes and one central strutted process. When samples abundant in this taxon were examined with the SEM several other small centrics of this size range were also found, although not as abundant as Thalassiosira cf. profunda. Because of the silt common in all of the samples, the image of this small centric was often partly obscured. Thus, the counts representing T. cf. profunda most probably contain other taxa.

These taxa, plus 34 others, were chosen for the multivariate analyses and accounted for over 90% of all valves counted. In this study most of the rare taxa encountered were in the wash where presumably they were deposited within the branches of the host plant by wave action and subsequent settling. These diatoms were primarily from the epipelic assemblage, Chaetoceros or unidentified spores and other centrics from the plankton. Chaetoceros spores were most commonly found at Port Isabel during May of the second year. Thus, it seemed more appropriate to use the common taxa in these analyses because they contained the most information about the diatom assemblage associated with each host plant.

Diversity within the epiphytic community was calculated for each treatment of the host plant, as well as for the composite count of each host plant. In general the composite species diversity was high on each host plant, with values ranging from 1.74 to 4.67 (Appendix B). A maximum of 86 taxa was found on Gelidium crinale collected from Galveston in January 1978. The diatom diversity within the individual treatments of each host plant was more variable than that between host plants.

For Cladophora dalmatica, collected year-round in Galveston and during the spring in Port Aransas and Port Isabel, and for Centroceras clavulatum, collected during the fall and winter at Port Aransas and Port Isabel, the diversity of the wash was usually greater than either the tips or the bases (Fig. 7). Diversity was lowest on the tips and increased toward the base. One to four times more taxa were present in the wash than on the tips (Fig. 8).

The same diversity pattern was common with Gelidium crinale (Fig. 9), but the number of taxa in the wash usually ranged from one to two and a half times that found on the tips and often equaled that found on the base (Fig. 10). On Bryocladia cuspidata the entire diatom community was more abundant than on the other host plants. Although there was generally an increase in diversity from tip to base of the plant (Fig. 11), the number of taxa present was quite similar (Fig. 12). The wash usually has only a few more taxa and was usually not significantly more diverse.

Redundancy values greater than .500 were more frequently encountered on Cladophora dalmatica and on Centroceras clavulatum than

Figure 5. Light microscope photographs of selected taxa. Part I. Centrics and Araphids. Scale bar = 10 μm. Scale 1 for a,b,e-g,i-k. Scale 2 for h. Scale 3 for c,d.

a. Thalassiosira cf. profunda

b. small lineate Thalassiosira sp.

c. Minidiscus sp.

d. Cyclotella atomus

e. Cymatosira belgica

f. Grammatophora oceanica, valve view

g. as above, girdle view

h. Neodelphineis pelagica

i. Synedra fasciculata v. truncata

j. Licmophora abbreviata, girdle view

k. as above, valve view

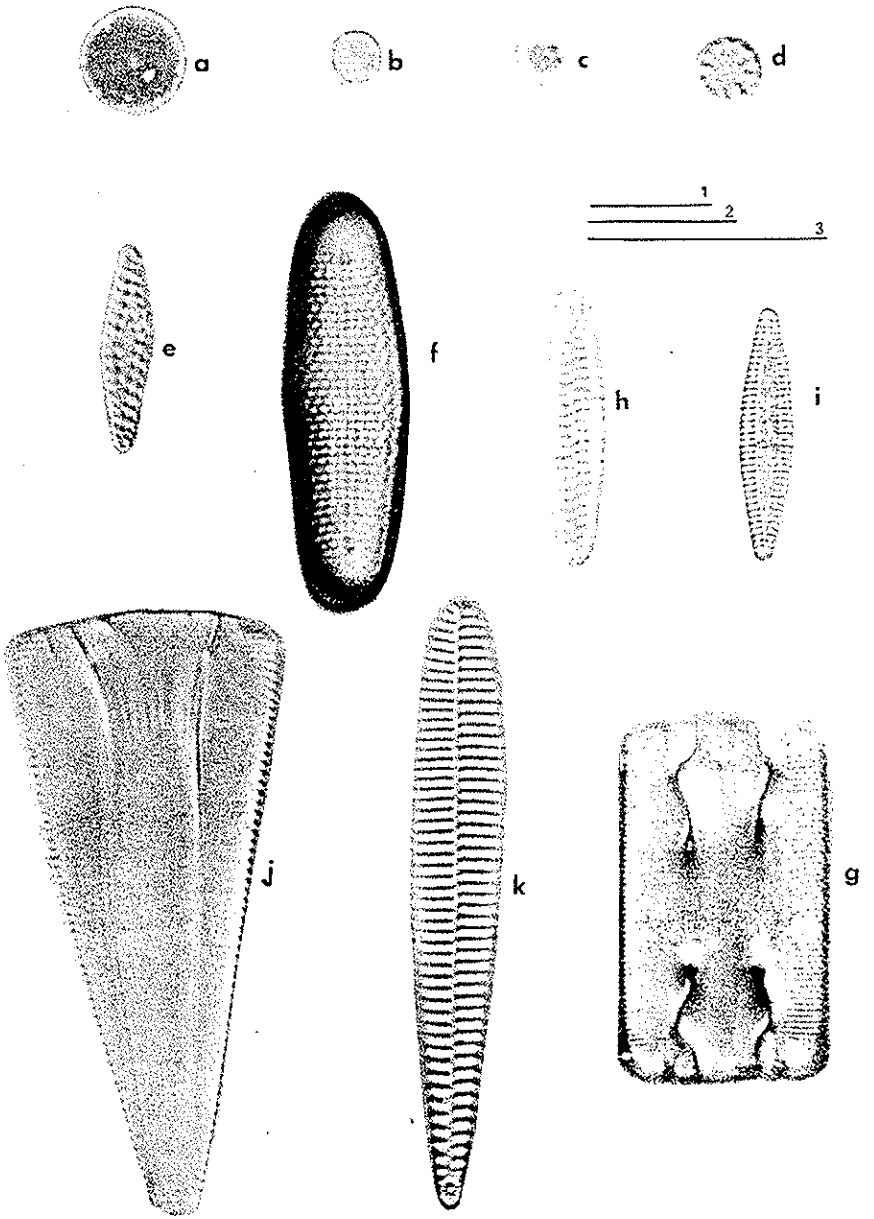
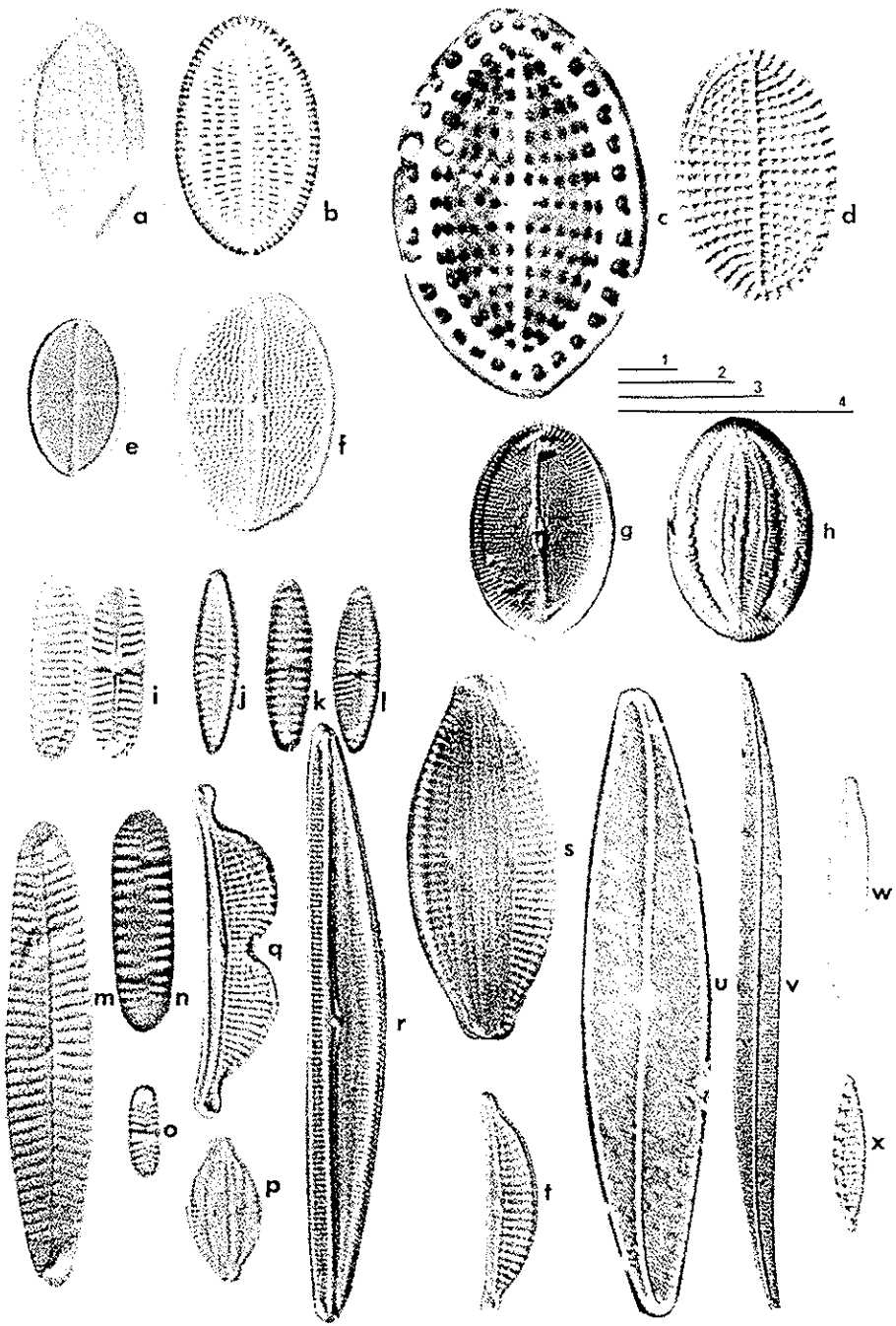


Figure 6. Light microscope photographs of selected taxa. Part II. Monoraphids and Biraphids. Scale bar = 10 μm. Scale 1 for u,v. Scale 2 for a-j,l,m,o-t,w. Scale 3 for n,x. Scale 4 for k.

a. Cocconeis placentula v. euglypta
b. as above, rapheless valve
c. Cocconeis scutellum raphe valve
d. as above, rapheless valve
e. Cocconeis cf. dirupta, raphe valve
f. as above, rapheless valve
g. Cocconeis littoralis, raphe valve
h. as above, rapheless valve
i. Achnanthes brevipes v. intermedia, both valves
j. Navicula agnita
k. Navicula diserta
l. Navicula pseudocomoides
m. Navicula stompsii
n. Rhoicosphenia genuflexa, diminutive raphe valve
o. as above, raphe valve
p. Amphora tenerrima
q. Amphora bigibba
r. Amphora cymbelloides
s. Amphora acutiuscula, girdle view
t. as above, valve view
u. Pleurosigma barbadense
v. Gyrosigma sp. 1
w. Nitzschia incrustans
x. Nitzschia frustulum



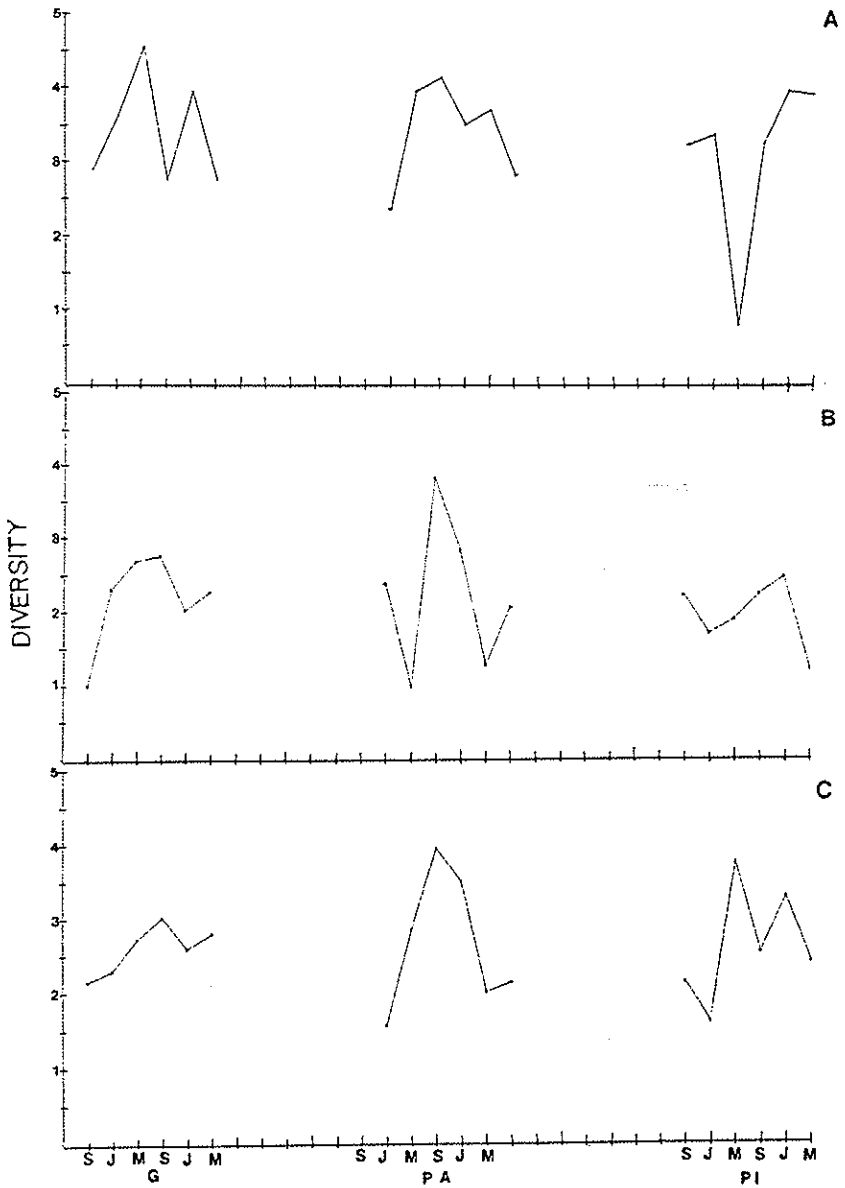


Figure 7. Diversity (H") of the wash, tips, and bases of Cladophora dalmatica and Centroceras clavulatum. C. dalmatica collected all months in Galveston and in May at Port Aransas and Port Isabel. C. clavulatum collected in September and January at Port Aransas and Port Isabel. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

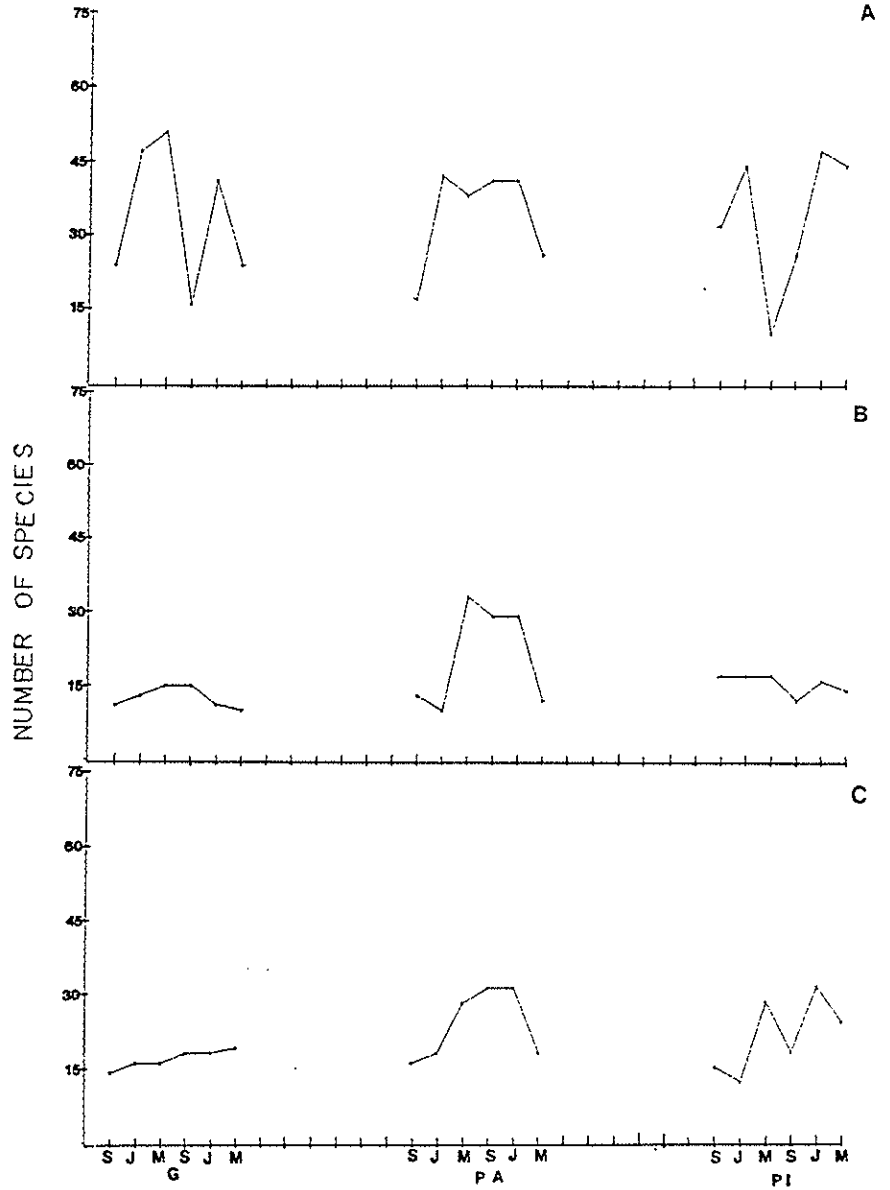


Figure 8. Number of taxa in the wash, tips, and bases of Cladophora dalmatica and Centroceras clavulatum. C. dalmatica collected all months in Galveston and in May at Port Aransas and Port Isabel. C. clavulatum collected in September and January at Port Aransas and Port Isabel. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

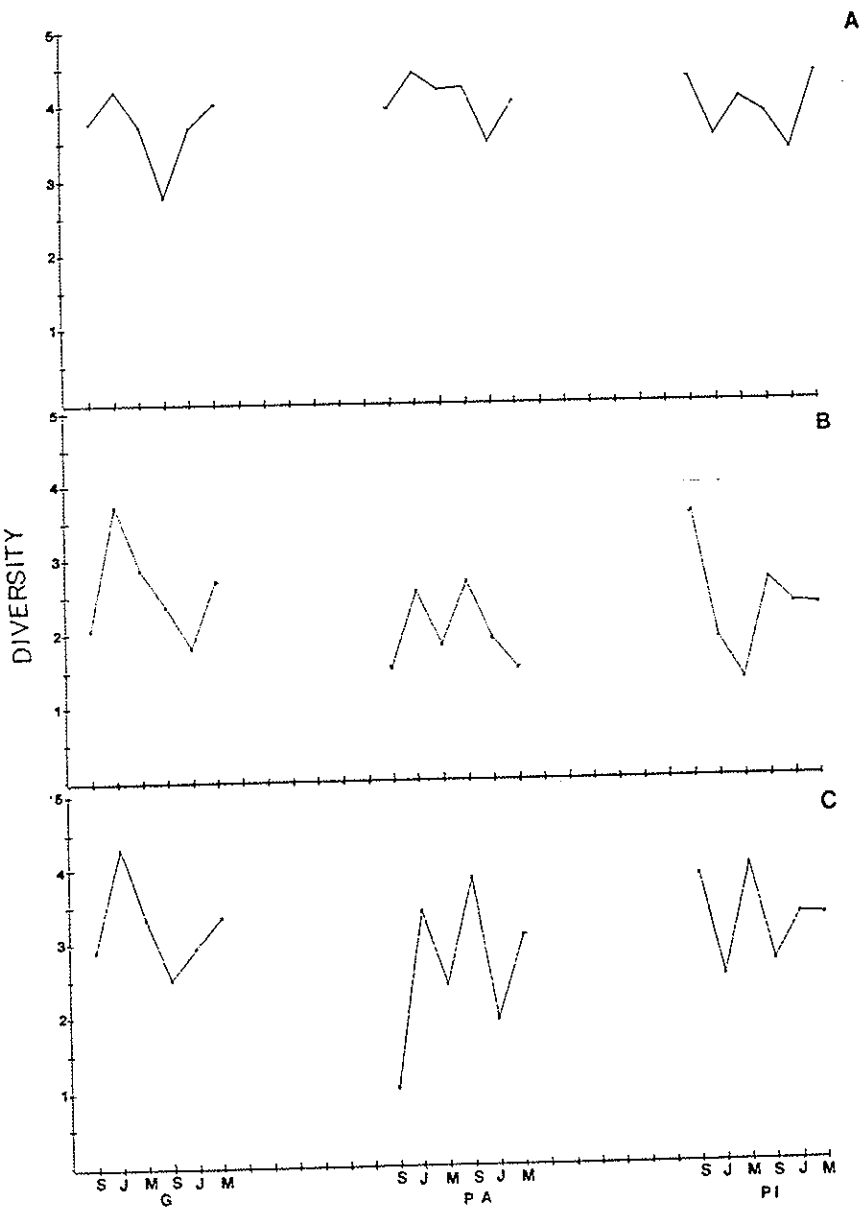


Figure 9. Diversity (H") of the wash, tips, and bases of Gelidium crinale. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

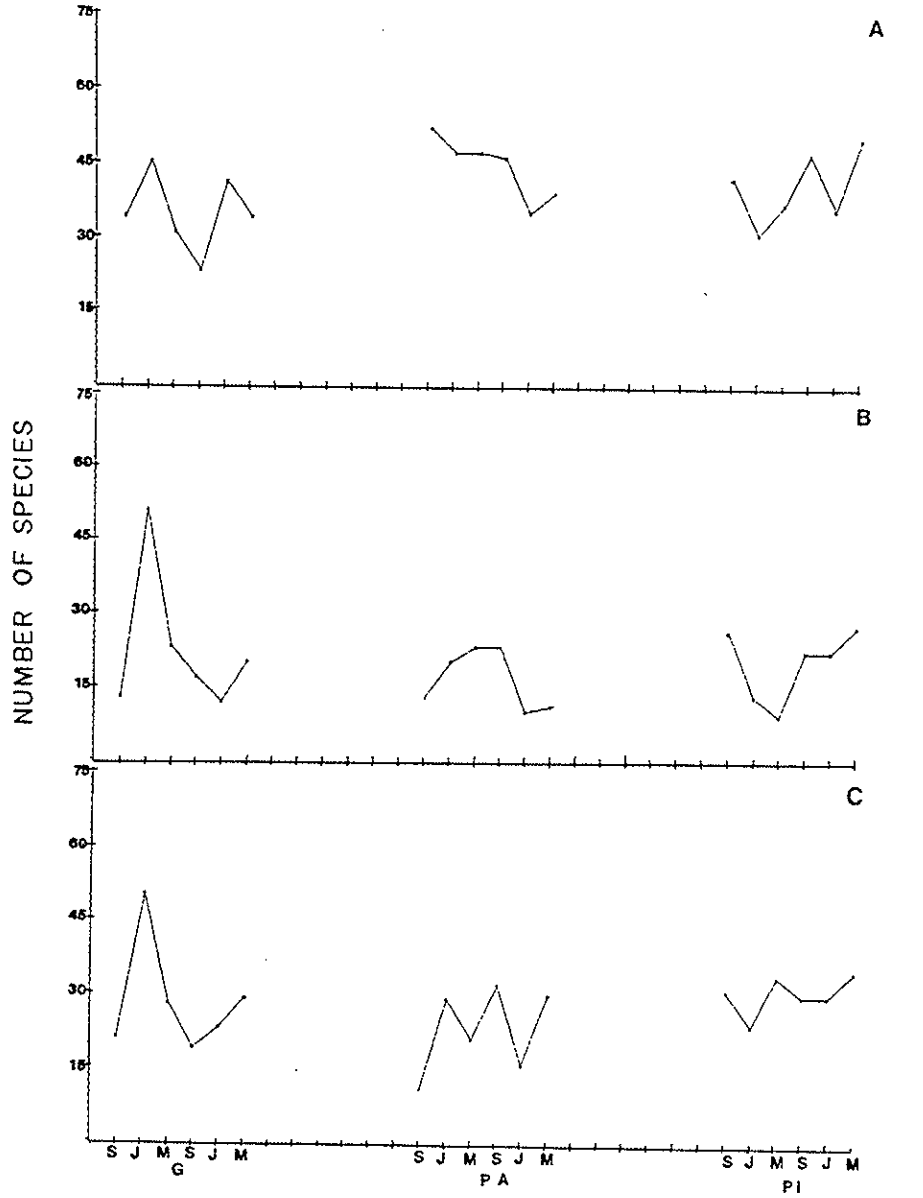


Figure 10. Number of taxa in the wash, tips, and bases of Gelidium crinale. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

