

AN ABSTRACT OF THE THESIS OF

Mark Carlos Whiting for the degree of Doctor of Philosophy in Botany
and Plant Pathology presented on May 2, 1983

Title: Distributional Patterns and Taxonomic Structure of Diatom
Assemblages in Netarts Bay, Oregon

Abstract approved: C. David McIntire
C. David McIntire

Epiphytic, planktonic and benthic diatom assemblages were investigated in Netarts Bay, Oregon. Samples were collected for a one-year period from February 1980 to March 1981. A planktonic flora was observed only during periods of off-shore enrichment when marine neritic species were abundant and were transported into the bay by tidal currents. Multivariate analyses demonstrated that epiphytic and benthic assemblages were distinct, with relatively little overlap in distribution of dominant taxa. The dynamics of the epiphyte assemblage were seasonal in nature, presumably related to the growth dynamics of the host plant (Zostera marina) as well as to seasonal changes in the physical environment. Intertidal exposure gradients exerted little influence on the distribution of dominant epiphyte taxa. In contrast to the epiphytic flora, dominant benthic taxa

demonstrated little seasonal variation in relative abundance. The effects of intertidal exposure gradients on benthic diatoms were dependent on interactions with different sediment types. Benthic taxa in silty sediments were virtually unaffected by intertidal gradients while many taxa in sandy sediments had marked intertidal preferences. Most of the variation in the distribution and relative abundances of benthic taxa could be explained by the physical properties of the sediment, especially mean particle diameter, sediment organic content, and the degree of sediment sorting.

**Distributional Patterns and Taxonomic Structure
of Diatom Assemblages in Netarts Bay, Oregon**

by

Mark Carlos Whiting

A THESIS

submitted to

Oregon State University

**in partial fulfillment of
the requirements for the
degree of**

Doctor of Philosophy

Completed May 2, 1983

Commencement June 1983

APPROVED:

C. David Mc Intire

Professor of Botany and Plant Pathology in charge of major

Thomas C. Moore

Head of Department of Botany and Plant Pathology

John C. Ringle

Dean of Graduate School

Date thesis is presented _____ May 2, 1983

Typed by WORD PROCESSING SPECIALISTS for _____ Mark Carlos Whiting

ACKNOWLEDGEMENTS

It would not be fair to present this thesis without acknowledging the many people who contributed, and to a large extent made this project possible. In particular, I extend heartfelt thanks to my major professor, Dr. David McIntire, who provided friendship, direction and support for my efforts. Without his enthusiasm for my work, the long hours spent at the microscope, at the computer center, or writing manuscripts would have been too discouraging. I have valued and enjoyed the tutorage of Dr. Harry Phinney in the fields of microscopy and phycology, and it was a shared fondness for chocolate ice cream that kept up my metabolism during critical phases in data analysis. I also extend thanks to the other members of my original committee, Dr. David Willis, Dr. James Hall and Dr. Jack Lyford and to Dr. Bruce Frey and Dr. Glenn Fisher who served as substitutes. These patient men were inconvenienced by committee meetings, preliminary and final exams, and helped edit a long thesis manuscript.

Graduate students with whom I have been fortunate enough to have been associated have also made valuable contributions. Mike Amspoker's own experience with estuarine diatoms provided a starting point for my own work. Michael Davis provided the majority of the environmental data that was used to make biogeographical interpretations of diatom distributions. Nancy Engst and Mary Kentula

accompanied me during my fieldwork and shared the anguish of cold, winter days and broken-down boat engines.

Finally, it is important to mention that funding for this project was made available by the EPA grant No. R 806780, made to Dr. McIntire.

TABLE OF CONTENTS

	<u>Page</u>
I. INTRODUCTION.....	1
II. LITERATURE REVIEW.....	8
Planktonic Diatoms.....	8
Epiphytic Diatoms.....	10
Benthic Diatoms.....	15
III. DESCRIPTION OF NETARTS BAY.....	23
IV. MATERIALS AND METHODS.....	27
Sampling Strategy.....	27
Sampling Methods.....	29
Diatom Assemblages.....	29
Physical Variables.....	31
Data Analysis.....	33
Community Composition Parameters.....	33
Multivariate Analysis.....	36
V. RESULTS.....	40
Analysis of Environmental Data.....	40
Raw Data.....	40
Structure of the Environmental Data.....	44
The Diatom Flora.....	47
Community Organization.....	69
Community Composition Parameters.....	69
Ordination Analyses.....	82
Community Structures Relative to Environmental Data.....	92
VI. DISCUSSION.....	101
BIBLIOGRAPHY	118
APPENDIX	128

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1 Map of Netarts Bay, showing intensive sampling sites: SAND site (A), FINE SAND site (B) and SILT site (C).	24
2 Monthly changes in sediment height at the intensive study sites in Netarts Bay.	42
3 Monthly changes in the ratio of surface chlorophyll <u>a</u> to deep chlorophyll <u>a</u> (4 to 5 cm below the surface) at all benthic sampling stations.	43
4 Reciprocal Averaging ordination of benthic and epiphytic samples.	83
5 Reciprocal Averaging ordination of benthic and epiphytic species.	85
6 Reciprocal Averaging ordination of epiphyte samples.	89
7 Reciprocal Averaging ordination of dominant epiphyte species.	90