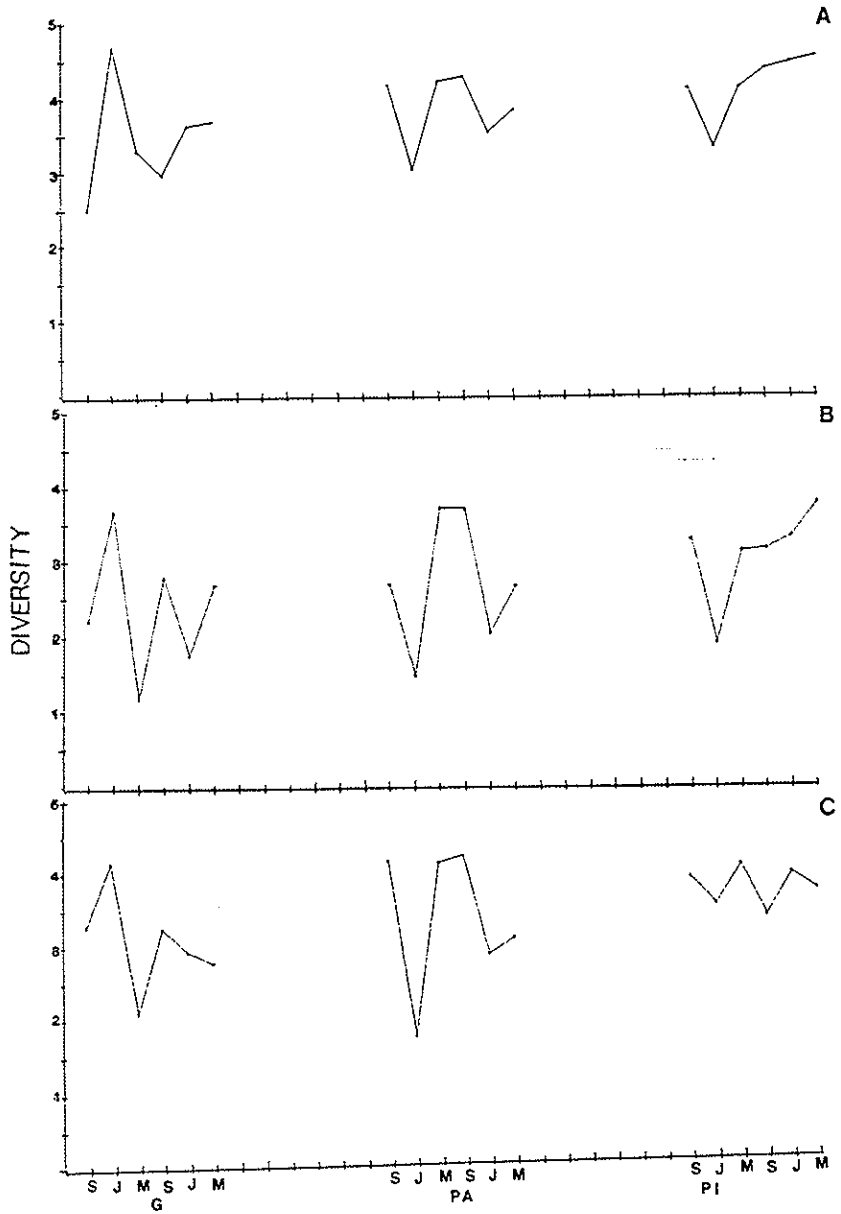


Figure 11. Diversity (H") of the wash, tips, and bases of Bryocladia cuspidata. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

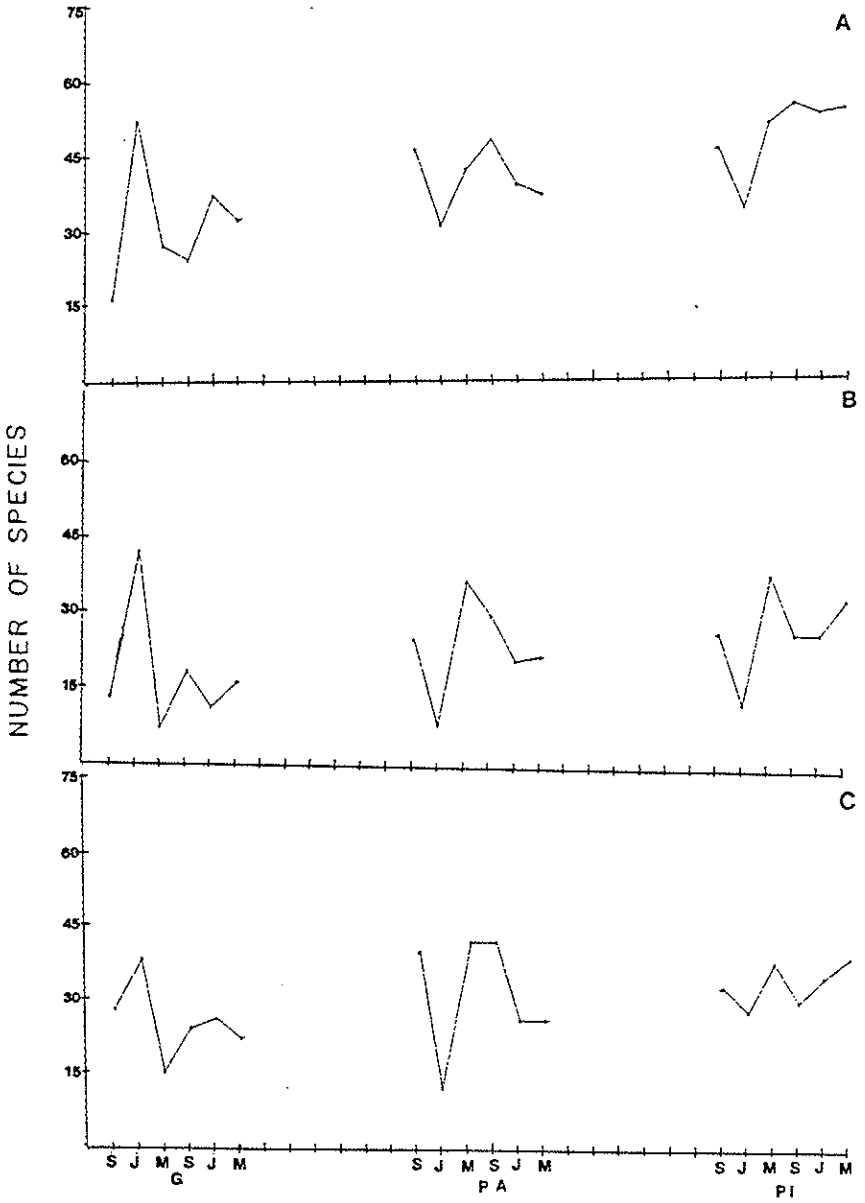


Figure 12. Number of taxa in the wash, tips, and bases of Bryocladia cuspidata. (A = wash, B = tips, C = bases) S = September, J = January, M = May; Replicates during the second year were averaged.

on the other two host plants (Appendix B).

If the data are pooled by treatment (wash, tip, or base) for each site, relative abundance of the dominate species and their niche breadth (Appendix C) in each treatment can be compared. The niche breadth values ranged from 1, if the taxon was present only in one portion of the plant, to 3 if equally represented in the wash and on the tips and bases of the host plant.

Certain taxa, such as Thalassiosira cf. profunda and the small lineate Thalassiosira sp., were more common in the wash (Fig. 13) (average Bj = 2.67). These taxa, which are planktonic (unpublished observations), undoubtedly have been trapped within the branches and mucilaginous waters surrounding the host plant and have continued to thrive there. Cymatosira belgica can be found not only in the plankton but also in the sediments and should probably be considered tychoplanktonic. Cymatosira belgica was easily washed off the host plant probably from the base of the plant where it was more numerous (Fig. 14).

These taxa had an average niche breadth of 2.03, 2.21, and 2.56, respectively. These three species, which were numerically important, along with others less prominent (such as Pleurosigma spp., Gyrosigma spp., and many of the Navicula spp. seen infrequently) are major components of the unattached community, the metaphyton, on the host plants. Choanoflagellates were also found in the wash.

Species that were more abundant on the tips of the plants were Achnanthes brevipes v. intermedia, Cocconeis scutellum, Grammatophora oceanica, and Licmophora abbreviata (Figs. 14,15,18, see pg. 61 for

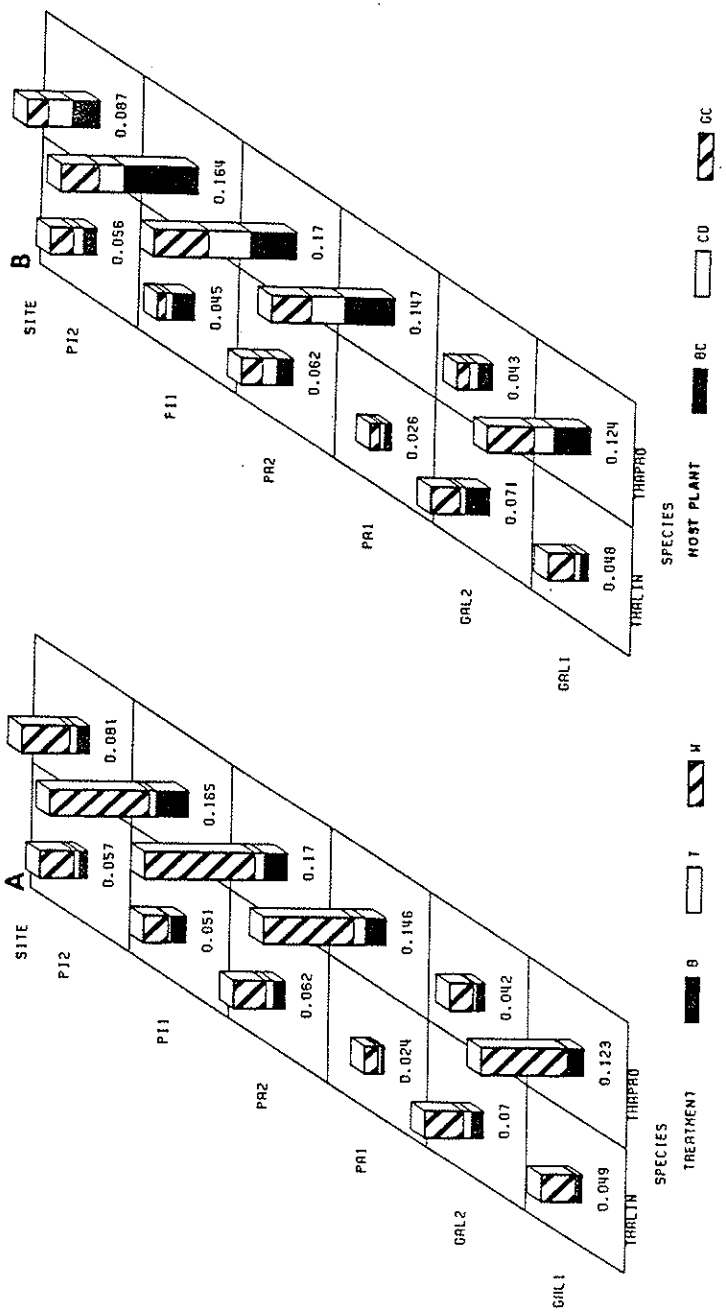


Figure 13. Relative abundance of Thalassiosira cf. profunda and lineate Thalassiosira sp. by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. GAL = Galveston, PA = Port Aransas, PI = Port Isabel. 1 = year one, 2 = year two. W = Wash, T = Tips, B = Base. BC = Bryocladia cuspidata, CD = Cladophora dalmatica and/or Centroceras clavulatum (see text for explanation), GC = Gelidium crinale. The total beneath each bar represents the summation of the relative abundances for each category.

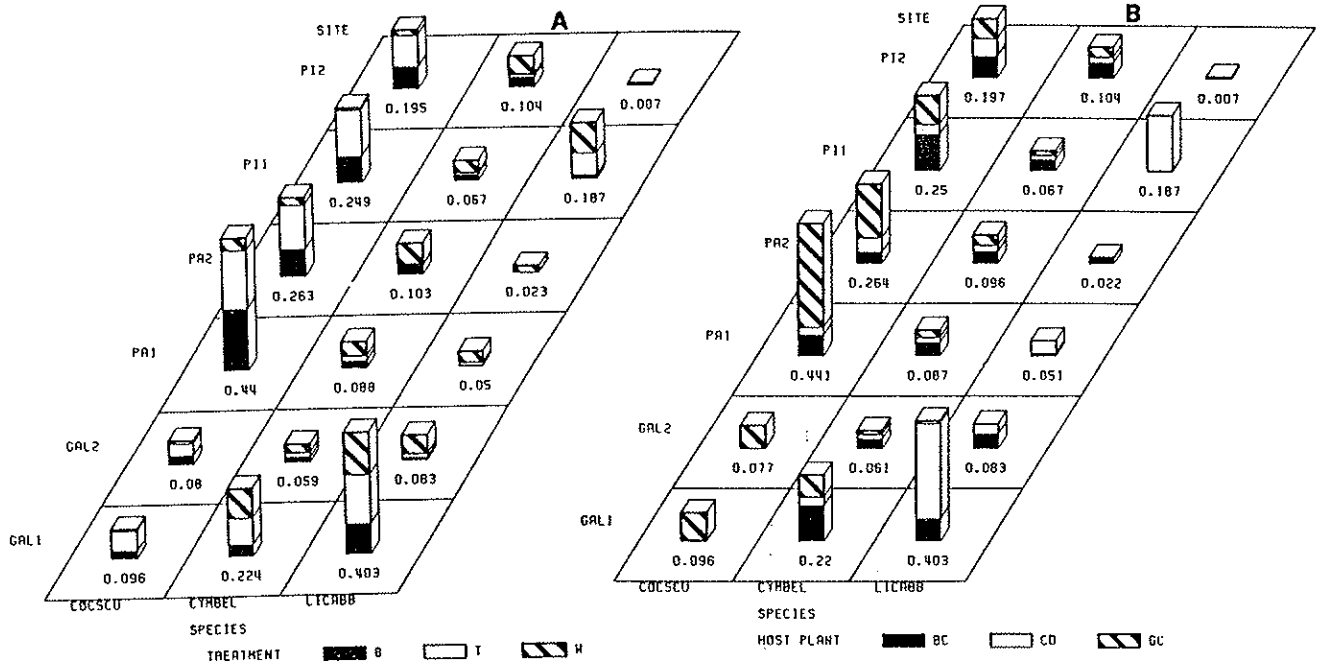


Figure 14. Relative abundance of Cocconeis scutellum, Licmophora abbreviata, and Cymatosira belgica by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. All other symbols as in Fig. 13.

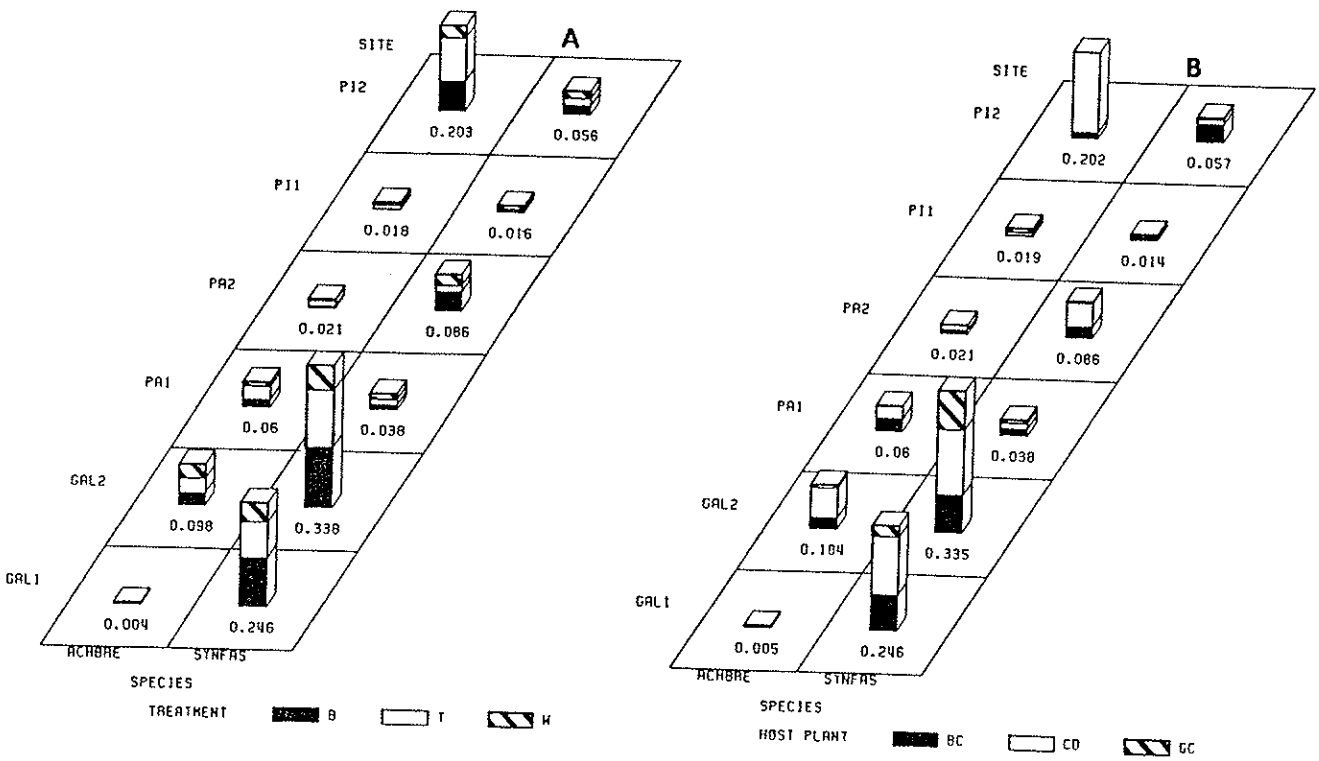


Figure 15. Relative abundance of Achnanthes brevipes v. intermedia and Synedra fasciculata v. truncata by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. All other symbols as for Fig. 13.

Fig. 18) (but see comments on Licmophora below). These taxa had an average niche breadth of 2.69, 2.35, 2.7, and 1.97, respectively.

Other taxa, whose distributions were more concentrated at the base of the host plant, were Navicula pseudocomoides and Nitzschia frustulum (Fig. 16). In Galveston, N. frustulum was more common on the bases and in the washes of the plants, but in Port Isabel, it was increasingly more important numerically and more equally distributed throughout the plant. The niche breadth of N. frustulum reflects this change as it changed from 2.64 to 2.95 along the coast from Galveston to Port Isabel.

Amphora acutiuscula and Amphora tenerrima were more prevalent at the bases of the host plants in Galveston and Port Aransas, but their abundance dramatically increased and their distribution spread more to the tips of the host plants at Port Isabel (Fig. 17). The distribution of Synedra fasciculata v. truncata was just the opposite (Fig. 15). It was quite abundant in Galveston, but decreased in importance southward.

Rhoicosphenia genuflexa, Navicula diserta, and Navicula stompsii were equally distributed throughout the tips and bases of the host plants (average Bj = 2.8, 2.93, and 2.91, respectively), and their abundance in the wash reflected the means of attachment to the host plant (Figs. 18,19). Navicula stompsii, a tube dwelling species, was commonly washed from the plant, perhaps, because the tubes were intermingled within the branches of the host plants. Navicula diserta, which was attached by its apex to the plant surface, was also readily removed from the host plant. The tensile strength of the

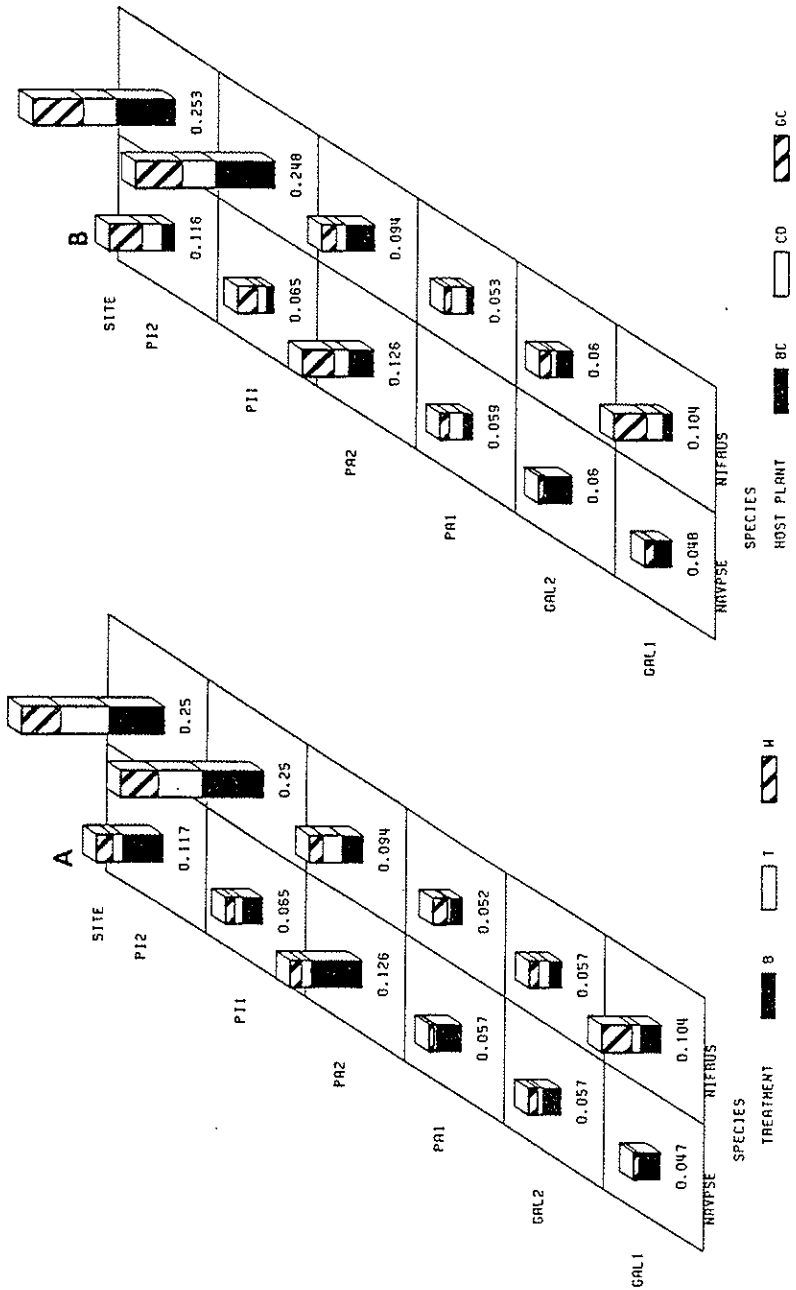


Figure 16. Relative abundance of Navicula pseudocomoides and Nitzschia frustulum by treatment and by plant. A = Pooled by Treatment, B = Pooled by Plant. All other symbols as for Fig. 13.