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1 Conversions for sediment particle diameters and Inman's phi coefficients.	45
2 Factor structure of the first three principal components generated from the environmental variables associated with benthic samples.	48
3 A list of planktonic species found in Netarts Bay during three months in 1980.	51
4 A list of 72 selected taxa, their total relative abundance (N_T), and their relative abundance in epiphyte (N_E) and benthic (N_B) samples.	55
5 A list of 36 selected benthic taxa with their total abundances in samples from the Sand (N_{SA}), Fine Sand (N_{FS}), and Silt (N_{SI}) sites.	60
6 The relationship between 22 selected epiphytic taxa and three environmental variables: intertidal height (TIDE), daylength (DAYL), and water temperature (TEMP).	63
7 The relationship between 36 selected benthic taxa and the first three principal components of the environmental data matrix.	66
8 Samples size (N), species richness (S), redundancy (RED), and species diversity (H'') for 36 samples of epiphytic diatoms.	70
9 Mean species diversity (\bar{H}'') and standard error ($S_{\bar{H}''}$) for epiphyte samples relative to sample date and to tidal height.	72
10 Sample size (N), species richness (S), redundancy (RED), and species diversity (H'') for the 22 samples of benthic diatoms from the Sand site.	74

LIST OF TABLES
(Continued)

<u>Table</u>	<u>Page</u>
11 Sample size (N), species richness (S), redundancy (RED), and species diversity (H") for the 19 samples of benthic diatoms from the Fine Sand site.	76
12 Sample size (N), species richness (S), redundancy (RED), and species diversity (H") for the 23 samples of benthic diatoms from the Silt site.	78
13 Mean species diversity (\bar{H}) and standard error ($S_{\bar{H}}$) for benthic samples relative to sample data, tidal height and sediment type.	80
14 A comparison of the similarity of pooled epiphytic and benthic samples using SIMI and Jaccard indices.	81
15 Correlations between environmental variables and two RA axes generated from an analysis of epiphyte data.	93
16 Correlations between environmental variables and two RA axes generated from an analysis of benthic data.	94
17 Correlations between environmental variables, 36 selected benthic taxa, canonical variables from a canonical correlation analysis of the benthic data.	96

**DISTRIBUTIONAL PATTERNS AND TAXONOMIC
STRUCTURE OF DIATOM ASSEMBLAGES IN
NETARTS BAY, OREGON**

I. I N T R O D U C T I O N

The unique and complex interactions between physical and biological processes in estuaries generate highly productive ecosystems of great scientific interest. Estuaries are coastal embayments where freshwater runoff from land mixes with tidal water from the ocean. Therefore, estuaries are ecotones, transitional zones between freshwater and saltwater ecosystems with tremendous biological and environmental diversity. While many of the characteristics of estuaries are the result of either fluvial or oceanic processes, their uniqueness is due to an interaction of these influences.

An appreciation for the diversity of estuaries may be obtained by an examination of classification schemes. For example, estuaries may be characterized by the relative influence of fluvial or oceanic processes (Pritchard, 1967). An estuary may be:

1. A highly stratified "salt wedge" type, where there is a pronounced vertical salt gradient, or halocline, caused by freshwater flow over a saltwater "wedge" of dense water. Such estuaries result when freshwater flow dominates over turbulences from tidal or wave action that would disrupt stratification by mixing the water masses. These estuaries are common on the Gulf Coast where tides have small amplitudes. They

are also typical of large rivers with high freshwater discharge.

2. A partially stratified type, where the influence of freshwater flow and tidal mixing are more nearly equal. The freshwater flow produces a halocline, but this becomes diffuse as tidal energy mixes waters of different density. This type of estuary is probably the most common type.
3. A non-stratified or mixed type, dominated by relatively powerful tidal forces and weak or diffuse sources of freshwater runoff. Temperature and salinity variations are along horizontal gradients, not vertical ones. These estuaries are common on the East Coast where intermediate tidal amplitudes and medium-size rivers merge in enormous estuaries like the Chesapeake Bay. Coastal embayments behind barrier islands are usually classified in this category.

Estuaries also may be classified on the basis of their geomorphological origins (Pritchard, 1967). Relative to this system, estuaries may be:

1. Drowned river valleys. Many of these are found on subsiding coastlines like the east coast of North America.
2. Fjords, which have terminal moraines forming bars at the mouth. These are common in Norway, Alaska and British Columbia.
3. Bar-built estuaries. These have submerged dunes or wave-built bars that enclose bays or sounds. These also are common on the east coast of North America.
4. Estuaries built by tectonic processes such as faulting or subsidence. San Francisco Bay is an example.
5. River deltas. The Mississippi delta is an example.