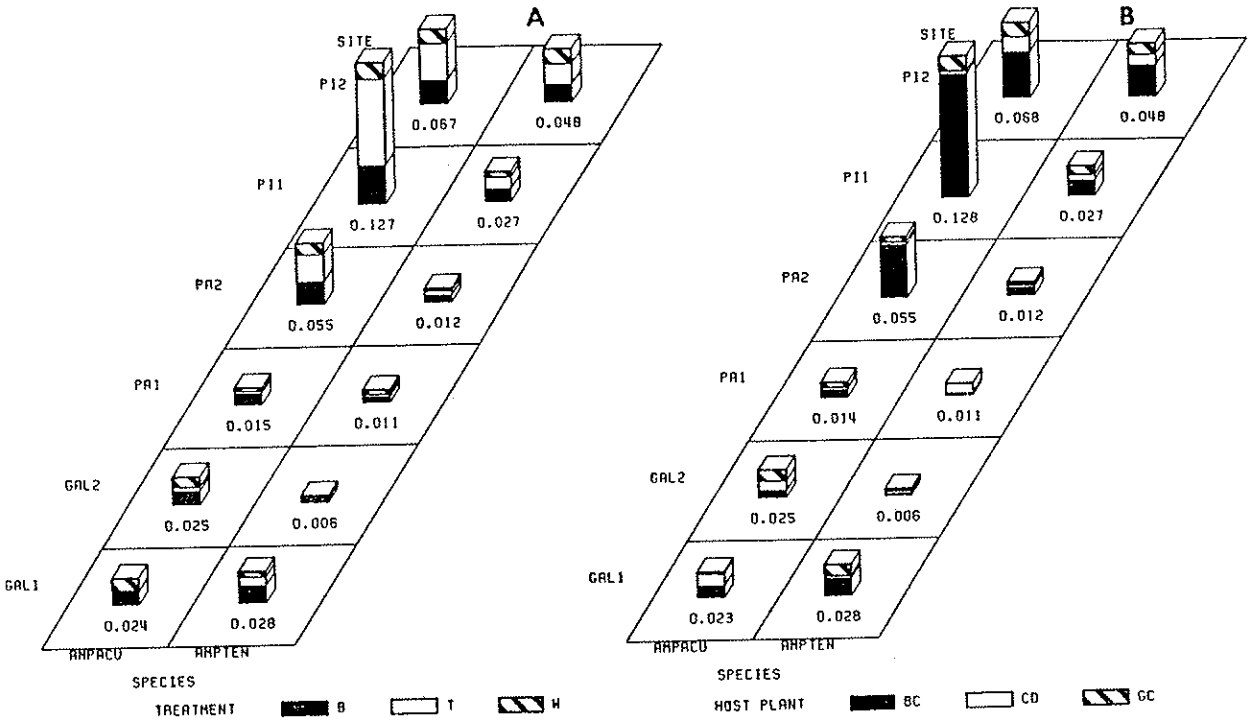


Figure 17. Relative abundance of Amphora acutiuscula and Amphora tenerrima by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. All other symbols as for Fig. 13.

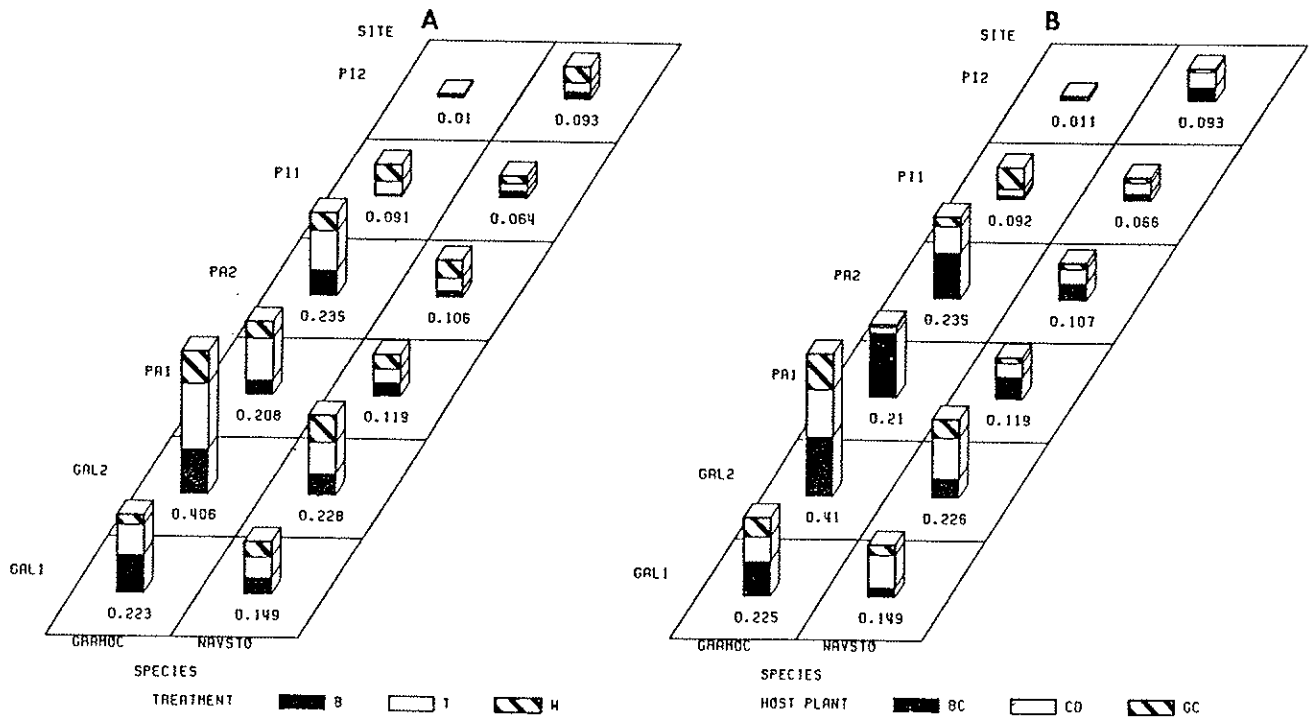


Figure 18. Relative abundance of Grammatophora oceanica and Navicula stompsii by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. All other symbols as for Fig. 13.

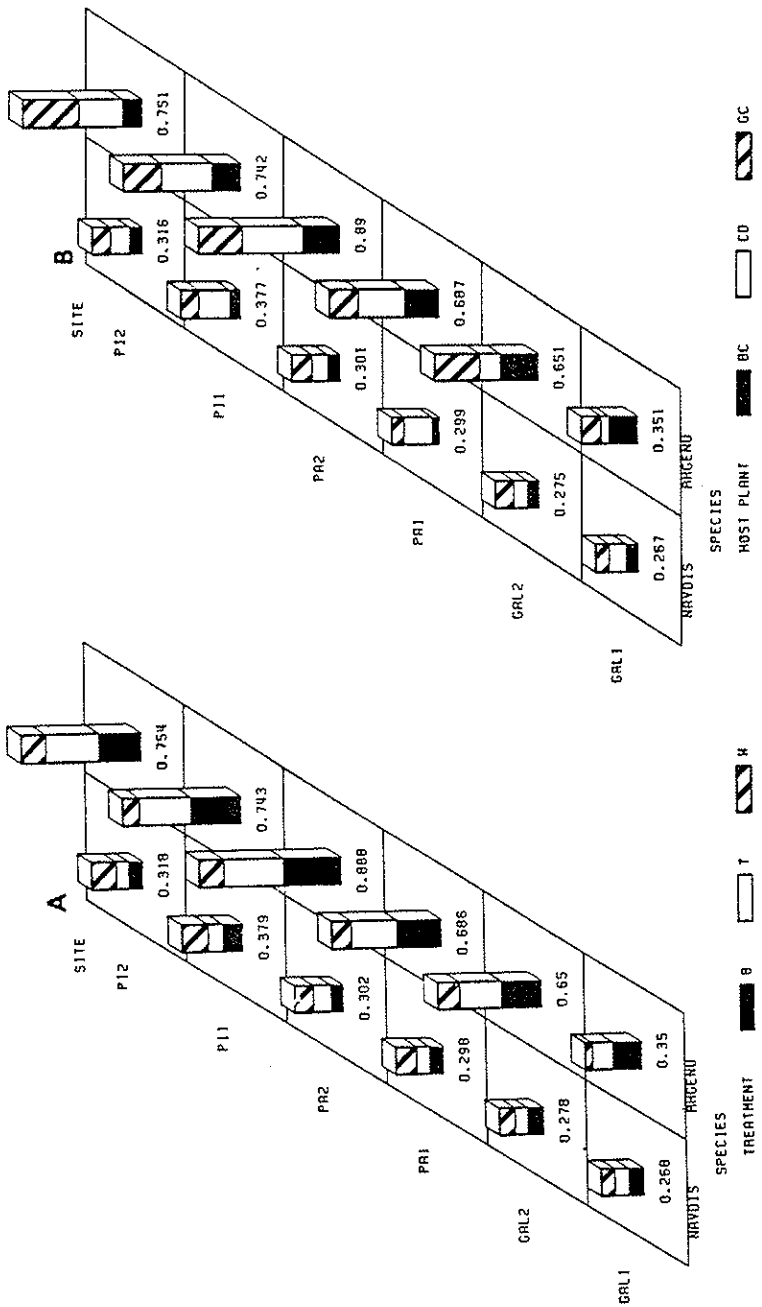


Figure 19. Relative abundance of Navicula diserta and Rhoicosphenia genuflexa by treatment and by plant. A = Pooled by Treatment. B = Pooled by Plant. All other symbols as for Fig. 13.

short mucilage stipe of Rhoicosphenia genuflexa enabled it to be more securely fastened to the host plant, thus attributing to its lower numbers in the wash.

The strength of the cell's attachment mechanism may be species specific. The numbers of those taxa belonging to the metaphyton would be expected to be greater in the wash, while true epiphytes would be more concentrated on the plant substrate. For example, of those species that attach directly to the host surface by the raphe (Cocconeis scutellum, Amphora acutiuscula, Amphora tenerrima), fewer cells of C. scutellum were found in the wash than the other two taxa. Presumably these are mostly rapheless valves, because host epidermal tissue grows around the raphe valve, which is attached to the plant substrate. Empty raphe valves still remain attached to the host plant long after the cell has died, and the rapheless valve sloughed.

The mucilage pads attaching Grammatophora oceanica and Synedra fasciculata v. truncata and the short mucilage stipe of Achnanthes brevipes v. intermedia are fairly effective attachment means (compare relative abundance in each treatment). However, by comparison, Licmophora abbreviata was more numerous in the wash than on the plant because the cells were easily broken loose from their longer stipe. During this study, dead or empty cells of Licmophora were never found attached to their stipe.

SIMI values were used to compare the similarity of the species assemblages associated with each treatment of each host plant. The variation in SIMI values throughout the year at each site reflected the changes in the relative abundances of primarily the major taxa.

During the first year at Galveston, the species assemblages washing off the host plants were significantly different from those attached to Bryocladia and Gelidium in September and May, while that washing off Cladophora more closely resembled the assemblages on the plant (Fig. 20). One primary reason for this similarity was the ease with which Licmophora cells were broken off their stipe, thus biasing the assemblage washing off Cladophora. Washes and host plant assemblages were most alike during January. The only plant to exhibit a distinct zonation pattern for the attached flora was Bryocladia during May.

This pattern was repeated the second year at Galveston (Fig. 20) and at Port Aransas both years (Fig. 21), although not as distinctly. Differences between tips and bases of the host plants were not found except on Gelidium in the spring of the second year and on Cladophora in the spring of the first year.

Centroceras was collected during September and January, but was replaced in the upper intertidal by Cladophora in May at Port Aransas. The assemblages washing off Centroceras during the winter of both years was not comparable to that found on the host plant itself.

The species assemblages within the host plants at Port Isabel are very dissimilar for both years (Fig. 22). During the first year, washes were incompatible with the host substrate for Gelidium, Bryocladia, and Centroceras in September and for Gelidium and Bryocladia in May. During January, all portions of Gelidium were unrelated to one another. Cladophora exhibited a distinct zonation pattern in May. The wash was very similar to the tips again because

Licmophora cells were broken loose from their stipes. The species assemblages within each host plant were remarkably similar during the second year. That washing off Centroceras in the fall and off Cladophora in the spring displayed the most dissimilarity to the other portions of the plants.

When the data were pooled by host plants, the relative abundance of the dominant taxa and their niche breadth (Appendix C) can be compared between plants. Niche breadth values ranged from 1, if the taxon was found only on one plant, to 3 if equally represented on all the host plants. Although none of the most abundant taxa were exclusively found on only one of the host plants (which would indicate obigate host specificity), some were evenly distributed among the host plants; the distribution of others was distinctly different between the host plants.

Bryocladia cuspidata had more epiphytes per unit area than the other host plants. Amphora acutiuscula and Amphora tenerrima were more prevalent on this host plant, but their preference for Bryocladia was most noticeable in Port Isabel (Fig. 17, see pg. 60). Navicula pseudocomoides was more common on Bryocladia than on other host plants in Galveston but became numerically important on Gelidium and Centroceras in Port Aransas and Port Isabel (average Bj = 2.55). It was almost completely absent from Cladophora in Galveston (Fig. 16, see pg. 59).

Achnanthes brevipes v. intermedia, Synedra fasciculata v. truncata, and Licmophora abbreviata (Fig. 15, see pg. 57) were more abundant on Cladophora in Galveston and on Centroceras in Port Aransas

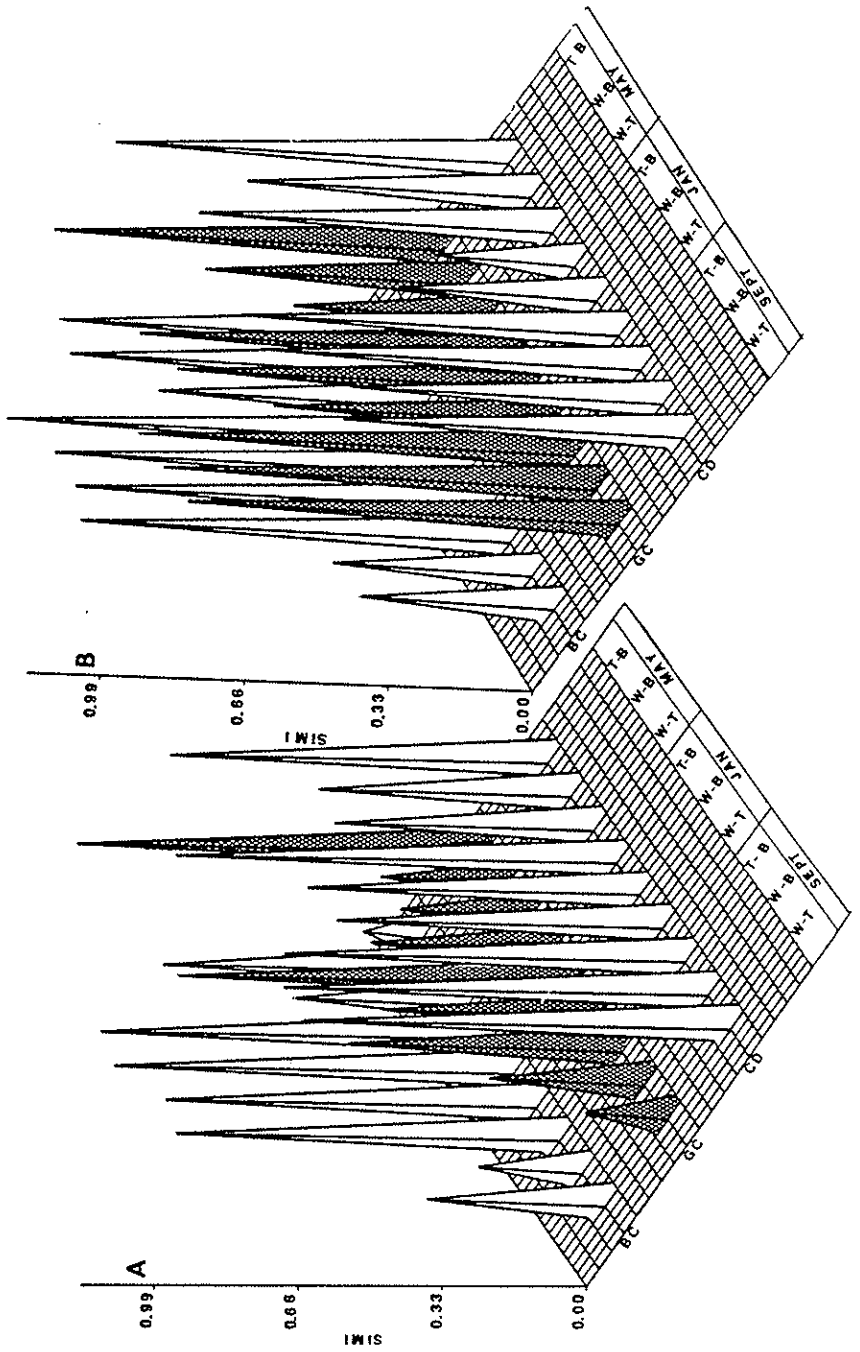


Figure 20. SIMI values for comparing the species assemblages within host plants collected at Galveston. (the first year (A) and the second year (B)) CD = Cladophora dalmatica; GC = Gelidium crinale; BC = Bryocladia cuspidata. W-T = Wash compared to Tip, W-B = Wash compared to Base, T-B = Tip compared to Base.

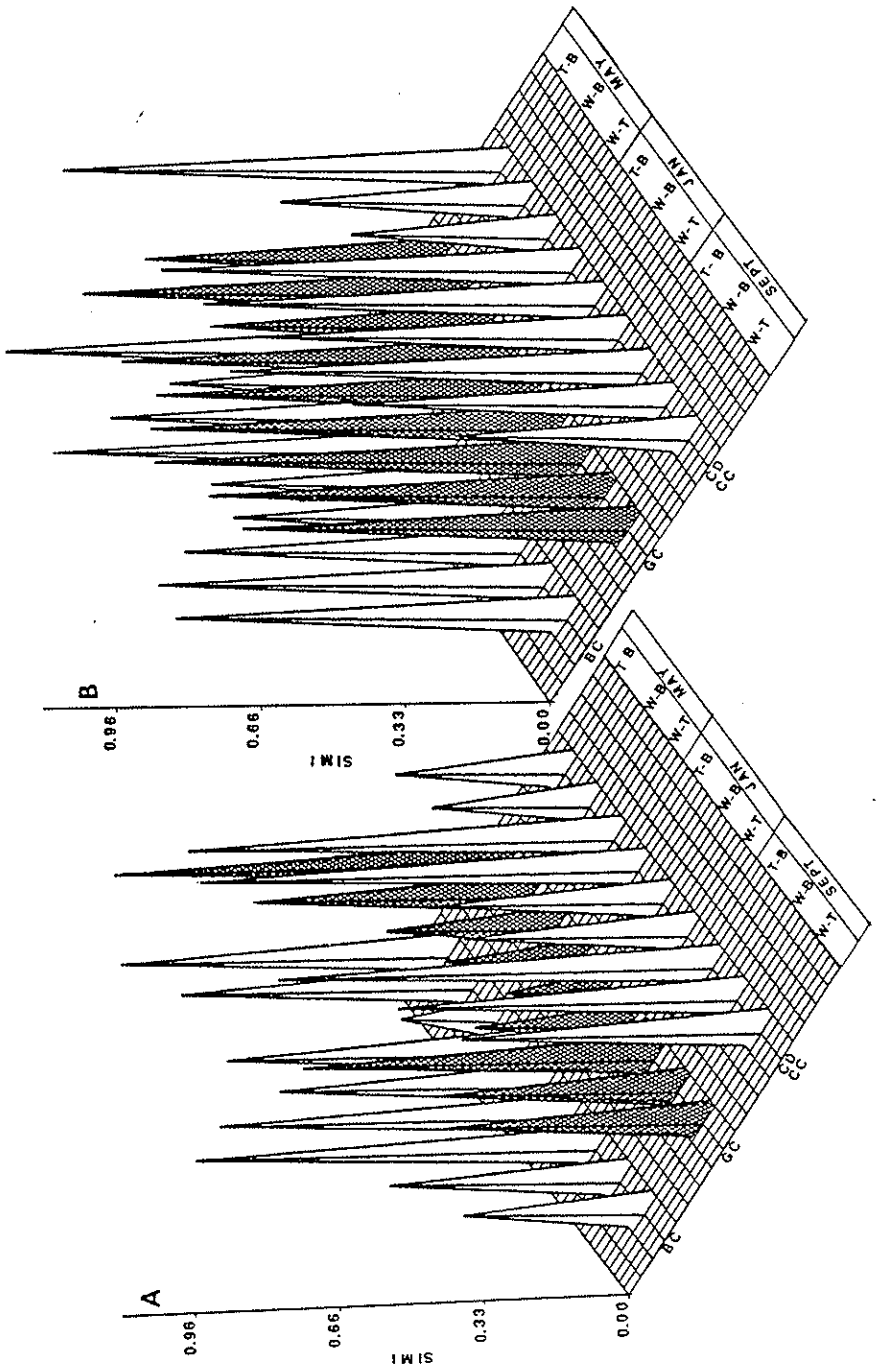


Figure 22. SIMI values for comparing the species assemblages within host plants collected at Port Isabel. (the first year (A) and the second year (B)) CC = Centroceras clavulatum; CD = Cladophora dalmatica; GC = Gelidium crinale; BC = Bryocladia cuspidata. Other symbols as for Fig. 20.

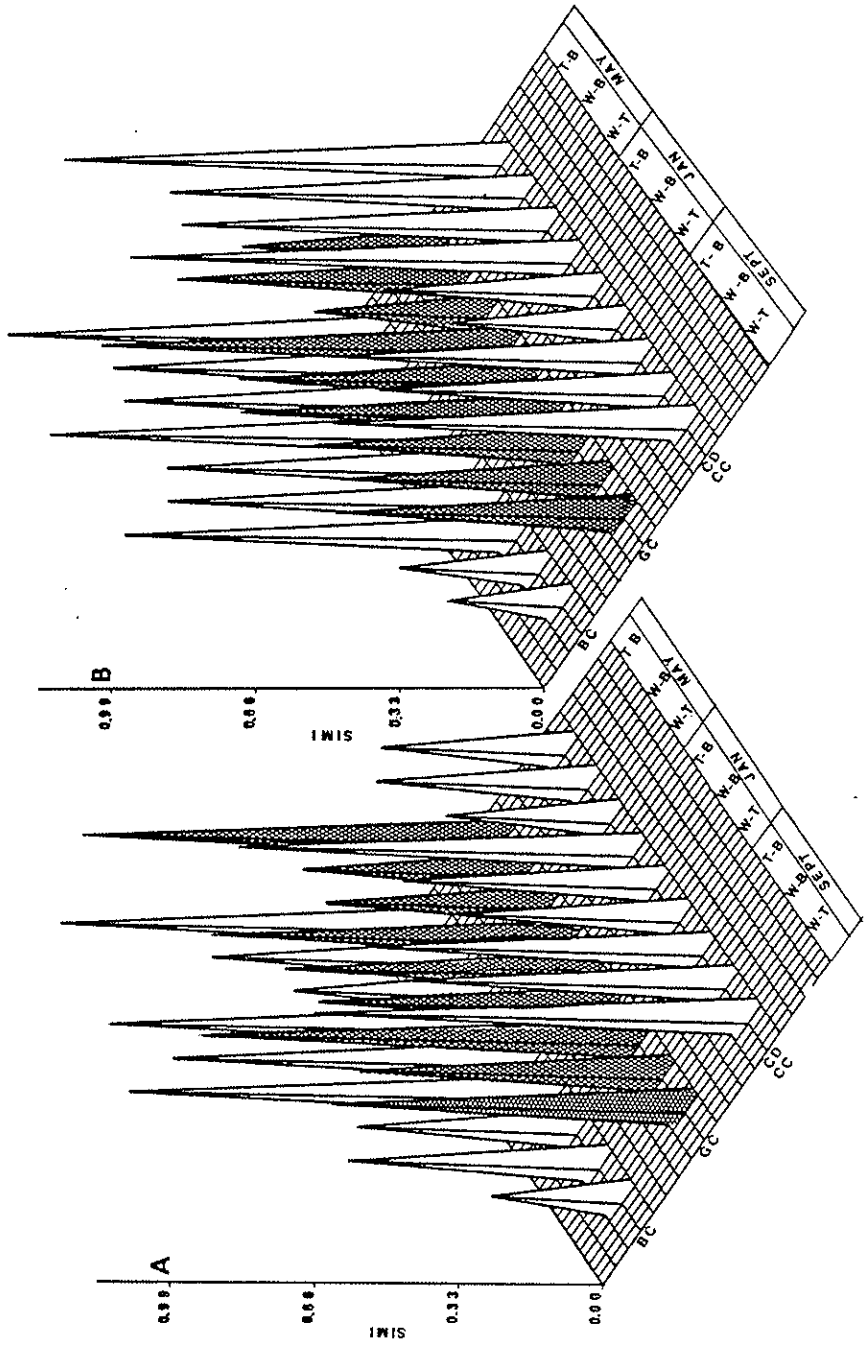


Figure 21. SIMI values for comparing the species assemblages within host plants collected at Port Aransas. (the first year (A) and the second year (B)) CC = Centroceras clavulatum; CD = Cladophora dalmatica; GC = Gelidium crinale; BC = Bryocladia cuspidata. Other symbols as for Fig. 20.

and Port Isabel than on other host plants (average Bj = 2.16, 2.57, and 1.86, respectively).

Navicula stompsii also was more abundant on Cladophora than the host plants collected from the mid-intertidal zone at all three sites but was not numerous on Centroceras at the two more southerly sites (Fig. 18, see pg. 61). Centroceras replaces Cladophora during the warmer months at the same height in the intertidal zone at Port Aransas and Port Isabel. Thus, the distribution of Navicula stompsii appeared, more or less, to be equally distributed among the host plants at Port Aransas and Port Isabel, but this is actually a reflection of its decreased distribution on Centroceras during the sampling period at Port Aransas and Port Isabel.

Nitzschia frustulum was not commonly found on Cladophora but was very common on Centroceras. Thus, its distribution in Galveston was more restricted to Gelidium and Bryocladia, while at Port Isabel it was more equitably reported from all the host plants (Fig. 14, see pg. 56).

The only taxon that was clearly more abundant on Gelidium than on any other host plant was Cocconeis scutellum (Fig. 14, see pg. 56), although its distribution spread to the other host plants southward from Galveston (average Bj = 1.15 at Galveston, 2.12 at Port Aransas, 2.83 at Port Isabel). Navicula diserta and Rhoicosphenia genuflexa (Fig. 19, see pg. 62) were more or less equally distributed among the host plants, as was Thalassiosira cf. profunda (Fig. 13, see pg. 55)(average Bj = 2.83, 2.84, and 2.88, respectively). However, the small lineate Thalassiosira sp. was not normally abundant on

Cladophora or Centroceras (Fig. 13, see pg. 55).

Cymatosira belgica and Grammatophora oceanica had very disjunct populations (Figs. 14,18, see pgs. 56 & 61). Cymatosira belgica was reduced in numbers on Cladophora and Centroceras throughout the sampling area; however it was very common on Bryocladia and Gelidium at Galveston the first year. Grammatophora oceanica was, more or less, equally distributed among the host plants in Galveston, more common on Bryocladia in Port Aransas, and numerically reduced on all plants in Port Isabel.

SIMI values were also used to compare the entire species assemblages on each plant to one another at each site on a seasonal basis for year one and year two (Fig. 23). For the second year the second replicates only were compared with one another because of missing data in the first replicate series at Galveston and Port Isabel. Also, the replicates of each host plant, with the exception of those in September at Galveston, were more similar to one another than to different host plants (compare Fig. 24 to Fig. 23), but the differences between the host plants were not statistically significant.

In general, the species assemblage on Cladophora was more similar to that on Bryocladia (average SIMI = .750) than to that on Gelidium (average SIMI = .222) at Galveston during September (Fig. 23). Moving southward, the species assemblage shifted, and that on Cladophora was more similar to that on Gelidium (average SIMI = .879) than to that on Bryocladia (average SIMI = .705) at Port Isabel. During January, assemblages on each host plant at each site were comparable; SIMI

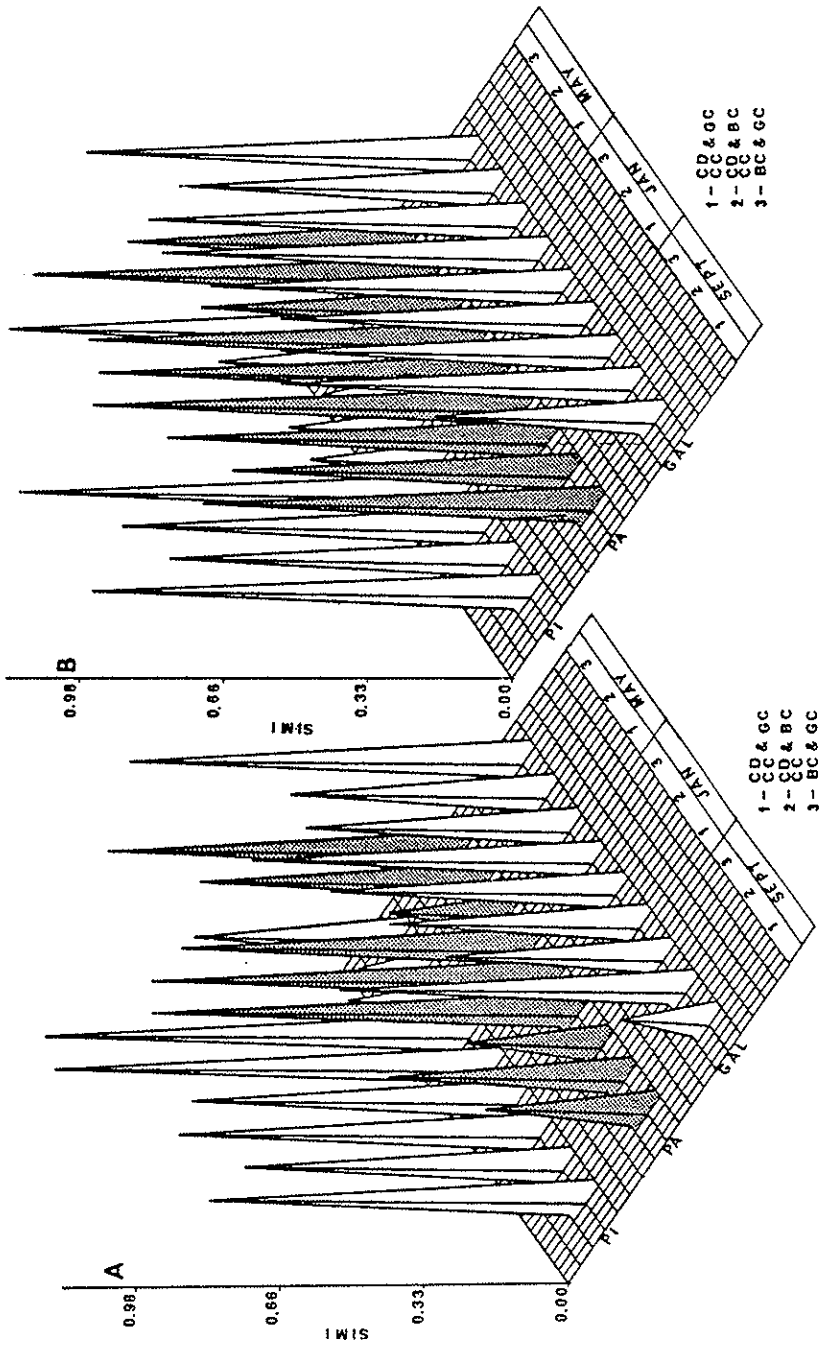


Figure 23. SIMI values for comparing the species assemblages between the host plants. Collections made during the first year (A) and the second year (B) at Galveston (GAL), Port Aransas (PA), and Port Isabel (PI). CC = Centroceras clavulatum; CD = Cladophora dalmatica; GC = Gelidium crinale; BC = Bryocladia cuspidata.

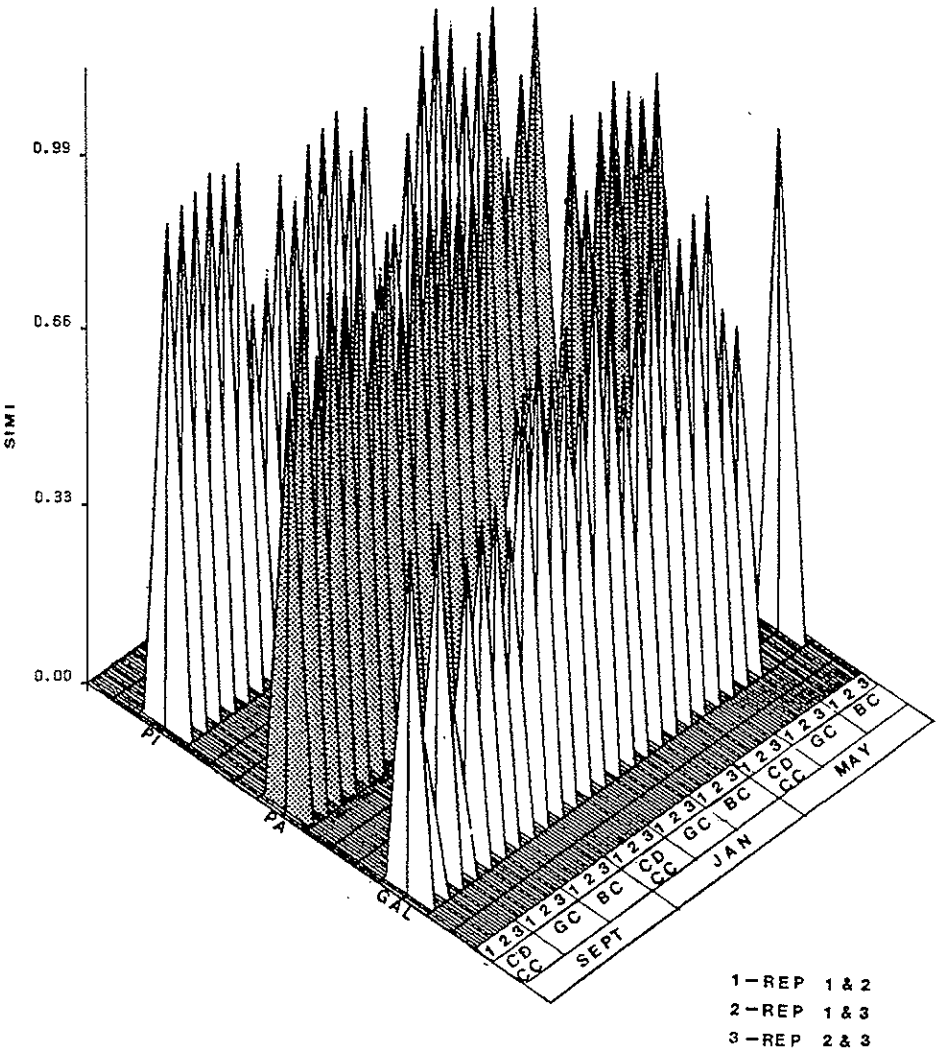


Figure 24. SIMI values for comparing the species assemblages between replicates of each host plant. Collections made during the first year (A) and the second year (B) at Galveston (GAL), Port Aransas (PA), and Port Isabel (PI). CC = Centroceras clavulatum; CD = Cladophora dalmatica; GC = Gelidium crinale; BC = Bryocladia cuspidata.

values ranged from .500 to .978 (with the exception of the disjunct assemblages on Bryocladia in January at Port Isabel).

In May, the pattern was more variable. The assemblages on Cladophora were similar to both Bryocladia (average SIMI = .604) and Gelidium (average SIMI = .682) at Galveston, but became more separated from these host plants toward Port Isabel (average SIMI = .171 to Gelidium and .229 to Bryocladia). The assemblages associated with Gelidium and Bryocladia responded similarily, when compared to one another for both years (although less dramatically), despite the fact that the similarity between the diatom assemblages was generally higher than that obtained when either host plant was compared to Cladophora.

The Duncan's multiple range test of the means of the similarity indices showed that the host plants collected in September were statistically different from those collected in May. This reflects the shift in the similarity of the diatom communities from September to May with January being a month when the diatom assemblages on all host plants were most alike.

There was a subtle seasonal change in the diatom flora, which was more pronounced the first year. SIMI values, comparing seasons for each year, are presented in Table IV. During the first year the winter samples more closely resembled those collected in the fall. During the second year the differences between the spring and winter assemblages were less pronounced. When the data were pooled by year the diatom community sampled over the two year period was 95% similar. Bj values ranged from 1, if present only in one season, to 3 if

Table IV. SIMI Values for Comparison of the Three Sampling Seasons Pooled for the Two Year Sampling Period. S = September, J = January, M = May.

	YEAR 1			YEAR 2		
	S	J		S	J	
J	.899		J	.934		
M	.887	.744	M	.841	.890	

equally present in all seasons (Appendix C).

In the fall Licmophora spp. were characteristic members of the community. In Galveston Licmophora abbreviata (Fig. 25) and Licmophora gracilis v. anglica co-occurred. Moving southward, this latter species was gradually replaced by two other taxa, Licmophora jeurgensii and Licmophora cf. hyalina.

Navicula diserta, Rhoicosphenia genuflexa, and Nitzschia frustulum were also common in the fall and into the winter. Their importance in the community increased southward to Port Isabel (Fig. 26).

Cocconeis scutellum, present more or less equally year-round, was most prominent in Port Aransas (Fig. 25). In Port Isabel, Cocconeis littoralis and Cocconeis cf. dirupta became more competitive with Cocconeis scutellum.

During the winter three taxa, Rhoicosphenia genuflexa, Navicula diserta, and Grammatophora oceanica accounted for nearly 50% of all cells present. Rhoicosphenia genuflexa composed from 26 to 31% of the total winter samples for both years.

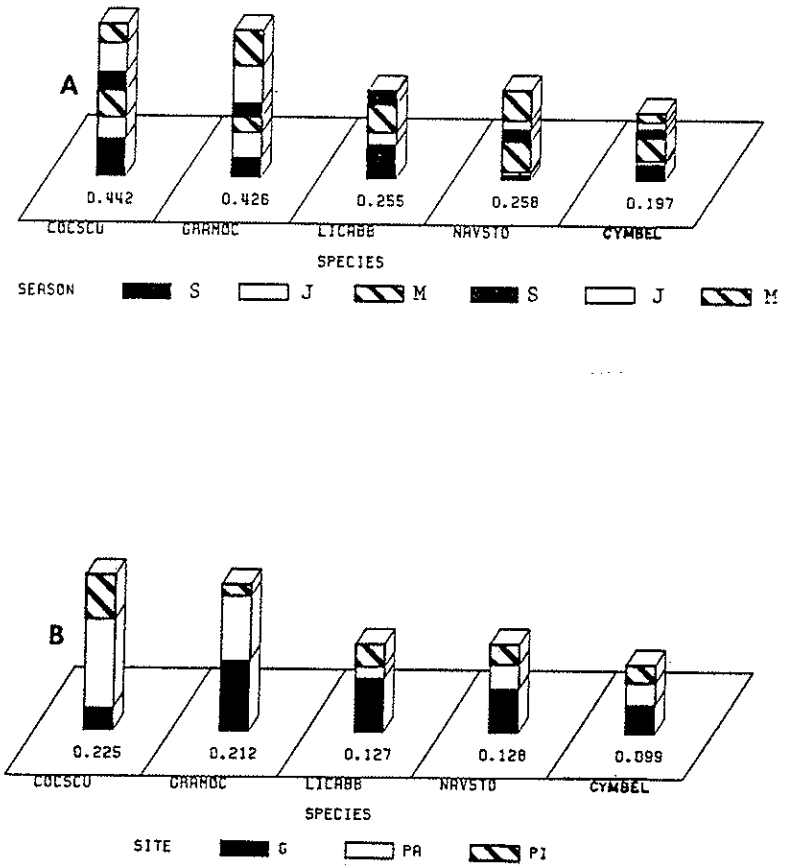


Figure 25. Relative abundance of C. scutellum, G. oceanica, L. abbreviata, N. stompsii, and C. beligica pooled by season (A) and by site (B). (S = September, J = January, M = May repeated for each year) (G = Galveston, PA = Port Aransas, PI = Port Isabel) The total beneath each bar represents the summation of the relative abundances for each category.

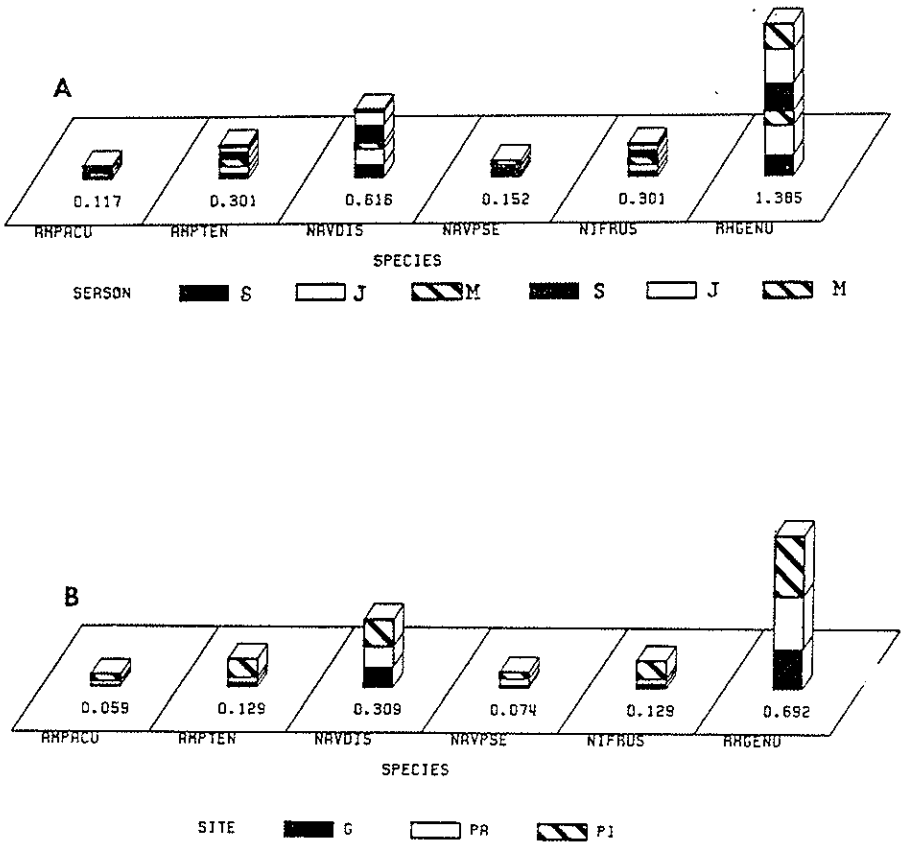


Figure 26. Relative abundance of A. acutiuscula. A. tenerrima, N. diserta, N. pseudocomoides, N. frustulum, and R. genuflexa pooled by season (A) and by site (B). All other symbols as in Figure 25.

Grammatophora oceanica, present in the fall, steadily increased as the temperatures dropped. During January, it was the third most abundant taxon, especially at Galveston and Port Aransas (Fig. 25). It reached maximum relative abuandance during March, a sampling month that was not counted for the statistical analysis. During the second year, Grammatophora oceanica continued to flourish into May, mainly at Port Isabel, because growth of the taxon was delayed at the most southern station until March of that year. Thus, the seasonal change in Port Isabel can lag behind that in Galveston and Port Aransas.

During the spring, the metaphytic members of the community, Thalassiosira cf. profunda, the small lineate Thalassiosira, and Cymatosira belgica flourished (Figs. 25,27). Achnanthes brevipes v. intermedia returned after being poorly represented during the winter, especially at Port Isabel (Fig. 27). Although this species was never significantly abundant, its presence during the spring indicated a change in the community from that found in the winter. Synedra fasciculata v. truncata, commonly found year-round during the first year, was a prominent member of the spring community, especially in Galveston during the second year (Fig. 27).

Samples and species were ordered along axes by three ordination methods: Polar Ordination (PO), Principal Components Analysis (PCA), and Reciprocal Averaging (RA). Of these methods, RA analysis of both species and samples maximized correspondence between sample and species ordinations and provided the greatest clarity of interpretation. Thus, only RA ordinations were presented for this study.

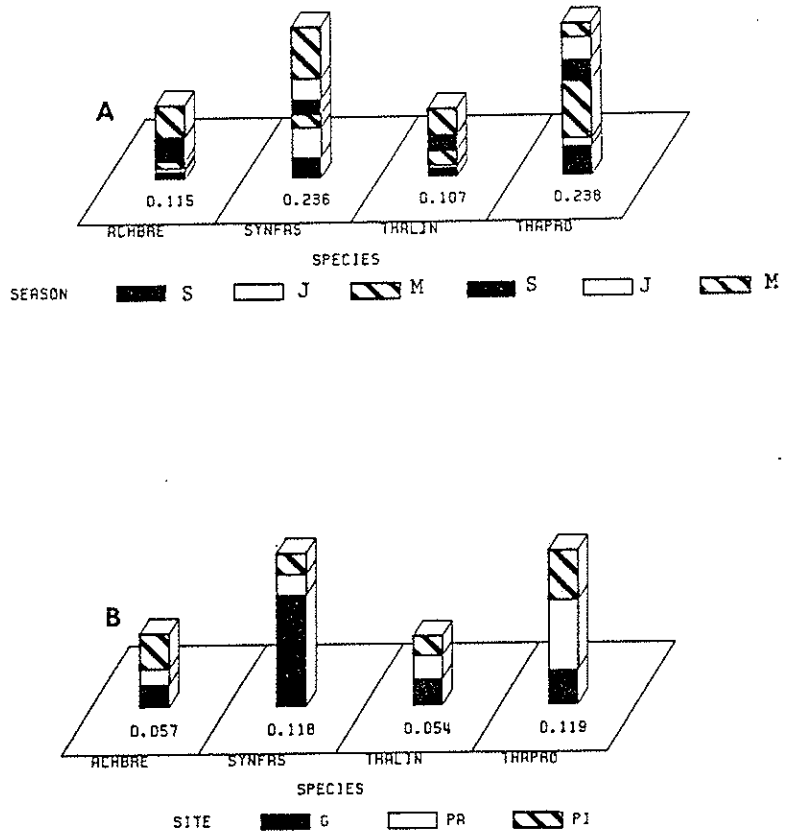


Figure 27. Relative abundance of A. brevipes v. intermedia, S. fasciculata v. truncata, T. cf. profunda, lineate Thal. sp. pooled by season (A) and by site (B). All other symbols as in Fig. 25.