Estuaries trap fluvial and marine sediments that are constantly shifting in response to waves and currents (Odum, 1971; Anderson,

1973). Estuarine organisms must tolerate erosion and deposition of sediment, wide ranges in salinity and temperature, and water with high turbidity. Nevertheless, estuaries are highly productive ecosystems. Waves and currents can be important energy subsidies. As long as turbulence is moderate and scouring does not occur, organisms may benefit from the renewal and mixing of nutrients and the aeration of water. Turbulence may also suspend microflora which allows bivalves and other sessile animals to feed and to flush away waste products.

Estuarine productivity is enhanced by nutrient inputs that may come from land runoff, from the sea, or from the rich sediments within the system. Burrowing animals and the roots of aquatic vascular plants aid in the release of nutrients from sediments which subsequently become available to planktonic organisms.

From an economic point of view, estuaries are important as rearing areas for many coastal and marine fishes. Most of the crabs and shrimp of commercial value spend part of their life cycles in estuaries. Moreover, juvenile stages of many marine organisms depend on tidal creeks, marsh fringes and seagrass beds for feeding and refuge (Weinstein, 1979).

In general, estuaries have rates of gross primary production that are in excess of their community respiration rates (Odum, 1971). Therefore, these ecosystems may export a large proportion of their organic matter, usually as detritus from macrophytes and by

emigration of fishes and crustacea. Detritus and benthic algae may be entrained by flood tides and carried shoreward as an organic input to beaches and saltmarshes (Anderson, 1973; Baillie and Welsh, 1980). Another fraction of estuarine detritus may be entrained by ebb tides and become an export to offshore communities and ocean beaches (Josselyn and Mathieson, 1980).

Temperate zone estuaries are often very different from estuaries in the tropics. Tropical estuaries usually are highly modified by biological activity (e.g. by processes associated with corals, mangroves, and seagrasses) and often have minimal seasonal variation. In contrast, temperate estuaries are largely controlled by physical processes, often with definite seasonal cycles with respect to photoperiod and lunar (tidal) periodicity (Odum, 1971).

One of the keys to survival for estuarine organisms is their spatial and temporal variability. Often communities respond to physical changes by a seasonal succession of organisms. Saltwater species often spend only a part of their life history in estuaries, and freshwater species may enter only when periods of freshwater discharge are high. Species that spend their whole lives in estuaries may have resting stages such as spores or seeds that allow them to survive through the most difficult periods. Other organisms may have an alternation of generations, such as the polyp-medusae stages of coelenterates or the sporophyte-gametophyte stages of plants, so that different stages of a life cycle may predominate during certain

environmental conditions. Nevertheless, some macrophytes and some of the longer-lived animals may spend their whole lives in estuaries, and have correspondingly broad tolerances for a variety of environmental conditions.

Among estuarine plants, diatoms are one of the most abundant and ubiquitous groups. They are important components of phytoplankton, epiphytic and epilithic assemblages, and of sediment associated assemblages (Odum, 1971; Round, 1971). Also, they are often common in the shifting sands of beaches where there are few other plants (Amspoker, 1977; Gunter, 1979). Diatoms have high rates of photosynthesis, often greater than what their biomass would suggest (Beardall et al., 1976; Thomas et al., 1978). Epiphytic diatoms may represent one-third of the joint primary production of seagrass-epiphyte associations (Jones, 1968), and assemblages of benthic diatoms may have gross primary production rates of $100-325 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ or more (McIntire and Moore, 1977).

Diatoms play important roles in estuaries other than that of primary producers. Benthic algal floras may help to stabilize sediments (Frostick and McCave, 1979), while epiphytic diatoms may be related to the dynamics of nutrients and detritus. Furthermore, epiphytic diatoms may be involved in the senescence and sloughing of the leaves of aquatic angiosperms (Phillips et al., 1978). Because such epiphytes surround the leaves with a layer of cells and quiescent water, they may alter the quantity and quality of nutrients

leached from the leaves of aquatic angiosperms (McRoy and Goering, 1974).

The research reported in this thesis was conducted in Netarts Bay, a bar-built estuary located on the Oregon coast. The bay is protected from excessive human activity, as nearly half the bay is a state shellfish reserve. In 1979, the Environmental Protection Agency conducted a preliminary investigation of the hydrology and nutrient dynamics of the bay. This research indicated that nutrient dynamics were greatly influenced by biological processes, especially in the vicinity of eelgrass beds. The EPA funded several follow-up studies to investigate the species composition of plant communities, plant biomass, primary production, and nutrient uptake and dispersal. The research presented in this thesis was part of these investigations.

The general objective of this study was to generate and examine hypotheses concerning mechanisms that account for spatial and temporal patterns in the diatom flora of Netarts Bay, Oregon. To achieve this goal, seasonal floristic patterns were examined in planktonic, epiphytic and benthic diatom assemblages for a period of one year. Floristic patterns were examined relative to substrate characteristics, temperature, and available light.

In this thesis, the term "benthic" will be used to refer to organisms that are associated with submerged or intertidal sediments. Other terms that are often used synonymously with this usage

are "epibenthic" and "edaphic." Unfortunately, these terms may be somewhat misleading, each in its own way. "Epibenthic" seems to refer only to those organisms found on the top of sediment, and not to those buried in it, while "edaphic" indicates an association with soil. The term "soil" usually is avoided in reference to marine sediment. While the term "benthic" is sometimes used in reference to macrophytes and associated epiphytes, this thesis considers epiphytes separately, and "benthic diatoms" will refer to both epipsammic diatoms (attached to sediment particles) and to epipelagic diatoms (free living in the sediment).

II. L I T E R A T U R E R E V I E W

Planktonic Diatoms

The published information on the ecology of diatoms is voluminous, especially with respect to the planktonic forms. However, a large fraction of this information is related to freshwater ecosystems, and very little of it concerns the Pacific Northwest coast specifically. Nevertheless, there are some generalizations that can be made. For example, in both freshwater and saltwater ecosystems, planktonic assemblages are mainly regulated by hydrographic characteristics, light intensity, nutrients, and grazing.

Freshwater ecosystems can be characterized by the amount and nature of nutrient inputs, the shape of the water basin, water discharge and flow rates, and the occurrence, timing, and duration of thermal stratification. These influences are important in marine and estuarine ecosystems, with the addition that haloclines may also be important. In some estuaries, summer stratification and low discharge rates may promote phytoplankton blooms by allowing a buildup of biomass as flushing and mixing rates decrease (Welsh et al., 1972). In other cases, mixing and high runoff from land may fertilize estuarine or coastal water and stimulate plankton blooms (Loftus et al., 1972; Ragothaman and Rao, 1978; Samuels et al., 1979). In general, phytoplankton blooms are initiated by upwelling, mixing of water masses by turbulence, runoff from land, or by nutrient regener-

ation during winter (Guillard and Kilham, 1977). Initially, planktonic blooms are characterized by fast growing species which are replaced by other taxa as nutrients become depleted. The floristic patterns of phytoplankton succession are thought to be governed by competition and by grazing (Guillard and Kilham, 1977). Short winter days, especially when accompanied by overcast skies, can limit phytoplankton production (Bruno et al., 1980; Lewin, 1977). The importance of grazing in regulating phytoplankton standing crop is emphasized in a review by Cushing (1964).

There are two general types of phytoplankton blooms noticed in the coastal water of the Pacific Northwest. One type is associated with off-shore upwelling which is initiated by strong northern winds (Lewin, 1977; Fox and Davis, 1979), and is characterized by an abundant and diverse diatom flora (Lewin, 1977). A second type of bloom occurs in the surf-zone along the coastline. These blooms are distinct in their origin, species composition, and timing (Lewin, 1977). Wrack that is left on the strand line of beaches decays and enriches interstitial water. These nutrients may be washed by heavy rains into the surf-zone where blooms may develop if water turbulence subsides after the passing of the storm (Gunter, 1979). Surf-zone blooms are dominated by only two diatom species: Chaetoceros armatum and Asterionella socialis. Lewin and Norris (1970) reported that the surf-zone blooms on the coast of New Zealand are likewise dominated by Chaetoceros armatum and a species of Asterionella (A. japonica).

In the Yaquina River estuary, Karentz (1975) found that the planktonic diatoms in spring, summer and fall were distributed as a continuum, gradually changing from a marine flora to freshwater plankton as one proceeds up river. In the winter, high discharge rates from winter runoff tended to flush the river of planktonic taxa, and a homogeneous assemblage of tychoplanktonic species became suspended in the water column.

Floristic accounts of the marine plankton of the North Pacific Ocean are few in number. Two of the most useful floristic treatments were presented by Gran and Angst (1931) and Cupp (1943).

Epiphytic Diatoms

Because of the shallowness of estuaries and the relative importance of the littoral zone, epiphytes and their host plants are often important contributors to estuarine production and standing crop. Epiphytes may compose one-fourth of the above-ground standing crop in a Zostera marina-epiphyte association (Penhale, 1977). Unlike the net production of most macrophytes, epiphyte production is immediately available to estuarine food chains through the process of grazing. In contrast, Zostera marina, and probably most seaweeds, enter the food chain mainly on a seasonal basis as detritus (Zimmerman et al., 1979).

Epiphyte growth and density are influenced by photoperiod and insolation, salinity, temperature, tidal exposure and the nature of

the host plant (Main and McIntire, 1974). Host plants are not passive substrates. McRoy and Goering (1974) demonstrated that rooted aquatic vascular plants may act as nutrient pumps, mobilizing regenerated nutrients from sediments and translocating them to leaves. Some fraction of these nutrients are leached from the leaves, either as inorganic nutrients or as organic compounds which must pass through the epiphyte layer before they enter the water column. These authors suggest that these nutrients may stimulate epiphyte growth. In return, the vascular host may derive some benefit from the protective layer of algal cells and mucilage during exposure at low tides.