Reciprocal averaging of the samples documented that there was a continuum in the diatom community from Galveston (left of the figure) to Port Isabel (right of the figure) (Fig. 28). The first axis appears to be a geographical axis, although regression of the sample rankings from the first axis against salinity explained only 16% of the variation. Temperature was not significantly correlated with the sample rankings. The September and May samples at Galveston were found at the left of axis 1; progressing to the right along axis 1 and slightly up axis 2, the January samples from Galveston could be located. The Port Aransas samples followed the same pattern, with the September and May samples being encountered first along axis 1. The Port Isabel samples were more homogeneously mixed, and the January samples were not separated from the other sampling months along the first axis.

The correspondence of the sample and species ordinations can be evaluated by comparing Fig. 28 and 29. Species, such as Licmophora gracilis v. anglica, Licmophora abbreviata, Pleurosigma barbadense, Grammatophora oceanica, Synedra fasciculata v. tabulata, Podosira montagnei, Amphora helensis, and Navicula stompsii were more abundant in Galveston and were typically found to the left on axis 1. Moving along axis 1 to the right, one encounters species whose abundances gradually increased southward from Galveston to Port Isabel. The species found at the extreme right of axis 1, such as Cocconeis littoralis, Cocconeis cf. dirupta, Amphora angusta, Cocconeis placentula, Cocconeis placentula v. euplypta, and Navicula platyventris, were most abundant at Port Isabel. By comparing the

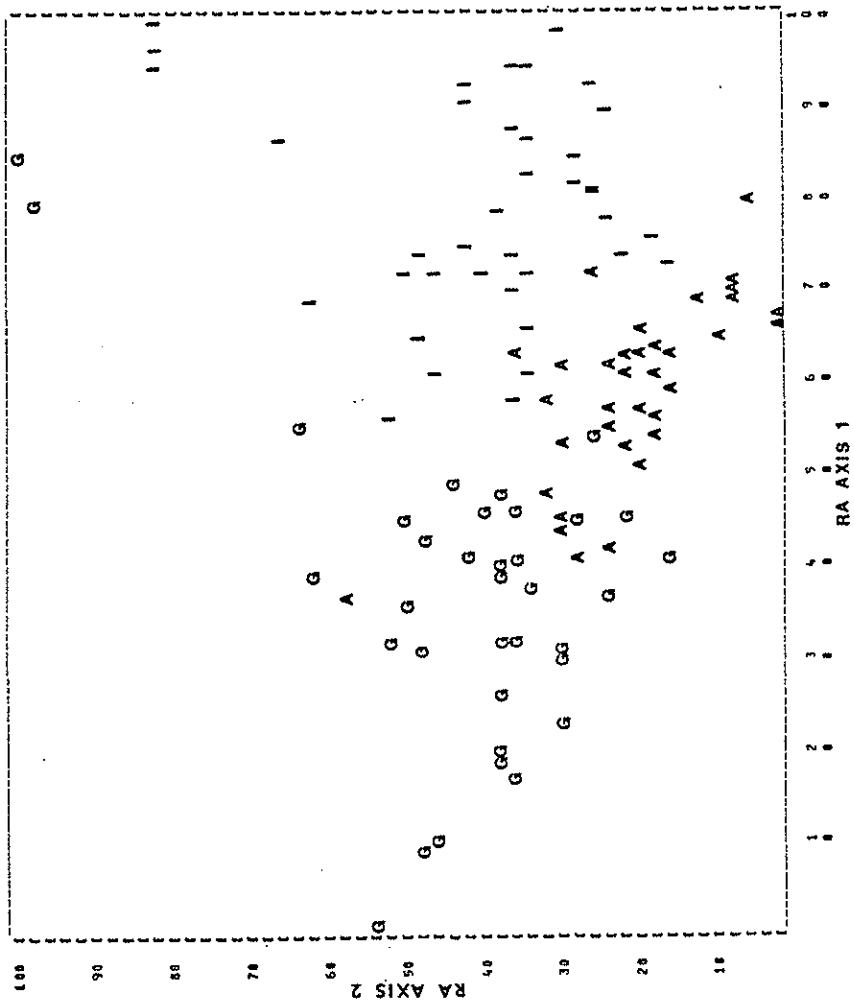


Figure 28. Reciprocal averaging ordination of epiphyte samples. G = Galveston, A = Port Aransas, I = Port Isabel.

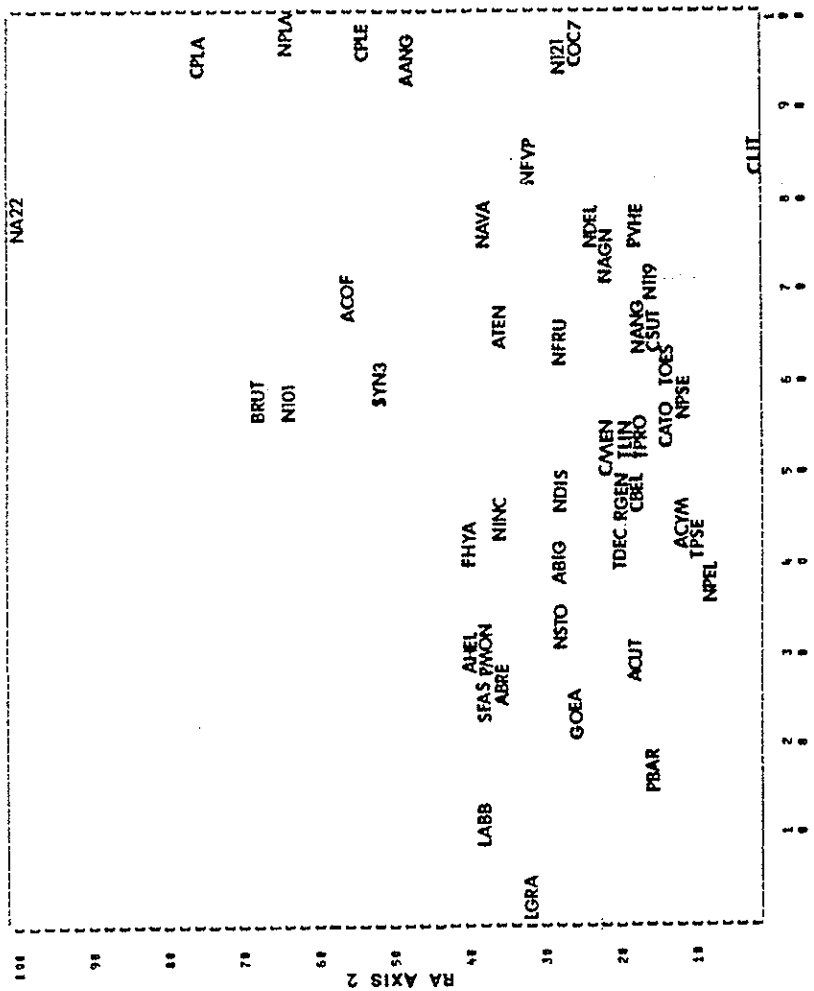


Figure 29. Reciprocal averaging ordination of epiphyte species. See Appendix A for species codes.

relative abundances of the more abundant taxa pooled by site in Figs. 25,26, and 27 (see pgs. 80,81, and 83) with the species patterns revealed by RA ordination, the change in species and their relative abundances from Galveston to Port Isabel can be documented.

When the data are pooled by site the similarity between the sites appears even more dramatic (Table V). Galveston is more similar to Port Aransas than it is to Port Isabel, which would be expected as the community gradually changes from Galveston southward to Port Isabel.

Table V. SIMI Values for Comparison of the Three Sampling Sites Pooled for the Two Year Sampling Period. G = Galveston, A = Port Aransas, I = Port Isabel.

	G	A
A	.870	
I	.843	.914

Colonization Sequences of Epiphytes

Among the epiphytic diatoms, there are a variety of attachment mechanisms, which are species specific. The most commonly encountered structure was the stipe (Fig. 30a,b, and c), which could be secreted either through the areolae (e.g. Podosira or Rhoicosphenia) or through a specialized pore field at one end of the diatom cell (e.g. Licmophora). Licmophora spp. were attached to the host plant via this mechanism, although each species formed a unique stipe. Licmophora abbreviata secreted a thickened bipartite stipe (Fig. 38d, pg. 110), which implied that there were two sources for mucilage secretion, much

Figure 31. Host plants collected from Port Aransas, Texas.

a,b,c - 48 mm working diatance, 12.5 KeV.

a. Centroceras clavulatum. 20 X.

b. Bryocladia cuspidata. 15 X.

c. Gelidium crinale. 30 X.

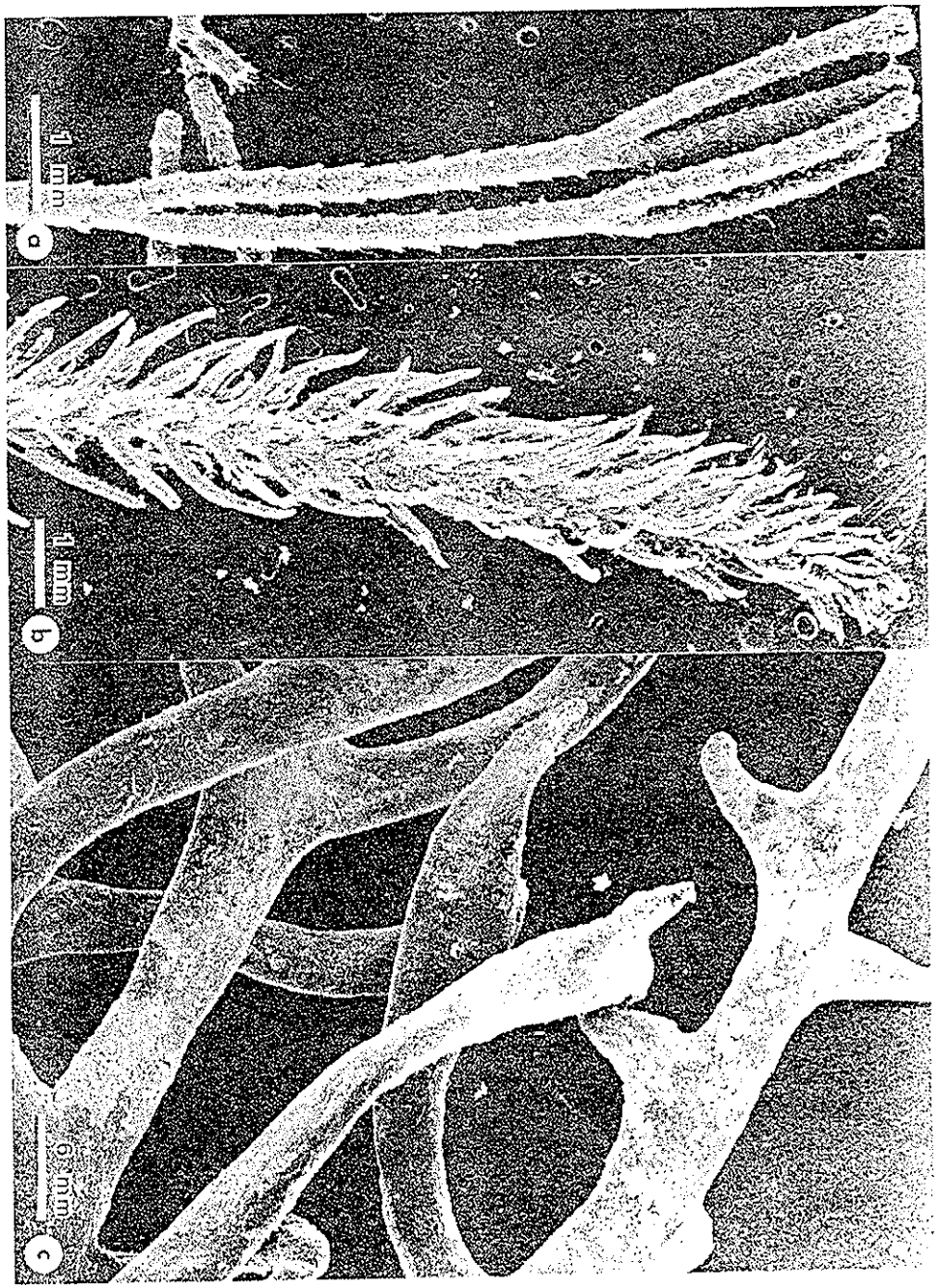


Figure 32. Successional sequence of epiphytes on Centroceras Part I.

a,b,c - 10 mm working distance, 15 KeV.

a. Tip of Centroceras showing delay of diatom colonization and initiation of bacterial colonization close to tip within the ring of cells and spines marking the node. 300 X.

b. Rhoicosphenia genuflexa attached to corticating cells with a long stipe (arrow), same specimen in lower left of a. 2000 X.

c. Licmophora gracilis v. anglica attached with a short stipe or pad to the node and Navicula diserta (arrow) attached in a perpendicular fashion behind the spine. 1000 X.

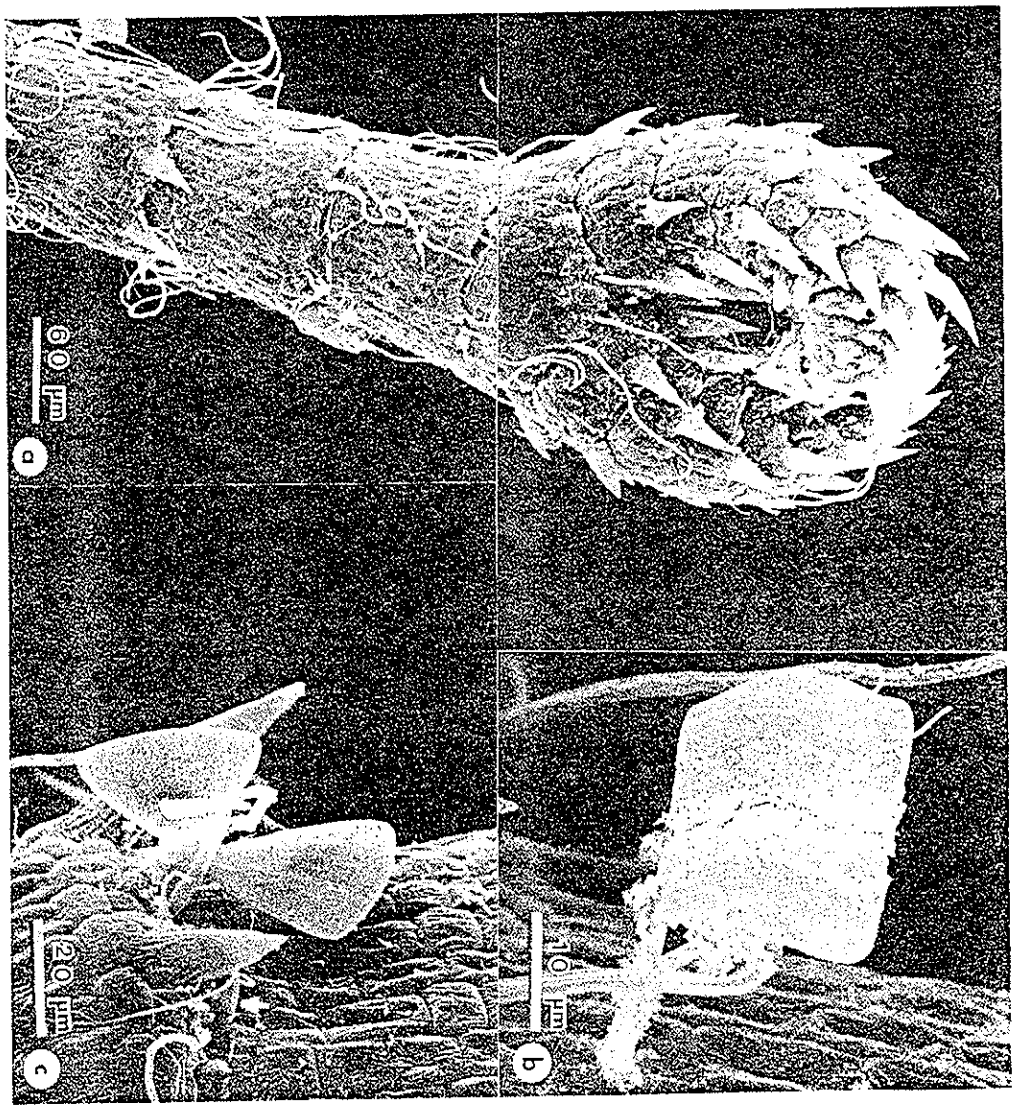


Figure 30. Attachment mechanisms of epiphytic diatoms.

a,b,c - 10 mm working distance, 15 KeV. d,e - 48 mm working distance, 12.5 KeV.

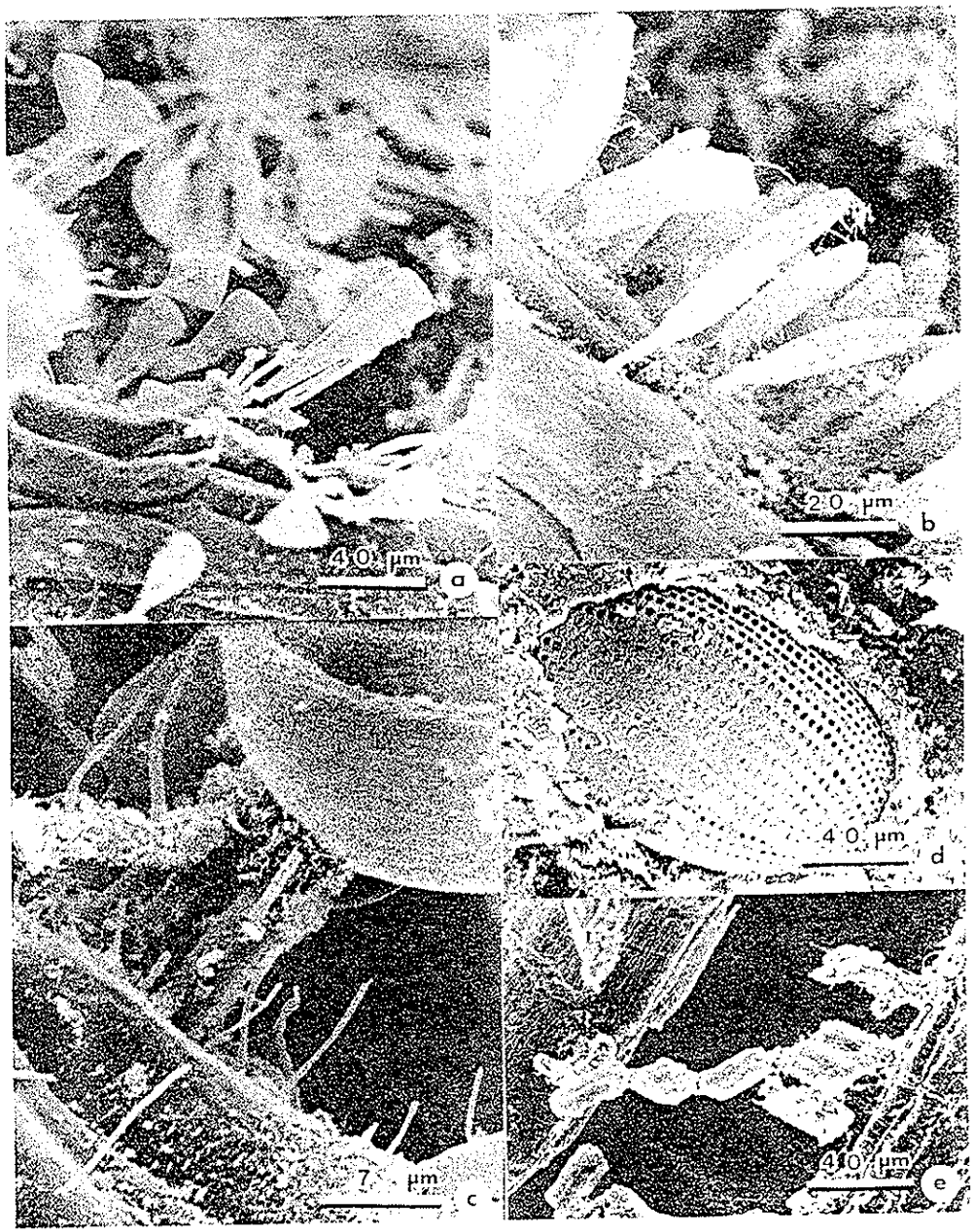
a. Licmophora cf. hyalina attached to branchlet of Bryocladia with a simple branched stipe. 450 X.

b. Achnanthes brevipes v. intermedia attached to branchlet of Bryocladia with a short stipe. 1000X.

c. Podosira montagnei attached to branchlet of Bryocladia with a six part stipe. 3000X.

d. Amphora acutiuscula embedded in a mucilage coat and attached valve side down to the main axis of Bryocladia. 4500 X 55°Tilt.

e. Zig-zag chain of Grammatophora oceanica attached to Bryocladia with a mucilage pad. 450 X.



as there is in Rhoicosphenia abbreviata, which secretes mucilage from both valves to form a similar stipe. Licmophora cf. hyalina secreted a thinner single stipe (Fig. 30a, pg. 89).

Achanthes brevipes v. intermedia (Fig. 30b, pg. 89) and Rhoicosphenia genuflexa (Fig. 32b) secreted single stipes, whose length varied with the position on the host plant. Multiple stipes from a single cell were secreted by Podosira montagnei (Fig. 30c, pg. 89).

Mucilage pads were characteristics of Synedra (Fig. 38c, pg. 110), Grammatophora (Fig. 30e, pg. 89), and Licmophora gracilis v. anglica (Fig. 34b, pg. 100). Chain formers, such as Grammatophora (Fig. 30e, pg. 89) and Biddulphia (Fig. 36c, pg. 105), formed pads to bind cells together within the chain.

Certain taxa attached directly to the host plant surface. Navicula diserta and other naviculoid species attached by the valve apex (Fig. 38b, pg. 110). Presumably the raphe, or slit in the valve, is involved with the production of secretions that result in the adherence of one pole of the cell to the substrate. In the genera, Cocconeis (Fig. 33c, pg. 97) and Amphora (Fig. 30d, pg. 89), the cell is fastened flat against the host substrate, apparently by the raphe. Both secreted protective mucilage around the cell.

The relationship between attachment mechanisms and position of the epiphyte on three host plants, as well as the colonization sequence from tip to base of that plant, was studied using SEM (Fig. 31). Any variation in the attachment mechanism for a given species

may indicate a response to either the host plant itself or to varying abiotic factors.

Centroceras clavulatum, which occurs in the upper littoral zone, is a dichotomously branched uniseriate filament with pincer-like apices (Edwards, 1970) (Fig. 31a). The uniseriate axes are completely covered by regular, longitudinal rows of rectangular cells (Fig. 32a). Short, colorless spines, one to three cells long, demarcate the nodes of the uniseriate filament (Fig. 32c). The host plant was initially colonized by filamentous bacteria, possibly Leucothrix (Sieburth, 1975), which settled first within the ring of cells and spines at the nodes (Fig. 32c). The surface of the corticating cells remained relatively free of epiphytes, but flocculant material (silt or, perhaps, coccoid bacteria) was randomly scattered over these internodal cells. The first diatom to appear was Rhoicosphenia genuflexa at approximately the fifth or sixth node from the apex, where it attached by a long stipe (Fig. 32b). Other diatoms, such as Licmophora gracilis v. anglica., which attached by a small pad, and Navicula diserta, which attached in a perpendicular fashion by one pole of the cell, began to colonize the ring of cells and spines at the nodes (Figs. 32c, 38b, pg. 110).

Epiphytic colonization in the nodal area and behind the spine increased distally from the apex (Fig. 33a). Silt and mucilage easily accumulated behind the spines. Finally, epiphytic settlement progressed onto the corticating cells, and this surface was immediately covered initially with filamentous bacteria (Fig. 33b). Diatoms were still primarily found at the nodes, and their presence

Figure 33. Successional sequence of epiphytes on Centroceras Part II.

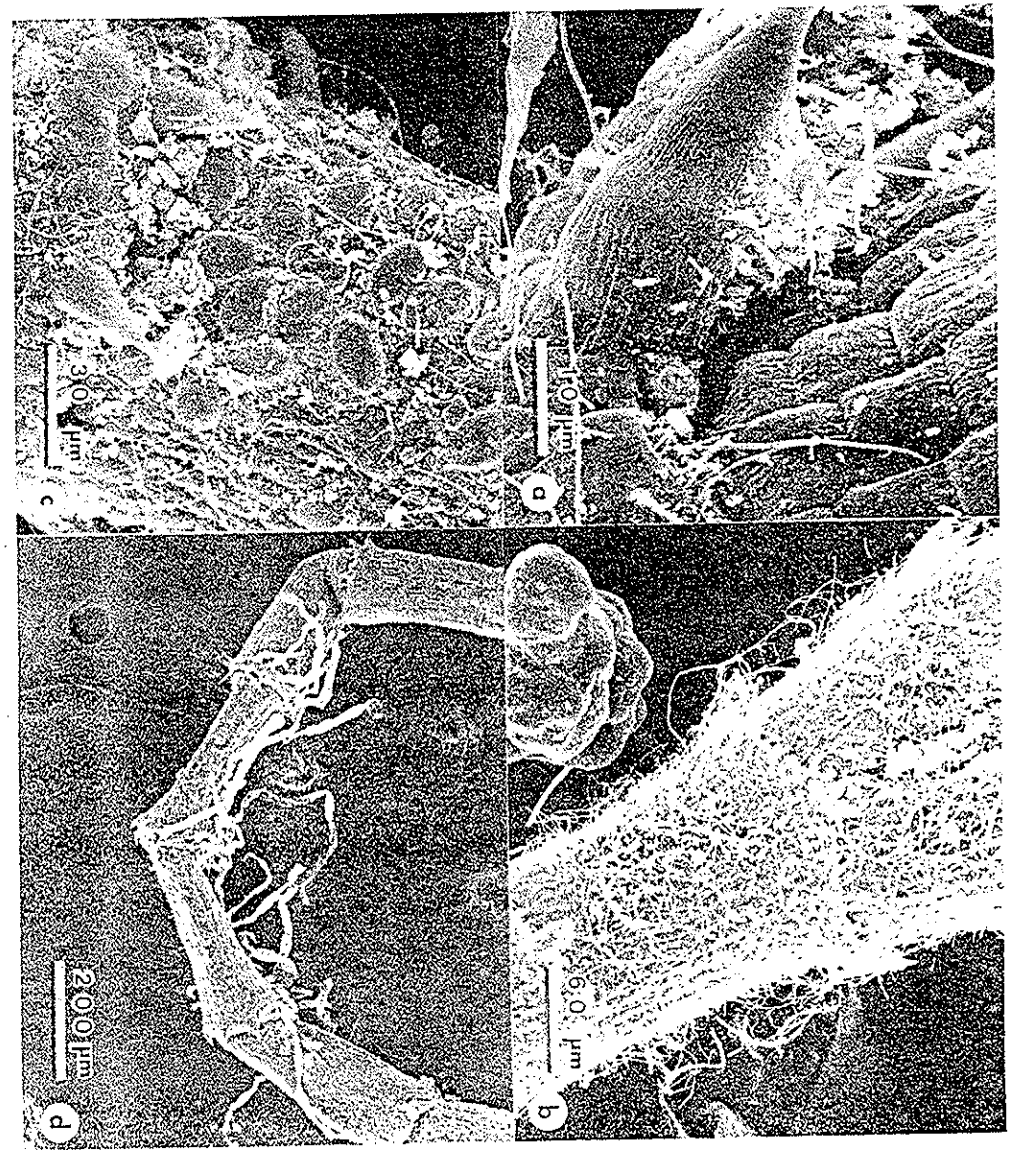
a,c,d - 10 mm working distance, 15 KeV. b. - 48 mm working distance, 15 KeV.

a. Accumulation of silt and bacterial filaments behind the spine. 2000 X.

b. Colonization of corticating cells by bacteria. 300 X.

c. Replacement of bacteria by diatoms. 700 X.

d. Rhizoids with occasional Cocconeis cells. 300X.



was partially obscured by the bacteria. These bacteria were subsequently replaced by heavy diatom populations. Cocconeis scutellum and Cocconeis placentula, which attached directly to the macroalga by the raphe valve, colonized the internodal surface so heavily that often the corticating cells are no longer visible (Fig. 33a). Naviculoid diatoms were still present within the nodes. Diatom settlement gradually decreased until at the rhizoids only scattered Cocconeis cells were found (Fig. 33d).

Bryocladia cuspidata occurs in the mid-intertidal zone just below Centroceras. The plants are sparingly branched and are densely covered with short, lateral branchlets arranged spirally on the main axis (Edwards, 1970) (Fig. 31b). Diatom settlement began almost immediately at the plant apex, but always within the fork where the branchlets attached to the main axis (Fig. 34b). Colonization of the branchlets was slower; however in general, a greater variety of species and attachment mechanisms were found there. Licmophora abbreviata C. Ag., attached with its thickened bipartite stipe (Fig. 34a, 38d, pg. 110). and Licmophora cf. hyalina with a thinner single stipe (Fig. 30a) created a dense overstory cover to the branchlet. Rhoicosphenia genuflexa also occurred on the branchlet and on the main axis but was attached to Bryocladia by a short stipe rather than the longer one secreted to attach the cell to Centroceras (Fig. 35a). Synedra fasciculata v. truncata (Fig. 38c, pg. 110) and Grammatophora oceanica (Fig. 30e, pg. 89) were attached by mucilage pads in isolated clusters on the branchlet. Flat, embedded cells, such as Cocconeis (Fig. 34a and b, 35c), were present on the branchlet but not in great

numbers. Instead their presence increased on the main axis (Fig. 34d). Another flat, embedded species, Amphora acutiuscula, was also more frequently found on the main axes than on the branchlets where the cells covered themselves with a sheet of mucilage (Fig. 30d, pg. 88).

Bacterial settlement followed the same sequential colonization pattern with initial recruitment within the branchlets and subsequent movement onto the branchlets (compare Fig. 34a to Fig. 34c). Often bacterial growth on the branchlets was so prolific that the diatoms were overgrown (Fig. 34c, 35b). Filamentous bacteria on the inner side of the branchlets were loosely arranged, while on the outside of the branchlet, the filaments were compacted, flattened, and possiblly overgrown with a coccoid bacterial colony or mucilage secretions from the host plant (Fig. 34c, 35b).

Bacterial growth, mucilage secretions, and silt accumulation increased toward the base of the alga (Fig. 35d, 36a). Diatoms were easily overlooked because of this dense overgrowth. Podosira montagnei was found predominately at the base of the alga where it was usually covered by a thick mucilage coat (Fig. 36b). When this mucilage layer was removed, the six-part stipe used for attachment to the host plant was seen (Fig, 30c, pg. 89). Also a long, zig-zag chain of Biddulphia biddulphiana was hidden among the mucilage and bacterial filaments surrounding the branchlets at the base of the plant (Fig. 36c). Rhizoids were relatively clear of epiphytic colonization (Fig. 36d).

Figure 34. Successional sequence of epiphytes on Bryocladia Part I.

a,b - 10 mm working distance, 15 KeV. c,d - 48 mm working distance, 15 KeV.

a. Early colonization of branchlet with Licmophora abbreviata and Cocconeis scutellum, few bacterial filaments. 200 X.

b. Early colonization of main axis by Licmophora gracili v. anglica, few bacterial filaments. 450 X.

c. Later colonization of branchlet, outer surface of branchlet with smooth coccoid bacterial colony overgrowing diatoms, inner surface of branchlet with free filamentous bacteria. 1000X.

d. Later colonization of main axis, Cocconeis scutellum predominates 1000X.

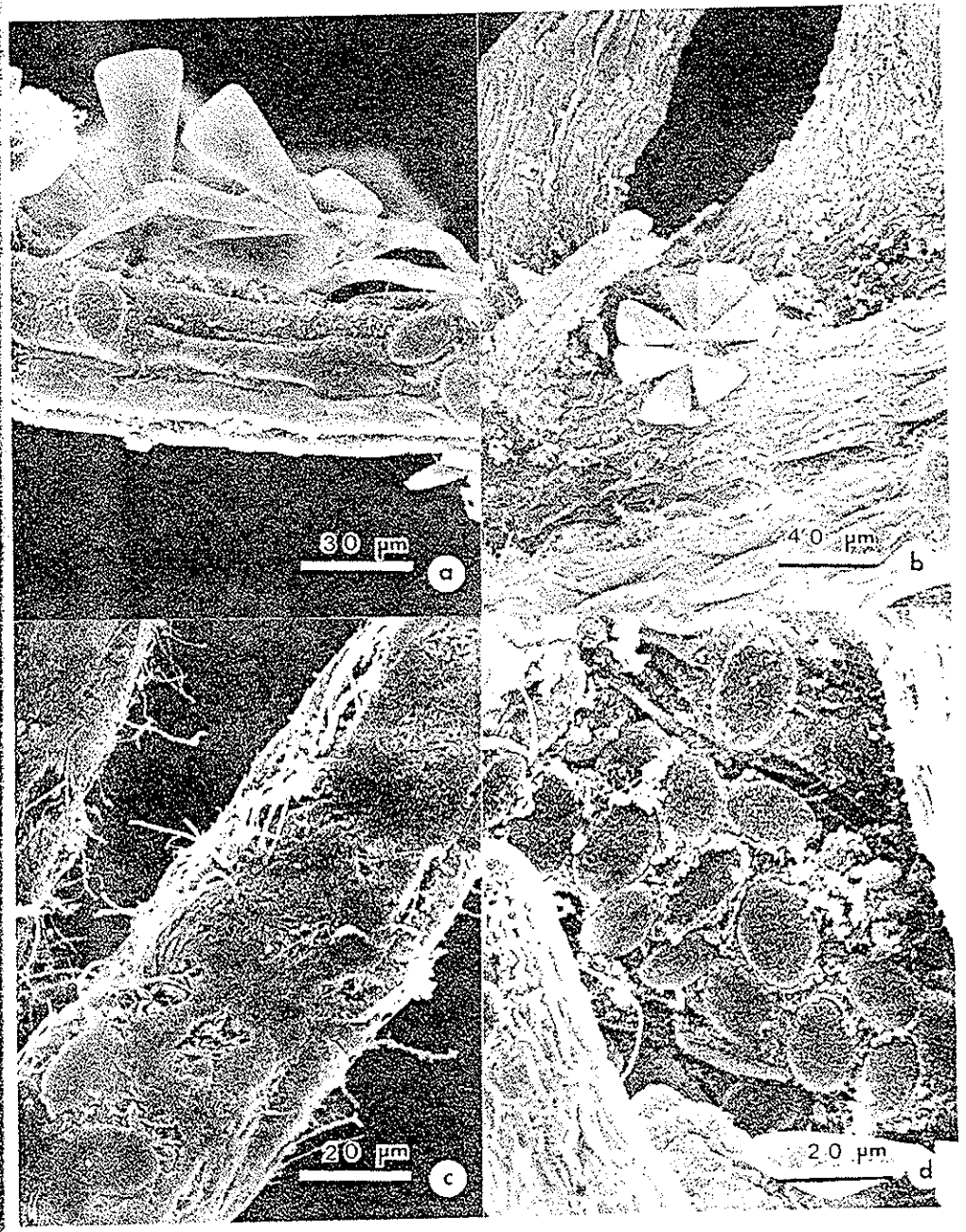


Figure 35. Successional sequence of Bryocladia Part II.

a,b,c,d, = 48 mm working distance, 12.5 KeV.

a. Rhoicosphenia genuflexa attached without a stipe. 1000 X.

b. Differential colonization of bacteria on the outer (smooth) and inner (floculant) sides of the branchlet. 1000 X.

c. Accumulation of silt within branchlet. 1000 X.

d. Colonization of Licmophora cells within forks. 700 X.

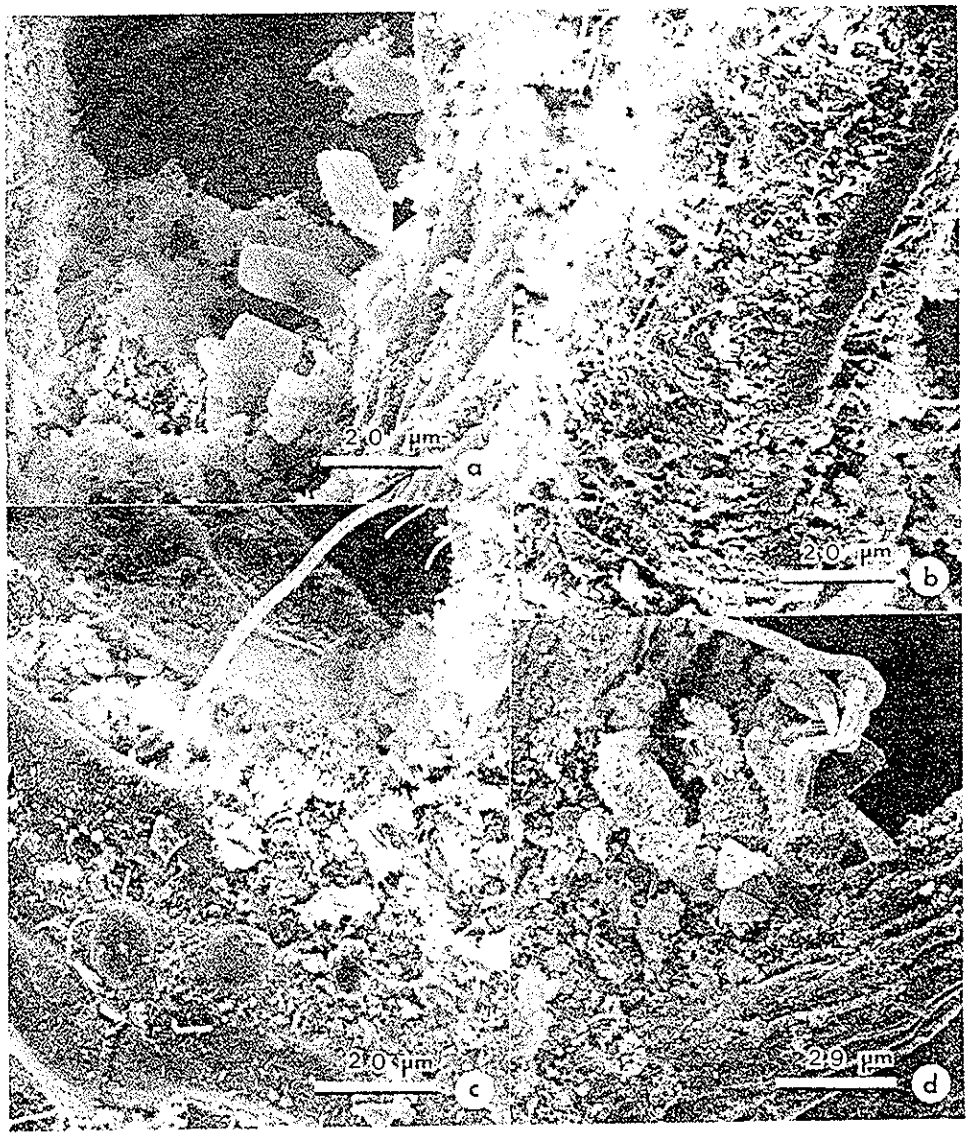


Figure 36. Successional sequence of epiphytes on Bryocladia Part III.

a,b - 48 mm working distance, 15 KeV. c - 48 mm working distance, 12.5 KeV. d - 10 mm working distance, 15 KeV.

a. Accumulation of silt and detritus, overgrowth of filamentous bacteria near base of alga. 1500 X.

b. Podosira montagnei attached to branchlet near base of alga, note mucilage coat around the diatom (arrow indicates mucilage coat around stipe, compare to Fig. 30c). 1000 X.

c. Zig-zag chain of Biddulphia biddulphiana hidden among the silt, mucilage, and bacterial filaments (arrow points to cell). 2000 X.

d. Rhizoid of alga with no fouling. 150 X.

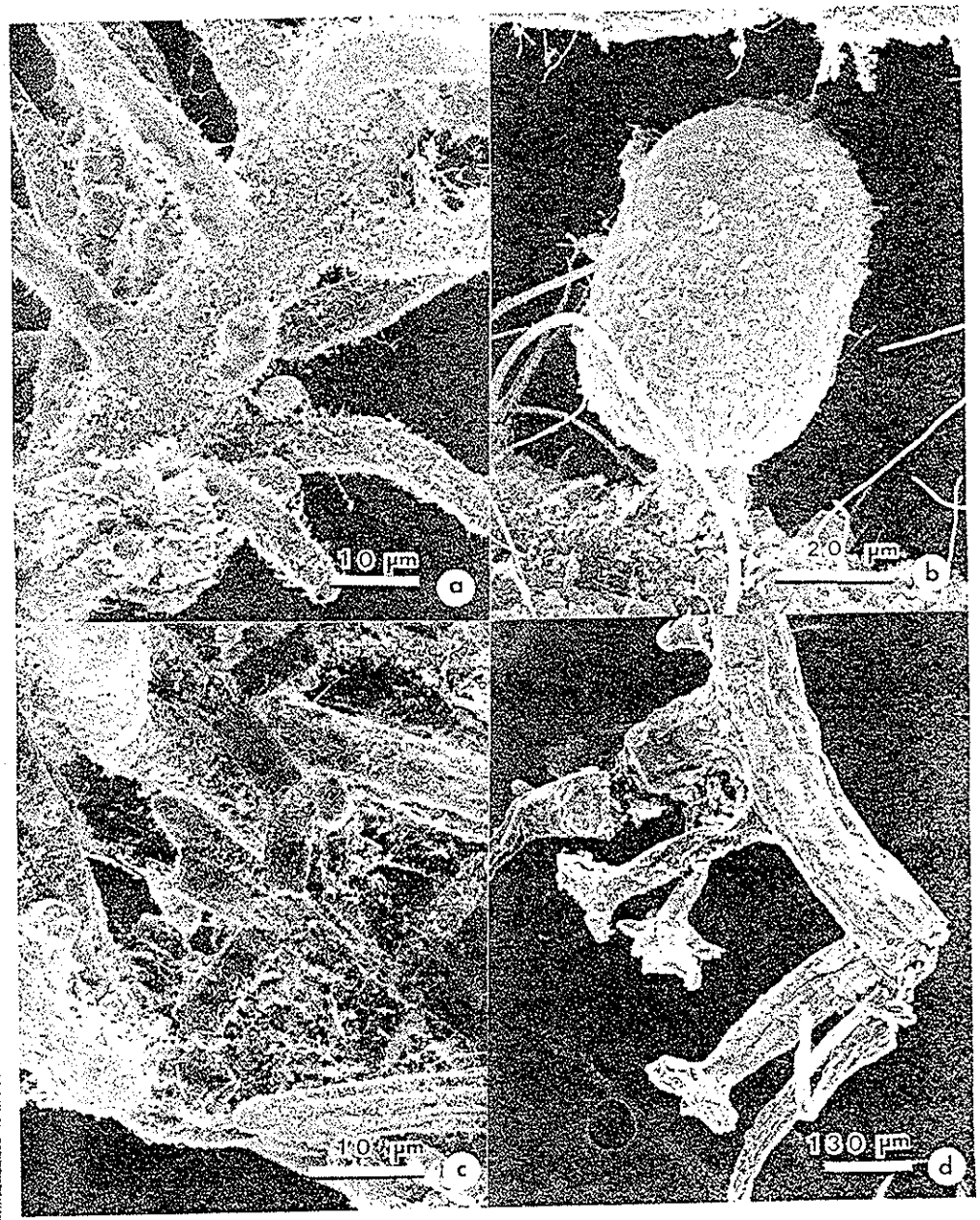


Figure 37. Successional sequence of epiphytes on Gelidium.

a,b,c,d, - 48 mm working distance, 12.5 KeV.

a. Tip of alga with few bacterial cells and silt deposited on surface. 450 X.

b. Coccoid bacterial colonies interspersed with filamentous bacteria and silt accumulation. 200 X.

c. Isolated cells of Cocconeis littoralis. 1500 X.

d. Rhizoids overgrown with filamentous bacteria. 45 X.

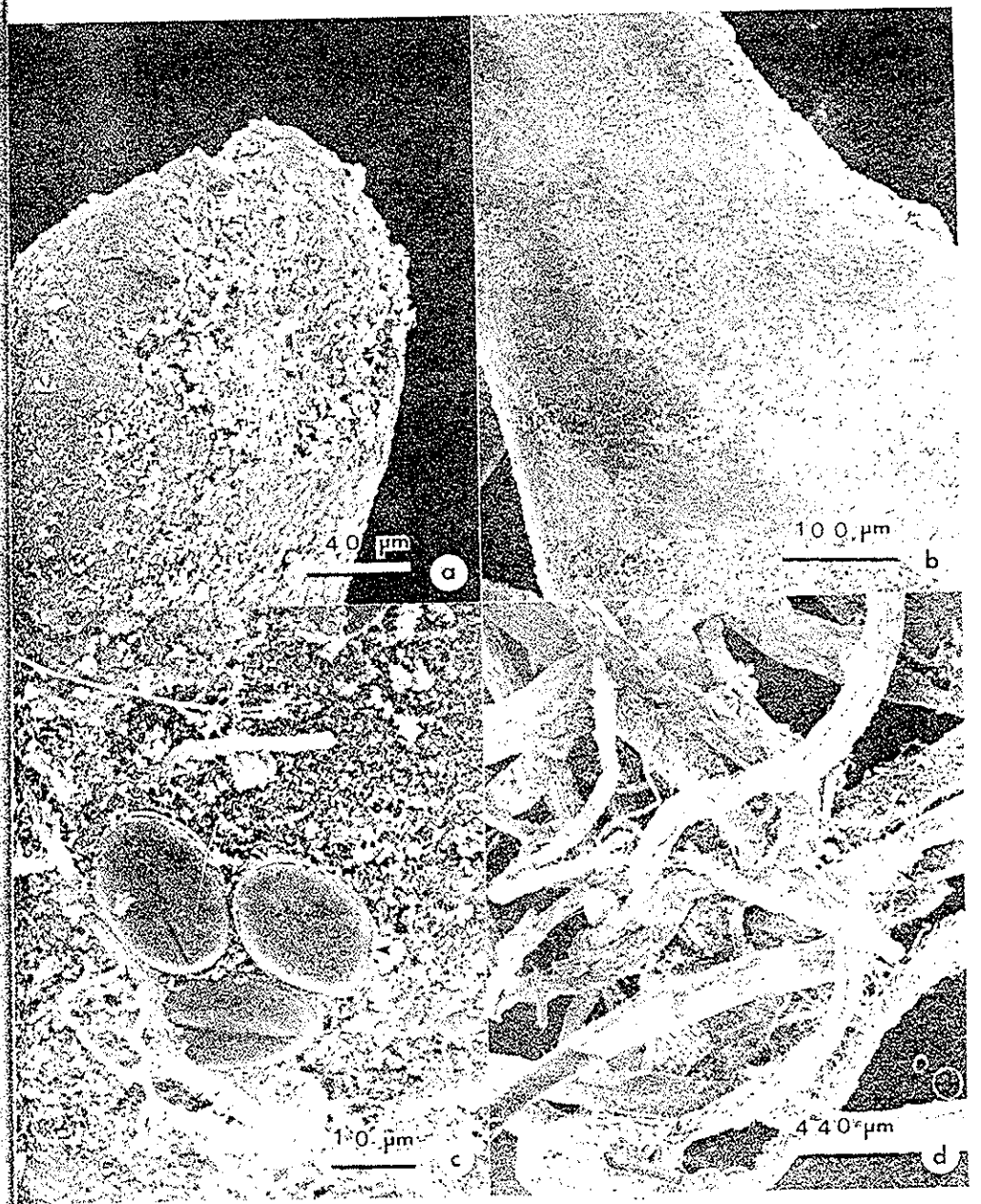


Figure 38. Stereo-images of epiphytic diatoms

a,b,c,d - 48 mm working distance, 12.5 KeV, 5-8° Tilt.

a. Cluster of Licmophora cells where Bryocladia branchlet attaches to main axis. 200X.

b. Silt accumulation and colonization of filamentous bacteria within node of Centroceras. 700 X.

c. Cluster of Synedra fasciculata v. truncata on branchlet of Bryocladia. 450 X.

d. Detail of Licmophora abbreviata showing bipartite stipe. 1000 X.