The exchange of nutrients and other possible benefits accruing to the host or epiphytes suggest that a commensal or even a mutualistic relationship may exist. On the other hand, commensal and mutualistic interactions are generally dependent on intricate coadaptations. If epiphytes and their host plants commonly have such interactions and if they were important, then some degree of host-specificity would be expected. In most instances, host-specificity among diatoms is the exception and not the rule. Cattano and Kalff (1979) found that epiphyte biomass and production were the same on plastic ribbons as on live Potamogeton. The epiphytes of three different species of seagrasses in Mississippi Sound were found to be virtually identical in species composition (Sullivan, 1979). In the Yaquina River, no specificity was found among various host plants studied by Main and McIntire (1974). Even epilithic floras, or at

least floras associated with solid substrates in estuaries, closely resemble epiphytic assemblages. Comparisons of the species composition on glass or plastic plates with epiphytic floras indicated these assemblages often have many species in common (Moore and McIntire, 1977; Tuchman and Blinn, 1979). The differences between these assemblages were mainly a matter of differences in relative abundances, not an obligate specificity for a substrate.

While most diatom taxa are broadly distributed across a range of natural and artificial substrates, there are some exceptions. Certain species of Cocconeis seem to have strong preferences for living substrates (Main and McIntire, 1974; Jacobs and Noten, 1980). There may be a slight tendency for taxa with narrow points of attachment to prefer the more delicately branched hosts. Conversely, epiphytes with coarser attachments may be more common on broadly branched or foliose hosts (Ramm, 1977). Endophytic diatoms often exhibit more host-specificity than do epiphytic species. Taasen (1972) discusses the ecological properties of Navicula endophytica, a taxon that lives in the conceptacles of Fucus and Ascophyllum, and Navicula dumontia (Taasen, 1974) which lives in the internal mucilage of the red alga Dumontia incrassata.

The usual sequence of epiphyte colonization and succession is described by Patrick (1977). The first colonizers are usually unicellular and attach to the host on their valve surface. Species of Cocconeis are common in this stage of colonization in both freshwater

and saltwater habitats. As competition for space increases, such taxa as Synedra become established. This genus is needle-shaped and attaches by mucilage pads on one end of the cell. Colonies of these cells resemble pins in a pincushion, and add a three-dimensional aspect to the epiphytic assemblage. As the assemblage becomes more mature, species that attach by mucilage stalks or form colonies in mucilage tubes become more common. Stalk forming genera include Gomphonema and Rhoicosphenia. Examples of tube forming estuarine diatoms include Navicula comoides, Navicula grevillei, and Berkeleya rutilans. Species such as these form an overstory that is analogous to a forest canopy. The early colonizers (e.g., Cocconeis) usually remain in the mature assemblage as an understory, but decrease in relative abundance as the other species establish themselves (Siver, 1978).

The colonization process is enhanced by moderate water movement and an ample nearby standing crop of established epiphytes to act as a source of colonizers (Patrick, 1978; Gale et al., 1979). Epiphytic algae seem to prefer irregularities on the host surface such as slight indentations where adjoining cells meet (Godward, 1934) and on leaf margins (Cattano, 1978). The preference for margins is probably due to physical factors related to water movements, as concentrations of epiphytes are also found along the margins of plastic ribbons (Cattano, 1978).

A dense coating of epiphytes can be a serious problem for aqua-

tic plants. An epiphytic flora may shade the leaves of the host plant, or epiphytes may act as a barrier to gas exchange (Sand-Jensen, 1977). Epiphyte loads are believed to contribute to the decline of aquatic macrophytes in eutrophic waters (Moss, 1981; Phillips et al., 1978; Fitzgerald, 1969).

Monocots, such as Zostera marina, grow from a basal meristem. The distal ends of the leaves are the oldest parts of the leaves and are the most heavily epiphytized (Siver, 1978). This results from the older leaves having had sufficient time to develop mature epiphytic assemblages. The production of new leaf tissue ensures that the host plant has photosynthetic surfaces that are relatively free of epiphytes.

Aquatic plants may react to epiphyte fouling with allelopathic interactions. For example, many seaweeds produce tannins, antibiotics and other toxins (Conover and Sieburth, 1966; Khfaji and Boney, 1979; Sieburth and Tootle, 1981). In addition, many freshwater and marine algae produce coats of mucilage that prevent attachment of epiphytes to host surfaces (Godward, 1934). On the other hand, aquatic vascular plants rarely exhibit allelopathy and do not produce mucilage. In general, these plants make prime hosts for an epiphytic microflora and probably cope with the fouling problem by rapid production of new leaves and the senescence and sloughing of the old leaves.

At least in temperate marine and estuarine habitats, the epi-

phytes of large seaweeds and aquatic angiosperms are likely to include species of Cocconeis, Licmophora, Achnanthes, Melosira and Synedra (McIntire and Moore, 1977). Floristic treatments of marine and estuarine epiphytic assemblages include Drum and Webber (1966), Castenholz (1967), Edsbacke (1968), Aleem (1973), and Main and McIntire (1974).

Benthic Diatoms

Benthic microalgae are influenced by such environmental variables as light intensity and photoperiod, water temperature, salinity, tidal exposure, water turbulence, sediment stability, sediment particle size, the concentration of nutrients and organic matter in the sediment, vascular plant cover, and grazing. Many studies have emphasized the importance of available light as a factor governing rates of photosynthesis in benthic assemblages (e.g., Marshall et al. 1971; Hartwig, 1978; Sorsa, 1979; Admiraal and Peletier, 1980; Aykulu, 1982). In a review of the productivity of aquatic ecosystems, Mann (1974) found that factors governing available light (e.g., cloud cover and latitude) had a greater influence on the overall productivity of an ecosystem than did nutrient factors. Factors governing nutrient availability accounted more for seasonal patterns of production than for overall productivity. While there are sometimes seasonal changes in species composition (Bacon and Taylor, 1976; Cox, 1977; Admiraal and Peletier, 1980), seasonality is

expressed most strongly in patterns of primary production rather than in floristics. Round (1960) states that most benthic taxa are present during the entire year. The seasonal succession of taxa is probably an imposition of a weak seasonality upon a more fundamental distribution (Cox, 1977; Baillie and Welsh, 1980).

Benthic algae grow best when given adequate light without desiccation (McIntire and Wulff, 1969). However, benthic diatoms require very little light, and are not even light limited in Spartina marshes (Darley et al., 1981). In laboratory experiments, Davis (1982) demonstrated that photosynthesis of benthic diatoms is saturated at 10-20% of full sunlight, only about $200-400 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$. In Oregon estuaries, such floras usually are not light limited, except on overcast days or when covered by deep or turbid water (Davis, 1982). Similarly, in an English estuary, benthic primary production ceased when the flora was covered at high tide (Joint, 1978).

Benthic microalgae are affected by temperature extremes, such as freezing weather in winter, or the warming of exposed sediment in the summer sun. Temperature also affects water stratification and nutrient dynamics. The combined effects of high temperature, high light intensity, and exposure to atmospheric oxygen can lead to photoinhibition of photosynthesis (Admiraal, 1977a).

In spite of wide ranges of salinity in estuaries, salinity is generally a factor of secondary importance in determining estuarine microalgal production or species distribution. Estuarine taxa are

tolerant of a wide range of salinity. For example, the growth of Melosira nummuloides is not noticeably affected by salinities ranging from 1‰ to 50‰ (McLean et al., 1981). Also Admiraal (1977b) noticed little effect on the rates of photosynthesis of mixed cultures of estuarine diatoms in salinities ranging from 4‰ to 60‰. Such wide tolerances are typical of many estuarine diatoms (Drum and Webber, 1966; Cook and Whipple, 1982). Benthic diatoms in the Yaquina River, Oregon, are brackishwater or marine taxa that tolerate a wide range of salinity, or they are freshwater taxa that do not tolerate salinities greater than 5‰. This discontinuity between brackishwater and freshwater floras at 5‰ moves up or down the estuary depending on the amount of freshwater discharge (McIntire, 1978; Amspoker and McIntire, 1978). Moreover, the relative abundances of brackishwater taxa changes gradually from the bay mouth to the upper reaches of the river. Therefore, it appears that the diatom taxa most influenced by salinity are the stenohaline marine or freshwater species.

Exposure to desiccation during low tide and exposure to low light conditions during high tide influences both microalgal primary production (McIntire and Wulff, 1969) as well as species distributions (Cox, 1977; Aleem, 1950a; Dexter, 1979; Bacon and Taylor, 1976). In general, the lower intertidal regions have the highest biomass and sites above or below this level tend to have lower biomass (McIntire and Moore, 1977).

The distribution of benthic diatoms is also affected by wave action, turbulence, and sediment stability. In a study of the benthic flora of a sandy beach, Amspoker (1977) found that sediment mixing from wave action produced a very homogeneous flora along an intertidal gradient. The assemblage had a very low biomass and a high species diversity. Riznyk and Phinney (1972) suggested that hydrographic factors determine the distribution of benthic diatoms in the Yaquina River estuary. Moore and McIntire (1977) identified these factors as the determinants of sedimentation and the distribution of sediment type. In general, sands are present in areas where wave action and turbulence are greatest, and typically have little organic content. Muddy sediments are deposited in calmer waters and are composed of smaller particles and are richer in organic matter. The decomposition of organic matter in sediments in anaerobic conditions may release compounds that inhibit the growth of many diatom species. A few species tolerant of these conditions dominate these assemblages, which typically have low species diversity (Admiraal and Peletier, 1979b).

Hendey (1964) suggested that mean grain size and sediment organic content are important factors influencing the distribution of benthic diatoms in British coastal waters. Amspoker and McIntire (1978) came to the same conclusion during a study of the Yaquina River estuary. Round (1960) states that sandy sediments have a distinct flora that is not found in any other habitat.

An overstory of vascular plants can affect the distribution and abundance of diatom populations in the associated sediments. Estrada et al. (1974) and Darley et al. (1981) concluded that Spartina so dominates nutrient dynamics in Eastern coastal marshes, that the benthic algae are probably nutrient limited in these areas. However, this is not the case when diatoms grow in open sediments in the same general location (Darley et al., 1981). Sullivan (1978, 1982) found strong positive correlations between certain diatom associations and the vascular plants that formed the overstory above them. This is probably the result of a combination of shading, nutrient dynamics, and the slight differences in sediment moisture and intertidal height that also determine the distribution of the vascular plants.