Gelidium crinale also occurs in the mid-intertidal zone, usually in the same location as Bryocladia. This plant is flattened with pinnate or irregular branches (Fig. 31c) Bacterial colonization of this alga was predominant. Silt, detritus, and some filamentous bacteria were found near the tip (Fig. 37a and b). This increased substantially from the tip, and areas characterized by flocculant particles and filamentous bacteria were easily distinguished from those overgrown by coccoid bacterial colonies (Fig. 37b). Diatoms were not dense on this host plant; Cocconeis spp., being the most common, was found in isolated clusters (Fig. 37d). Bacterial colonization continued throughout the rhizoids (Fig. 37c).

DISCUSSION

The diatom flora associated with the selected species of macroalgae in this study from the Texas coast of the Gulf of Mexico is a diverse and abundant assemblage that is typical of open coast areas rather than estuarine waters (Stowe, 1982; Sullivan, 1980). Qualitiative examination of a wide variety of host plants within the three major macroalgal classes revealed that not all plants were utilized equally as host substrates. Certain genera, such as Bangia, have been previously shown to support an impoverished epiphytic community. Other species, such as Porphyra, Petalonia, Enteromorpha, Ulva, and Polysiphonia spp. require further investigation. The epiphytic community may have been slow to develop on these seasonal algae, and therefore may have been undetected by the periodic sampling strategy employed in this study. However, differential epiphytism, even on this relatively gross scale, raises more questions about host-epiphyte interaction and about community response to abiotic factors.

In general, Rhodophytes and Phaeophytes supported heavier epiphytic diatom assemblages than did Chlorophytes along the Texas coast. This bias toward two algal classes as host substrates may reflect their abundance in a subtropical habitat, especially that of the Rhodophytes.

Most Phaeophytes did not develop heavy epiphytic growth until after their growing season was well underway. The holdfast area of the plants were the most heavily colonized.

Of those Chlorophyceae sampled, only Cladophora and Chaetomorpha developed substantial epiphytic growth. Stevensen and Stoermer (1982)

noted that epiphytic growth on Cladophora lagged behind that of the host substrate until the growth cycle of Cladophora had peaked. Possibly Cladophora was more efficient at nutrient uptake than its epiphytes and could, at any rate, out-compete them, both for space and nutrients early in the growing season.

Nearly all Enteromorpha and Ulva spp. had very sparse epiphytic growth. Both Enteromorpha and Ulva are ephemeral algae, which may account for the reduced epiphytic community. These host plants are rapidly replaced during their peak growing season, and epiphytic settlement may be deterred. Yet, in estuarine and low salinity areas, Enteromorpha and Ulva spp. support heavy epiphytic communities (Hopkins, 1964; Lee et al., 1976; Main and McIntire, 1974; Ramm, 1977). Open coast stands of Enteromorpha are poor host substrates (Edsbagge, 1966; and this study). Perhaps in estuarine and low salinity areas, such as the Baltic, both host plants and their epiphytes have evolved to co-exist in a more physiological stressful environment, while in open coast areas, the biological interaction between host plant and epiphyte plays a more dominant role.

The Rhodophyceae are, by far, more representative of the Texas coast than the other two algal classes. They also offer a wide variety of host plant shapes for epiphyte settlement. Filamentous thalli, except for Polysiphonia and Bangia, were heavily epiphytized. Cartilaginous, cylindrical species, such as Gelidium, Hypnea, and Gracilaria, and foliose plants, such as Rhodymenia, do support diverse epiphytic communities, but these communities are not as dense per unit area as the filamentous hosts. Cocconeis spp. played an important

role on all of these host plants. The family Rhodymelaceae offered the best substrate for epiphytic community development. This same family also produces biotoxins, which will retard epiphytic growth. A more intensive sampling program, involving a single species, such as Bryocladia, coupled with standard bacteriological tests for the production of antibiotics may help document spatial differences within the host plant or preferential epiphytism of certain plants within the life cycle.

In areas where long term epiphytic studies have been conducted (refer to Introduction), samples have been taken throughout an intertidal zone of several meters. In most cases, distinct macroalgal and diatom zonation patterns could be documented (Aleem, 1950; Simonsen, 1962; Edsbagge, 1966; Main and McIntire, 1974). Along the Texas coast of the Gulf of Mexico, the annual tidal range rarely exceeds one meter. More specificially, in this study, the host plants, whose epiphytic communities were taxonomically analyzed, were actually spatially separated in the intertidal zone by 20 centimeters or less. Yet, within this small distance some zonation patterns could be documented. Light-loving species, such as Achnanthes brevipes v. intermedia and Licmophora spp. were consistently more abundant on the tips of Cladophora and Centroceras, which were the host plants sampled from the high intertidal zone. On Bryocladia these taxa were more numerous on the branchlets than on the main axis. They did not flourish on Gelidium. Their abundance in spring through late summer in this and other studies (Aleem, 1950; Castenholz, 1964; Hopkins, 1964; Main and McIntire, 1974; Stevensen and Stoermer, 1982; Jacobs

and Noten, 1980; Simonsen, 1962) also indicates a tolerance of high light intensities.

In more temperate areas, Navicula pseudocomoides and Grammatophora oceanica are more restricted to lower intertidal or subtidal areas (Simonsen, 1962; Edsbagge, 1965). Along the Texas coast, these species exhibit different adaptations to the environment. Grammatophora oceanica, although present year-round, reaches maximum abundance during the winter, a time when light intensities would be at their lowest. This response is similar to that of Grammatophora spp. in the Ouse, Estuary, U.K. (Hopkins, 1964). Navicula pseudocomoides is more restricted to the bases of the host plants, especially those of the mid intertidal zone, where it would be shaded by the uppermost branches of the host plant.

The diatom communities associated with the sediments rarely exhibit any seasonal variation (McIntire and Moore, 1977; Whiting, 1983), while the epiphytic and epilithic assemblages usually have distinct seasonal changes. Along the Texas coast the seasonal changes in the epiphytic flora were very subtle. Except for a few minor exceptions, the dominant taxa were present year-round; only their relative abundance changed seasonally.

During the spring there were usually about ten taxa that co-dominated the community. The planktonic members of the metaphytic assemblages were numerically important at this time. As the season progressed the number of numerically dominant taxa steadily decreased. Achnanthes brevipes v. intermedia reached maximum abundance during the warmest part of the year; while Licmophora spp. did during the late

summer and early fall. By winter, three taxa, Rhoicosphenia genuflexa, Navicula diserta, and Grammatophora oceanica, comprised the majority of taxa.

These seasonal changes are not drastically different from those of more temperate areas. Many taxa are shared, although some, such as Rhoicosphenia abbreviata (=curvata) are replaced by more tropical (?) forms, e.g. Rhoicosphenia genuflexa. Rhoicosphenia abbreviata is commonly cited as one of the most numerous members of the epiphytic community in more temperate studies where it is very common year-round, but can reach maximum development in the winter (Taasen, 1974; Rautianinen and Ravanko, 1974; Ronnberg and Lax, 1980; Main and McIntire, 1974; Stevensen and Stoermer, 1982; Whiting, 1983). Rhoicosphenia genuflexa follows the same pattern in this study.

In temperate areas, Cocconeis scutellum co-occurs with Cocconeis placentula and Cocconeis pediculus. Cocconeis scutellum is also numerically important along the Texas coast, but its importance decreases southward as it competes with more tropical taxa, such as Cocconeis woodii, Cocconeis littoralis, and Cocconeis cf. dirupta.

During the winter the diatom communities associated with each host plant were more alike,, perhaps because as seasonal growth of the host plants decreased so would the production of any inhibitory compounds. Greater variation between diatom communities occurred during May and September as host plants were actively growing. Replicate host plants supported remarkably similar diatom assemblages (except for those collected at Galveston during September, 1978), which would indicate that possibly biological interaction between host

That there was such a gradual change in the diatom community from Galveston southward to Port Isabel was surprising, especially because Hendey (1977) found such a descrepancy in epiphytic species composition between collecting sites established along a relatively short length of coastline in northern Cornwall, U.K. The water quality along the Texas coast of the Gulf of Mexico improves from Galveston to Port Isabel as evidenced by the sediment load into the basins behind each collecting jetty, as well as by the reduction in the amount of shipping traffic in the area. The Galveston jetties mark the entrance into the heavily utilized Houston Ship Channel, where oil spills and other pollution can be locally heavy. The growing season increases gradually from Galveston to Port Isabel and undoubtedly affects the epiphytic diatom community structure as it surely does the macroalgal community. Thus, the improved water quality, the lengthened growing season, as well as the decreased salinity range southward to Port Isabel, may all be involved in creating the gradual change in the epiphytic diatom community southward from Galveston to Port Isabel. Certainly, salinity could only explain 16% of the variation in the continuum from Gaveston to Port Isabel.

Each of the host plants displayed distinct colonization and successional sequences and showed evidence of host-related differences in these patterns. A vertical zonation of epibionts was evident on each host plant, but this was usually within a few milimeters of the tips. Thus, the halving of each host plant was not on a scale that could detect these differences, which could be shown with the SEM.

Fouling occurred sporadically near the extreme tips and was, in most cases, initiated by bacteria and later replaced with diatoms.

With Centroceras, species diversity and relative abundance of the epiphytes increased distally from the tip as the microcommunity established itself first within the nodes and behind the spines and later on the surface of the corticating cells. This alga occurs in the high intertidal zone, and this type of successional sequence may be in response to light inhibition. Alternatively, inhibitory compounds may be produced in such abundance by this alga that colonization of the algal surface is inhibited until the effect of these compounds has dissipated or are no longer being produced by the host cells. A change from diatoms attached by stipes to those attached directly to the host surface occurs distally from the apex. A simple time differential explanation for this zonation pattern may not be adequate because of the change in attachment mechanisms from the tip to the base of the plant and because of the unique spatial colonization sequence on the host plant.

On Bryocladia, species diversity and relative abundance of the epibionts increased somewhat from tip to base. Toward the base of the plant, those diatom species requiring high light intensities, such as Licmophora and Achnanthes, no longer occur. These species are attached by long stipes near the apex and primarily on the branchlets. These stipes may serve to lift the diatom above the macroalgal surface in response to alleopathic compounds, as well as to lift the cells above the shading effects of the branchlets. Cocconeis spp. and Amphora spp. occur in higher numbers on the main axis than on the

plant and epiphyte played a greater role than interaction with the environment. Indeed, the changes in the diatom community were only weakly correlated with salinity changes and completely unrelated to temperature, except on a seasonal basis. This contrasts with the variation among v. between host plant reported by Main and McIntire (1974). Yet, here again, this study was in an estuary where adaptations to physiochemical stresses are of primary importance in the life strategies of organisms who live there. Thus, within host variation of the epiphytic diatom communities could easily exceed that between hosts, as biological interaction is downplayed.

From a worldwide biogegraphical point of view, it appears that many epiphytic diatoms have a cosmopolitan distribution, although the arctic taxa certainly disappear from the community as one moves toward the more tropical climates. Also, the number of species in certain genera change from temperate to tropical areas, (compare only 1 species of Mastogloia found by Hendey (1977) from British coastal waters to 12 found in this study), and some genera (Climacosphenia) are restricted to distinct temperature regimes. Thus, differences in abundances of taxa in local study areas may reflect more subtle reactions to their habitat, i.e. host plant, than to broadly changing environmental factors, such as temperature and salinity.

It is not surprising that, living within the branches of the macroalga, there is a very diverse community that are not securely attached to the host plant substrate. Intense wave action easily stirs up the silty sediments of the Gulf coast, and cells, both planktonic and benthic, settle within the branches. Small centrics,

primarily of the genera Thalassiosira, Cyclotella, and Minidiscus, were commonly washed from the host plants. Other centrics, e.g, Thalassiosira decipiens, Biddulphia biddulphiana, Odontella aurita, and Podosira montagnei, are true epiphytes. Characteristic taxa normally associated with the epipelic community were also present in the metaphytic community, but never abundant. Cymatosira belgica, Plagiogrammopsis vanheurckii, Pleurosigma spp., and Gyrosigma spp., however, were exceptions. Once trapped within the mucilaginous waters surrounding the host plants, these representatives of the planktonic and epipelic assemblages can continue to thrive as evidenced by this and other studies (Main and McIntire, 1974; Whiting, 1983).

Much of the diversity of the epiphytic assemblages was associated with the wash from the plant, especially for Cladophora and Gelidium. This tended to bias the degree of similarity between the host plants, and thus mask the possibility of detecting host specificity. However, direct observation and SEM observations of the host plants documented that the intensity of the epiphytic colonization per unit area was not uniform across the host plants studied. This was especially true for Gelidium and Bryocladia, which occurred side by side in the intertidal zone, and thus, environmental variables, which could influence the diatom community, were minimized between the two host plants on a relative scale. Thus, the host plant, whether by biochemical or structural means, was directly involved in shaping the epiphytic community associated with it, and the question of host specificity, or at least, intensity of epiphytes on different host plants, bears further investigation.

branchlets where they may be outcompeted for available space and nutrients and may even be somewhat light inhibited. Amphora spp. are coated with mucilage, and Cocconeis spp. are actually embedded in the host epidermal tissue. These attachment mechanisms could be interpreted as either responses to inhibitory compounds or to abiotic factors.

Species such as Podosira montagnei and Biddulphia biddulphiana consistently found at the base of the host plant, are inhibited by high light intensities or, perhaps, by antibiotic compounds. They are always found heavily coated with mucilage.

The notable decrease in diatom colonization per unit area of Gelidium may be related to inhibitory compounds being secreted by the host plant. Within a given area, the number of diatoms associated with Gelidum is far less than on the other plants. Most of the diversity of the diatom community associated with Gelidium was in the metaphytic community.

Often monospecific areas of Cocconeis could be found on Gelidium and on other cartilaginous hosts. Ramm (1977) has suggested that, perhaps these flat embedded taxa need a wider surface area for attachment. This would help explain the monospecific stands of Cocconeis reported consistently from cartilaginous hosts and seagrasses (refer to Introduction), but such a physical explanation cannot account for colonization of Cocconeis spp. on Chaetomorpha (this study) or of Rhopalodia on Ectocarpus (unpub. obs.).

The effect of thallus shape on the colonization sequence of the epiphytes is quite evident on those plants studied with SEM. As

projections extend from the main axes of both Centroceras and Bryocladia, not only cells, but also silt and detritus, are induced to settle out of the water column. The lack of projections on the surface of Gelidium may help to explain the paucity of the epiphytic community per unit area. These macroalgae occur in high energy environments, and it is evident that rapid, frequent water motion may enhance epiphyte removal, if not inhibit the cells from settling initially, unless the force of that motion is broken up by projections from the host plant.

The successional sequence normally encountered on artificial substrates follows in this fashion: organic coating, bacteria, low profile diatoms, high profile diatoms creating an overstory canopy (Hoagland et al., 1982). However, in this study, the high profile diatoms (especially those with long branched stipes) colonized the macroalgae first near the tips and on the branchlets, and the low lying forms occurred in greater numbers on the main axes and for certan taxa nearer the base. In fact, Rhoicosphenia genuflexa secreted a long stipe when it was attached to the upper portions of Centroceras and a shorter one or no stipe at all when it colonized the basal portions. The response of this diatom to Bryocladia was different, and a short stipe was secreted when the diatom was attached to the upper portion of this alga. Varying stipe length may be a response to possible inhibitory compounds being secreted by Centroceras rather than to abiotic factors because Rhoicophenia genuflexa is the most commonly encountered taxon, especially during the winter when light intensity is at its lowest.

Although mucilage plays an important role in binding sediments and contributing to the adhesion of cells to the substrate, its function as a protective coating for cells could also be inferred from in this study. Diatoms that were elevated above the host substrate were never seen with a mucilage coat surrounding them. However, low lying cells, both Cocconeis and Amphora were surrounded by such a coating, which could only serve as a protective device for the cell because it lies in close proximity to the host plant or because it needs some material to enhance shading. Mucilage secretions have been useful in species identification (Hoagland et al., 1982), and the variety of distinct mucilaginous structures, such as stipes and pads, can be correlated with known species. The strength of the attachment mechanisms may be species specific and not related to the actual mechanics involved to attach the cell to the surface.

The present study indicates that the microcommunity attached to these selected species of macroalgae along the Texas Gulf coast is spatially and temporally dynamic. Both metaphytic and epiphytic components of the diatoms species associated with the macroalgal host plants could be identified. There is a gradual change in the epiphytic community from Galveston to Port Isabel that is weakly correlated with salinity. The colonization sequences of the epiphytes respond to the macroalga in terms of both biological and physical factors. Such responses generate new hypotheses for understanding attachment mechanisms and possible control of fouling organisms in the marine environment.

SUMMARY

1. The metaphytic community could separated from the true epiphytic community primarily in the spring and the fall. This was due to the contribution that the phytoplankton and the epipelic diatoms made to the metaphytic assemblage at this time.

2. Differences in the diatom assemblages associated with distinct host plant species were greater than differences between replicates of the same host plant. The similarity of the metaphytic community helped mask the host-related differences. Almost unialgal stands of Cocconeis spp. could be found on the more cartilaginous host plants.

3. There was a subtle seasonal change in the diatom flora with ten taxa comprising 50-60% of the flora in the spring. The community gradually changed until only three taxa were dominant in the winter.

4. There was a gradual change in the community composition from Galveston to Port Isabel that could weakly correlated with salinity.

5. The spatial organization of the epiphytic community responded to the host plant shape and possibly to gradations in light intensity and insulation from desiccation. As the number of branches on the host plant increased, so did settlement of detrital particles and epibionts.

6. Rhoicosphenia genuflexa was the most commonly occurring diatom, comprising up to 27% of the total species counted.

7. There was a gradual increase in diversity from the tip toward the base of the host plant. Colonization of epibionts was restricted near the actively growing meristems of host plants, presumably because

of antibiotic activity. The length of the stipe of Rhoicosphenia genuflexa decreased as the diatom settled further away from the tip.

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APPENDIX A

TAXONOMIC LIST OF SPECIES

(Species Code) for Multivariate Analyses

Class Choanoflagellida
- *Acanthoeca brevipoda* Ellis

Class Chrysophyceae
- *Dictyocha fibula* Ehr.

Class Bacillariophyceae
Order Centrales
Suborder Coscinodiscineae
Family Melosiraceae
- *Melosira dubia* Kütz.
- *Paralia sulcata* (Ehr.) Cl.
- *Podosira montagnei* Kütz. (PMON)

Family Thalassiosiraceae
- *Cyclotella atomus* Hust. (CATO)
- *Cyclotella caspia* Grun.
- *Cyclotella kutzingiana* Thw.
- *Cyclotella meneghiniana* Kütz. (CMEN)
- *Cyclotella* cf. *operculata* (Ag.) Kütz.
- *Cyclotella stylorum* Brightw.
- *Cyclotella stelligera* Cl. et Grun.
- *Cyclotella* sp. A
- *Cyclotella* sp. C
- *Cyclotella* sp. D1
- *Cyclotella* sp. D2
- *Cyclotella* sp. E
- *Minidiscus* sp.
- *Skeletonema costatum* (Grev.) Cl.
- *Skeletonema tropicum* Cl.
- *Thalassiosira angstii* (Gran) Mak.
- *Thalassiosira binata* G. Fryx.
- *Thalassiosira decipiens* (Grun.) Jørg. (TDEC)
- *Thalassiosira eccentrica* (Ehr.) Cl.
- *Thalassiosira exigua* G. Fryx. et Hasle
- *Thalassiosira licea* G. Fryx.
- *Thalassiosira lundiana* G. Fryx.
- *Thalassiosira minima* Mertz.
- *Thalassiosira nanolineata* (Mann) G. Fryx. et Hasle
- *Thalassiosira oestruppi* v. *venrickae* G. Fryx. et Hasle (TOES)
- *Thalassiosira* cf. *profunda* (Hend.) Hasle (TPRO)
- *Thalassiosira pseudonana* Hasle et Heim. (TPSE)
- *Thalassiosira tenera* Proschk-Lavr.
- *Thalassiosira weissflogii* (Grun.) G. Fryx. et Hasle
- *Thalassiosira* sp. lineolate (TLIN)

Thalassiosira cf. sp. lineolate
Thalassiosira sm clear
Thalassiosira sp. D
Thalassiosira sp. E
Thalassiosira sp. F
Thalassiosira sp. H
Thalassiosira sp. I
Thalassiosira sp. J
Thalassiosira sp. K
Thalassiosira sp. L
Thalassiosira sp. M
Unidentified centric sp.1
Small centric

Family Coscinodiscaceae
Coscinodiscus sp.
Unknown centric

Family Hemidiscaceae
Roperia tesselata (Roper) Grun.

Family Heliopeltaceae
Actinoptychus senarius Ehr.

Suborder Rhizosoleniineae

Family Rhizosoleniaceae
Guinardia flaccida (Cast.) Per.
Rhizosolenia setigera Brightw.
Rhizosolenia calcar-avis Schultze

Suborder Biddulphiineae

Family Biddulphiaceae
Subfamily Hemiauloideae
Cerataulina sp.
Hemiaulus sinensis Grev.
Eucampia sp.
Subfamily Biddulphioideae
Anaulus creticus Drebes et Schulz
Anaulus vallus Nik.
Biddulphia biddulphiana (J.E. Sm.) Boyer
Eunotogramma laeve Grun.
Eunotogramma marinum (Wm. Sm.) Per.

Family Lithodesmiaceae
Bellerochea sp
Ditylum brightwelli (T. West) Grun.

Family Chaetoceraceae
Chaetoceros breve (Schütt
Chaetoceros peruvianum Brightw.
Chaetoceros sp.
Chaetoceros spore
unidentified spores

Family Eupodiscaceae
Subfamily Eupodiscoideae
Cerataulus laevis Ralfs.
Cerataulus smithii Ralfs
Odontella aurita (Lyng.) Ag.
Odontella mobiliensis (Bail.) Grun.