Grazing by snails and sediment infauna often decreases both standing crop and primary production of benthic microalgae (Branch and Branch, 1980; Nicotri, 1977; Darley et al., 1981; Davis, 1982). Admiraal (1977c) found that ciliate protozoa in estuarine sediment can decrease microalgal biomass and select for diatom taxa of relatively larger size.

The euphotic zone in sediment is only a few mm in depth, the exact depth depending on the grain size and the concentration of organic matter. Most benthic diatoms live in the upper 2 mm of sediment (Harper, 1969). The raphid diatoms can detach from their substrate and move elsewhere. These movements are related to tidal rhythms, light intensity, and depth of burial (Round and Haphey,

1965; Harper, 1977; Aleem, 1950b). Harper (1969) suggested that mobile raphid diatoms and the non-mobile araphid diatoms may have different vertical distributions in sediment. In sand, motile forms were most common in the uppermost 1 mm, while the non-motile forms were most common between 2 and 10 mm below the surface.

Diatom migrations may take place in response to many types of adverse conditions (Harper, 1977). Too much light, exposure to desiccation, or exposure to water turbulence may cause motile diatoms to move downward into sediments. There is a possibility that motile diatoms may adjust their depth beneath the surface to obtain the most favorable illumination.

In some cases, diatoms may have endogenous migratory rhythms, moving upward before sunrise and down again after dusk. These rhythms may continue indefinitely under laboratory conditions, even with constant light or darkness (Harper, 1977). As estuarine sediments are constantly being shifted by turbulence, diatom motility may be an adaptation to avoid burial (Round and Haphey, 1965). Indeed, most benthic diatoms are raphid taxa (Aykulu, 1982). The exception to the rule is the epipsammic diatom flora. These organisms are small, generally without a raphe, and live attached to sand grains. Epipsammic diatoms are usually abundant only in sands that are exposed to considerable turbulence and wave action.

Many benthic diatoms may be capable of facultative heterotrophy, especially if interstitial dissolved organic matter is abundant

(McLean et al., 1981). In such situations, diatoms are certainly in competition with bacteria for these organic nutrients. Bacterial metabolism and surface-to-volume ratios clearly give the bacteria the advantage in competitive interactions. However, bacterial digestion is extracellular, and as long as dissolved organic matter is present, diatoms may supplement their nutrition by heterotrophic uptake. Saks and Kahn (1979) placed the estuarine diatom Cylindrotheca closterium in a competitive situation with the estuarine bacterium Aeromonas. The cultures were provided with a variety of low molecular weight organic molecules. Cylindrotheca metabolized 71% of the consumed glucose and from 33% to 73% of various amino acids. These results indicated that facultative heterotrophy by Cylindrotheca occurred even in the presence of competing organisms and at concentrations of organic compounds that are found in nature.

Facultative heterotrophy is more common among pennate diatoms than centric diatoms, especially among diatoms from muddy substrates that have a relatively high concentration of organic matter. Admiraal and Peletier (1979a) found that facultatively heterotrophic diatoms were relatively small in size and had greater surface to volume ratios than other species. A review of diatom heterotrophy is presented by Hellebust and Lewin (1977).

Benthic diatoms are often found in endosymbiotic association with the larger Foraminifera (Lee et al., 1980). Many of these species are common benthic taxa (e.g., Nitzschia frustulum, Amphora

tenerrima, Nitzschia panduriformis, and Nitzschia laevis). This symbiotic relationship is an example of the variability and adaptability of some estuarine diatoms.

Benthic algae are important, not only as part of the estuarine food chain, but as stabilizers of estuarine sediment. Algal mucilage cements particulates together, giving sediments some cohesion and some resistance to resuspension by water turbulence (Frostick and McCave, 1979). The importance of sediment stabilization is evident in the fact that estuarine water turbidity can have a limiting effect on primary production and that most of the suspended particles in the water column are particles that have been resuspended from sources within the estuary (Frostick and McCave, 1979).

Reviews of the ecology of marine littoral diatoms are given by Round (1971) and McIntire and Moore (1977). Floristic investigations of benthic diatoms in American estuaries include Hustedt (1955), Wood (1963), Drum and Webber (1966), and Riznyk (1973). The similarity of these floras with those studied in Europe (e.g., Hustedt, 1939; Aleem, 1950a; Aleem, 1950b; Brockman, 1950; Hustedt and Aleem, 1951; Hendey, 1964; Aleem, 1973) suggest that many marine and estuarine diatom species may be cosmopolitan in their distribution.

III. DESCRIPTION OF NETARTS BAY

Netarts Bay is a bar-built estuary located in west-central Tillamook County, about 12.5 km west of the town of Tillamook (Fig. 1). The bay is Oregon's sixth largest estuary and covers 941 hectares. The basin of the bay was formed by erosion of soft sedimentary rock (the Astoria Formation) between basaltic headlands, Cape Lookout to the south and Cape Meares to the north. A sand spit separates the bay from the Pacific Ocean except for an opening at the northern end. The spit is a remnant of coastal dunes that were partially inundated at the end of the last glacial epoch.