Family Cymatosiraceae
Arcocellus mammifera Vonstosch et Hasle
Camplyosira cymbelliformis (A.S.) Grun.
Cymatosira belgica Grun. (CBEL)
Plagiogrammopsis vanheurckii (Grun.) Vonstosch et Hasle (PVHE)

Order Pennales

Suborder Araphidineae

Family Diatomaceae
Asterionella glacialis Cast.
Dimerogramma minor (Greg.) Ralfs.
Dimerogramma inane Giff. (SYN3)
Fragilaria hyalina (Kütz.) Grun. (FHYA)
Fragilaria striatula Lyng.
Fragilaria small
Grammatophora oceanica Ehr. (GOEA)
Grammatophora oceanica v. macilienta (Wm. Sm.) Grun.
Grammatophora angulosa Ehr.
Licmophora abbreviata Ag. (LABB)
Licmophora gracilis v. anglica (Kütz.) Per. et Per. (LGRA)
Licmophora hyalina (Kütz.) Grun.
Licmophora cf. juergensii Ag.
Licmophora sp. 1
Neodelphineis pelagica Tak. (NPEL)
Opephora marina (Greg.) Petit
Opephora martyi Her.
Opephora sp. 2
Plagiogramma brockmanni Hust.
Rhaphoneis surirella (Ehr.) Grun.
Rhabdonema adriaticum Kütz.
Synedra fasciculata v. truncata Patr. (SFAS)
Synedra cf. investiens Wm. Sm.
Synedra no mark
Synedra sp. 2
Synedra sp. 6
Thalassionema nitzschioides Grun.
Thalassiothrix sp.

Suborder Raphidineae

Family Achnanthaceae
Achnanthes amoena Hust.
Achnanthes brevipes v. intermedia (Kütz.) Cl. (ABRE)
Achnanthes hauckiana Grun.
Achnanthes pseudogroenlandica Hend.
Achnanthes temperei Per.
Achnanthes sp. 4
Achnanthes sp. 6
Achnanthes sp. 9
Achnanthes sp. 10
Cocconeis cf. brittanica Naegeli
Cocconeis californica Grun.
Cocconeis costata Greg.
Cocconeis cf. dirupta Greg. (COC7)
Cocconeis cf. dirupta v. flexella (Jan. et Rab.) Grun.

Cocconeis diruptoides Hust.	
Cocconeis cf. disculoides Hust.	
Cocconeis cf. flumiensis (Grun.) Per et Per.	
Cocconeis formosa Brun.	
Cocconeis littoralis Subr.	(CLIT)
Cocconeis cf. nitens Eds.	
Cocconeis placentula Ehr.	(CPLA)
Cocconeis placentula v. euglypta (Ehr.) Grun.	(CPLE)
Cocconeis pseudiruptoides Foged	
Cocconeis stpauli Heid. et Kolbe	
Cocconeis scutellum v. parva (Grun.) Cl.	(CSUT)
Cocconeis scuttellum v. ?	
Cocconeis woodii Reyes-Vasquez	
Cocconeis sp. 10	
Cocconeis sp. 11	
Cocconeis sp. 13	
Cocconeis sp. 14	
Family Naviculaceae	
Amphiprora paludosa Wm. Sm.	
Amphiprora alata (Ehr.) Kütz.	
Amphora acutiuscula Kütz.	(ACUT)
Amphora angusta Greg.	(AANG)
Amphora beaufortiana Hust.	
Amphora bigibba Grun.	(ABIG)
Amphora coffeaeformis (Ag.) Kütz.	(ACOF)
Amphora cymbelloides Grun.	(ACYM)
Amphora exilitata Giff.	
Amphora granulata Greg.	
Amphora helenensis Giff.	(AHEL)
Amphora pestilenta Giff.	
Amphora profusa Giff.	
Amphora pusio Cl.	
Amphora strigosa Hust.	
Amphora tenerrima Hust.	(ATEN)
Amphora tenuissima Hust.	
Amphora terroris Ehr.	
Amphora sp. 1	
Amphora sp. 8	
Amphora sp. 9	
Amphora sp. 11	
Amphora sp. 12	
Amphora sp. 18	
Amphora sp. 19	
Amphora sp. 20	
Amphora sp. 100	
Amphora sp. 101	
Amphora sp. A	
Amphora small	
Berkeleya rutilans (Trent.) Grun.	(BRUT)
Berkeleya micans (Lyng.) Grun.	
Caloneis sp. 1	
Climaconeis scalaris (Meres.) Cox	

Diploneis pseudovalis Hust.	
Diploneis weissfloggi (Schmidt) Cl.	
Diploneis sp. 1	
Diploneis sp. 3	
Diploneis sp. 4	
Diploneis sp. 5	
Diploneis sp. 6	
Diploneis sp. 7	
Gyrosigma sp. 1	
Gyrosigma sp. 2	
Mastogloia amoyensis Voigt	
Mastogloia angulata Lewis	
Mastoglota binotata (Grun.) Cl.	
Mastogloia crucicula (Grun.) Cl.	
Mastogloia exigua Lewis	
Mastogloia omisa Voigt	
Mastogloia ovulum Hust.	
Mastogloia pseudexigua Voigt	
Mastogloia pumila (Cl. et Möll.) Cl.	
Mastogloia pusilla Grun.	
Mastogloia regula Hust.	
Mastogloia sp. 1	
Navicula abunda Hust.	
Navicula agnita Hust.	(NAGN)
Navicula ammophila Grun.	
Navicula bremeyeri Hust.	
Navicula cancellata Donk.	
Navicula cf. clamans Hust.	
Navicula clamans Hust.	
Navicula complanata Grun.	
Navicula cf. contenta Grun.	
Navicula delognei V.H.	(NDEL)
Navicula cf. destitutoides Hust.	
Navicula diploneoides Hust.	
Navicula directa (Wm. Sm.) Ralfs	
Navicula diserta Hust.	(NDIS)
Navicula distanoides	
Navicula forcipata Grev.	
Navicula gracilis Ehr.	
Navicula gracilis v. neglecta (Thw.) Grun.	
Navicula gregaria Donk.	
Navicula halophila (Grun.) Cl.	
Navicula johanrossi Giff.	
Navicula lyra Ehr.	
Navicula mutica Kütz.	
Navicula pavillardi Hust.	
Navicula cf. pelliculosa Hilse	
Navicula platyventris Meist	(NPLA)
Navicula protracta (Grun.) Cl.	
Navicula pseudony Hust.	
Navicula pseudocomoides Hend.	(NPSE)
Navicula radiosa Kütz.	

Navicula radiosa v. tenella (Breb.) Cl et Möll.	
Navicula ramosissima (Ag.) Cl.	
Navicula rynchocephala Kütz.	
Navicula salinarum Grun.	
Navicula salinicola Hust.	(NAVA)
Navicula stompsii Chol.	(NSTO)
Navicula cf. taedens Chol.	
Navicula tripunctata (Müll.) Bory	
Navicula sp. C	
Navicula sp. 2	
Navicula sp. 3	
Navicula sp. 7	
Navicula sp. 8	
Navicula sp. 10	
Navicula sp. 11	
Navicula sp. 13	
Navicula sp. 22	(NA22)
Navicula sp. 23	
Navicula sp. 24	
Navicula sp. 101	
Navicula sp. 102	
Navicula sp. 107	
Navicula sp. 109	
Navicula sp. 111	
Navicula sp. 112	
Navicula sp. 115	
Navicula sp. 119	(N119)
Navicula sp. 121	(N121)
Navicula sp. 124	
Navicula sp. 125	
Navicula sp. 127	
Navicula sp. 129	
Navicula sp. 130	
Navicula sp. 132	
Navicula sp. 133	
Navicula sp. 134	
Navicula sp. 135	
Navicula sp. 136	
Navicula sp. 137	
Navicula sp. 138	
Navicula sp. 139	
Navicula lg. punctate	
Navicula ?	
Navicula clear sp. 1	
Navicula clear sp. 2	
Navicula clear sp. 3	
Pleurosigma barbadense Grun.	(PBAR)
Pleurosigma cf. diverse-striatum Meist.	
Pleurosigma longum Cl.	
Pleurosigma sp. 3	
Pleurosigma sp. 4	
Pleurosigma sp. 5	

Pleurosigma sp. 6	
Pleurosigma sp. 10	
Pleurosigma sp. 11	
Stauroneis sp. 1	
Thalassiophysa hyalina (Grev.) Padd. et Sims	
Trachyneis aspera (Ehr.) Cl.	
Family Gomphonemataceae	
Rhoicosphenia genuflexa (Kütz.) Medl. nom. prov.	(RGEN)
Gomphonema sp. 1	
Family Nitzschiaceae	
Bacillaria paxillifer (Müll.) Hend.	
Cylindrotheca gracilis (Brèb.) Grun.	
Cylindrotheca closterium (Ehr.) Reim. et Lewin	
Cymatonitzschia sp.	
Gomphonitzschia sp.	
? Hantzschia isolita Giff.	
Nitzschia cf. acicularis (Kütz.) Wm. Sm.	
Nitzschia alandica Tynni	
Nitzschia angularis v. affinis Grun.	(NANG)
Nitzschia cf. apiculata (Greg.) Grun.	
Nitzschia coarctata Grun.	
Nitzschia compressa Bail.	
Nitzschia cf. dissipata (Kütz.) Grun.	
Nitzschia frustulum (Kütz.) Grun.	(NFRU)
Nitzschia frustulum v. perpusilla (Rab.) Grun.	(NFVP)
Nitzschia incrustans Grun.	(NINC)
Nitzschia laevis Hust.	
Nitzschia laevissimma Grun.	
Nitzschia longissima (Brèb.) Grun.	
Nitzschia lorenziana Grun.	
Nitzschia cf. media Hantz.	
Nitzschia obtusa v. parva Hust.	
Nitzschia ovalis Arn.	
Nitzschia paleaceae Grun.	
Nitzschia perminuta Grun.	
Nitzschia proxima Hust.	
Nitzschia pseudohybrida Hust.	
Nitzschia pseudonana Hasle	
Nitzschia pungens Grun.	
Nitzschia serpenticola Chol.	
Nitzschia cf. sibula Giff.	
Nitzschia sigma (Kütz.) Wm. Sm.	
Nitzschia sigma v. fonticola Hust.	
Nitzschia sigma v. ?	
Nitzschia sigmoidea (Nitz.) Wm. Sm.	
Nitzschia spiculum Hust.	
Nitzschia cf. stompsii Chol.	
Nitzschia cf. thermalis (Ehr.) Auerw.	
Nitzschia valdestriata Aleem et Hust.	
Nitzschia vidovichii Grun.	
Nitzschia sp. 1	
Nitzschia sp. 2	

Nitzschia sp. 5
Nitzschia sp. 6
Nitzschia sp. 7
Nitzschia sp. 8
Nitzschia sp. 9
Nitzschia sp. 11
Nitzschia sp. 101 (N101)
Nitzschia sp. 102 + CN
Nitzschia sp. 104
Nitzschia sp. 108
Nitzschia sp. 109
Nitzschia sp. 110
Nitzschia sp. 111
Nitzschia sp. 113
Nitzschia sp. 115
Nitzschia sp. 116
Nitzschia sp. 117
Nitzschia sp. 118
Nitzschia sp. 119
Pseudoeunotia doliolus (Wall.) Grun.

Family Epithemiaceae
Rhopalodia gibberula (Ehr.) Müll.
Rhopalodia gibberula v. vanheurckii Müll.
Rhopalodia musculus v. constricta (Bréb.) Per. et Per.
Rhopalodia operculata (Ag.) Hank.

Family Surirellaceae
Surirella ovata v. salina (Wm.) Sm.
Surirella fatuosa (Ehr.) Kütz.

APPENDIX B

COMMUNITY COMPOSITION STATISTICS

Comparison of Number of Species, Diversity (Both H" and Simpsons), and Redundancy Values for the Pooled Host Plants for the Two Year Study Period CD = Cladophora dalmatica, CC = Centroceras clavulatum, GC = Gelidium crinale, BC = Bryocladia cuspidata.

Sample	N	H"	Simp.	REDI
CD-G-9-77	28	2.25	.611	.556
CD-G-1-78	53	3.11	.808	.489
CD-G-5-78	55	3.75	.877	.377
CD-PA-9-77	26	2.33	.701	.525
CD-PA-1-78	49	3.15	.749	.468
CD-PA-5-78	56	4.45	.936	.250
CD-PI-9-77	39	2.79	.761	.499
CD-PI-1-78	48	2.62	.661	.567
CD-PI-5-78	36	2.70	.674	.502
CD-1-G-9-78	34	3.29	.849	.370
CD-2-G-9-78	20	3.33	.881	.236
CD-3-G-9-78	19	2.56	.711	.408
CD-1-G-1-79	39	3.20	.814	.417
CD-2-G-1-79	45	3.53	.868	.378
CD-3-G-1-79	46	3.14	.780	.458
CD-1-G-5-79	31	2.94	.806	.426
CD-2-G-5-79	35	2.98	.807	.441
CD-3-G-5-79	27	2.71	.778	.447
CC-1-PA-9-78	46	2.81	.713	.523
CC-2-PA-9-78	74	4.53	.926	.299
CC-3-PA-9-78	59	3.38	.789	.457
CC-1-PA-1-79	45	2.72	.675	.536
CC-2-PA-1-79	46	2.88	.733	.509
CC-3-PA-1-79	50	2.83	.709	.532
CD-1-PA-5-79	39	2.78	.771	.502
CD-2-PA-5-79	24	2.55	.760	.460
CD-3-PA-5-79	34	2.57	.717	.520
CC-1-PI-9-78	52	3.41	.831	.429
CC-2-PI-9-78	48	2.93	.739	.508
CC-3-PI-9-78	40	2.68	.719	.524
CC-1-PI-1-79	61	3.89	.888	.373

CC-2-PI-1-79	60	3.10	.741	.512
CC-3-PI-1-79	59	3.60	.835	.419
CD-1-PI-5-79	50	2.75	.630	.550
CD-2-PI-5-79	50	3.22	.783	.459
CD-3-PI-5-79	52	2.49	.577	.603
GC-G-9-77	40	3.66	.878	.329
GC-G-1-78	86	4.44	.915	.338
GC-G-5-78	49	3.84	.883	.337
GC-PA-9-77	57	2.58	.652	.601
GC-PA-1-78	63	3.98	.874	.363
GC-PA-5-78	57	3.30	.760	.467
GC-PI-9-77	60	4.37	.924	.281
GC-PI-1-78	43	3.37	.845	.400
GC-PI-5-78	50	3.62	.831	.384
GC-1-G-9-78	43	3.52	.859	.372
GC-2-G-9-78	21	1.74	.521	.623
GC-3-G-9-78	33	2.96	.809	.434
GC-1-G-1-79	50	2/96	.753	.508
GC-2-G-1-79	55	3.43	.827	.438
GC-3-G-1-79	40	S.96	.753	.470
GC-1-G-5-79	42	3.51	.846	.370
GC-2-G-5-79	53	4.24	.916	.279
GC-3-G-5-79	40	3.43	.844	.374
GC-1-PA-9-78	68	4.07	.892	.360
GC-2-PA-9-78	57	3.99	.891	.340
GC-3-PA-9-78	54	3.97	.892	.333
GC-1-PA-1-79	47	3.22	.805	.447
GC-2-PA-1-79	28	2.36	.702	.530
GC-3-PA-1-79	52	2.90	.745	.527
GC-1-PA-5-79	48	3.53	.841	.393
GC-2-PA-5-79	52	3.54	.817	.406
GC-3-PA-5-79	44	2.89	.747	.500
GC-1-PI-9-78	58	3.25	.803	.479
GC-2-PI-9-78	47	3.23	.805	.445
GC-3-PI-9-78	57	3.46	.820	.440
GC-1-PI-1-79	53	2.80	.702	.548
GC-2-PI-1-79	72	4.12	.881	.363
GC-3-PI-1-79	40	3.09	.801	.444
GC-1-PI-5-79	79	4.46	.911	.324
GC-2-PI-5-79	56	3.18	.746	.488
GC-3-PI-5-79	56	3.63	.847	.404
BC-G-9-77	32	3.17	.839	.382
BC-G-1-78	85	4.51	.906	.332
BC-G-5-78	34	2.91	.814	.449
BC-PA-9-77	66	4.22	.904	.329
BC-PA-1-78	34	2.30	.675	.576
BC-PA-5-78	62	4.39	.918	.282
BC-PI-9-77	65	4.19	.911	.331
BC-PI-1-78	48	3.28	.809	.440
BC-PI-5-78	73	4.20	.888	.353
BC-1-G-9-78	41	3.82	.892	.303
BC-2-G-9-78	33	3.50	.878	.320

BC-3-G-9-78	33	3.16	.844	.392
BC-1-G-1-79	50	3.62	.864	.384
BC-2-G-1-79	42	2.44	.651	.580
BC-3-G-1-79	42	3.17	.782	.437
BC-2-G-5-79	39	3.53	.869	.351
BC-3-G-5-79	40	3.33	.857	.395
BC-1-PA-9-78	66	4.48	.928	.281
BC-2-PA-9-78	63	4.24	.919	.315
BC-3-PA-9-78	77	4.63	.928	.287
BC-1-PA-1-79	52	3.88	.897	.342
BC-2-PA-1-79	61	3.53	.794	.437
BC-3-PA-1-79	29	1.95	.494	.626
BC-1-PA-5-79	44	3.66	.880	.350
BC-2-PA-5-79	45	3.62	.856	.362
BC-3-PA-5-59	53	3.58	.833	.401
BC-1-PI-9-78	34	2.88	.781	.465
BC-2-PI-9-78	70	3.98	.885	.382
BC-3-PI-9-78	73	4.19	.902	.353
BC-1-PI-1-79	83	4.51	.910	.323
BC-2-PI-1-79	56	3.86	.884	.360
BC-3-PI-1-79	69	4.59	.933	.270
BC-1-PI-5-79	83	4.67	.932	.295
BC-2-PI-5-79	58	4.02	.882	.339
BC-3-PI-5-79	77	4.58	.931	.296

APPENDIX C

NICHE BREADTH

Niche breadth values for dominant taxa at each site. Range of values are: BjA=1-3 for data pooled by plant; BjB=1-3 for data pooled by treatment; BjC=1-3 for data pooled by season; BjAB=1-9 for data showing the interaction of factor A and B.

GALVESTON-YEAR 1

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	2.42	2.33	2.98	4.80
Amphora acutiuscula	2.59	2.27	2.12	4.45
Cocconeis scutellum	1.20	2.21	1.75	2.48
Cymatosira belgica	2.61	2.77	1.97	6.10
Grammatophora oceanica	2.91	2.67	2.25	7.05
Licmophora abbreviata	1.82	2.94	2.05	4.77
Navicula diserta	2.96	2.99	1.83	8.78
Navicula pseudocomoides	2.20	1.71	1.62	3.52
Navicula stompsii	2.48	2.97	1.55	6.86
Nitzschia frustulum	2.64	2.68	1.59	5.75
Rhoicosphenia genuflexa	2.69	2.66	1.96	6.80
Synedra fasciculata v. truncata	2.53	2.82	2.81	6.86
Thalassiosira cf. profunda	2.82	1.62	2.26	4.52
lineate Thalassiosira sp.	2.37	1.62	2.14	4.16

Port Aransas-Year 1

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	2.37	2.74	2.04	6.11
Amphora acutiuscula	2.69	2.29	2.54	5.58
Cocconeis scutellum	1.92	2.56	2.37	4.85
Cymatosira belgica	2.79	2.72	2.84	6.82
Grammatophora oceanica	1.52	2.67	1.99	3.96
Licmophora abbreviata	1.80	2.05	1.79	3.52

Navicula diserta	2.54	2.92	2.80	7.27
Navicula pseudocomoides	2.96	1.91	2.27	5.44
Navicula stompsii	2.62	2.99	1.83	7.60
Nitzschia frustulum	2.84	2.55	2.40	6.66
Rhoicosphenia genuflexa	2.94	2.83	2.30	8.23
Synedra fasciculata v. truncata	2.89	2.98	2.74	8.05
Thalassiosira cf. profunda	2.95	2.15	2.47	6.15
lineate Thalassiosira sp.	2.80	2.46	2.69	6.44

Port Isabel-Year 1

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	2.87	2.81	2.03	6.62
Amphora acutiuscula	1.57	2.47	2.28	3.61
Cocconeis scutellum	2.68	2.22	2.33	5.62
Cymatosira belgica	2.70	2.48	2.44	6.38
Grammatophora oceanica	2.31	2.39	1.65	4.42
Licmophora abbreviata	1.12	2.39	1.05	2.67
Navicula diserta	2.73	2.92	2.82	8.35
Navicula pseudocomoides	2.71	2.73	2.95	6.61
Navicula stompsii	2.84	2.99	2.04	7.79
Nitzschia frustulum	2.91	2.93	2.71	7.96
Rhoicosphenia genuflexa	2.92	2.73	2.79	7.79
Synedra fasciculata v. truncata	2.89	2.62	2.37	5.40
Thalassiosira cf. profunda	2.69	2.05	2.23	5.42
lineate Thalassiosira sp.	2.56	2.25	2.17	5.59

Galveston-Year 2

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	1.80	2.98	1.15	5.50
Amphora acutiuscula	2.93	2.75	2.95	7.87
Cocconeis scutellum	1.10	2.06	1.72	2.90
Cymatosira belgica	2.78	2.88	2.40	6.78
Grammatophora oceanica	2.94	2.88	2.93	8.31
Licmophora abbreviata	2.32	2.06	1.30	4.36
Navicula diserta	2.92	2.98	2.56	8.65
Navicula pseudocomoides	1.81	2.62	2.27	4.58
Navicula stompsii	2.76	2.95	2.86	8.11
Nitzschia frustulum	2.75	2.98	2.45	7.96
Rhoicosphenia genuflexa	2.85	2.89	2.78	8.23
Synedra fasciculata v. truncata	2.89	2.82	2.20	8.13
Thalassiosira cf. profunda	2.94	2.19	2.68	6.28
lineate Thalassiosira sp.	2.55	2.39	1.111	6.08

Port Aransas-Year 2

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	2.23	2.59	1.97	5.64
Amphora acutiuscula	1.65	2.87	1.79	4.51
Cocconeis scutellum	2.32	2.53	2.85	5.78
Cymatosira belgica	2.91	2.07	2.85	7.83
Grammatophora oceanica	2.56	2.85	1.97	7.26
Licmophora abbreviata	1.84	1.26	1.17	2.31
Navicula diserta	2.92	2.94	2.19	8.37
Navicula pseudocomoides	2.84	2.26	2.99	6.31
Navicula stompsii	2.78	2.76	2.03	7.65
Nitzschia frustulum	2.69	2.95	2.52	7.81
Rhoicosphenia genuflexa	2.93	2.82	2.84	8.26
Synedra fasciculata v. truncata	2.17	2.74	1.56	5.49
Thalassiosira cf. profunda	2.98	1.97	2.84	5.86
lineate Thalassiosira sp.	2.95	2.46	2.03	7.12

Port Isabel-Year 2

Species	BjA	BjB	BjC	BjAB
Achnanthes brevipes	1.30	2.69	1.11	3.43
Amphora acutiuscula	2.55	2.79	2.94	6.78
Cocconeis scutellum	2.99	2.54	2.65	7.39
Cymatosira belgica	2.76	2.46	2.38	6.61
Grammatophora oceanica	2.44	2.83	2.21	6.20
Licmophora abbreviata	2.25	1.14	2.78	2.56
Navicula diserta	2.94	2.85	2.56	8.23
Navicula pseudocomoides	2.79	2.51	2.90	6.62
Navicula stompsii	2.55	2.81	2.20	7.04
Nitzschia frustulum	2.92	2.97	2.69	8.64
Rhoicosphenia genuflexa	2.75	2.87	2.93	7.87
Synedra fasciculata v. truncata	2.10	2.99	2.13	6.07
Thalassiosira cf. profunda	2.94	2.22	2.96	6.47
lineate Thalassiosira sp.	2.81	2.13	1.99	5.97

VITA

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