Netarts Bay has extensive tidelands, 612 hectares that include large sand and mudflats, large seagrass beds, and some sandy beaches near the bay mouth to the north. A narrow fringe of tidal marsh exists along the sand spit to the west and expands to a 40.5 hectare marsh at the south end. The subtidal area is restricted to narrow branching channels that merge near the bay mouth and connect with the Pacific Ocean.

The tidal regime is typical of the Pacific Northwest, a mixed semi-diurnal type, with two unequal high tides and two unequal low tides each lunar day (ca. 24 hr and 50 min). The maximum normal tidal range is 3 m, with mean high water (MHW) and mean low water (MLW) at 2.0 m and 0.5 m above the mean lower low water level (MLLW), respectively.

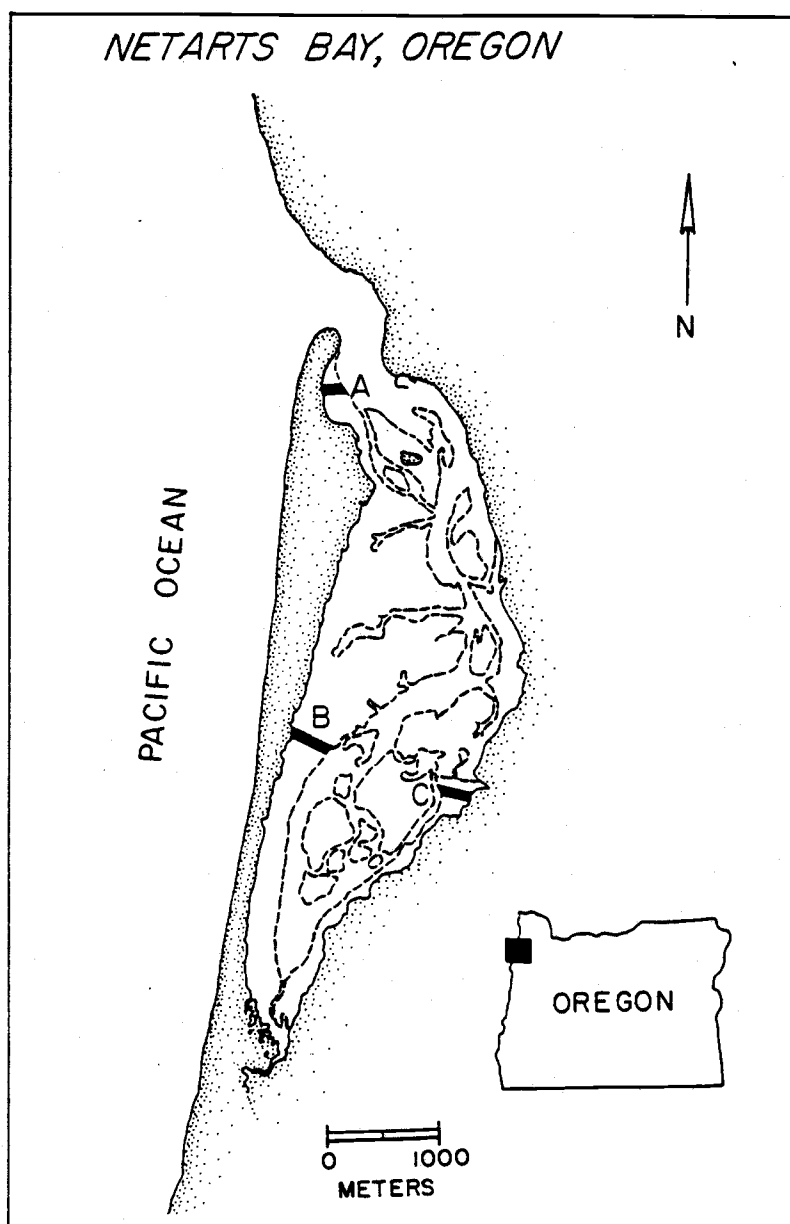


Figure 1. Map of Netarts Bay, showing intensive sampling sites: SAND site (A), FINE SAND site (B) and SILT site (C).

Netarts Bay has a relatively small watershed which feeds several small creeks that enter the bay. Because of the diffuse input and the relatively small volume of freshwater, Netarts Bay does not develop a stratified water column. However, recent studies by the Environmental Protection Agency (EPA, 1979) indicate that the bay water is not well mixed. The deep subtidal channels funnel seawater into the bay during flood tide which displaces, rather than mixes with, the bay water. The warmer, slightly less salty bay water is pushed up over the tidal flats and Zostera beds as the ocean water enters the channel. On the ebb tides, bay water slips back into the channel as the seawater withdraws. Dye studies indicated that many tidal cycles were necessary for enough mixing to take place to flush the dye from the estuary (EPA, 1979).

Salinity in Netarts Bay usually varies from 28 to 34‰ (Davis, 1982). The salinity of the interstitial water, the relevant salinity to which the benthic microflora is exposed, usually varies between 25‰ and 35‰. Higher intertidal areas (2.0 m or more above MLLW) may exhibit interstitial salinities as low as 5‰ during rain storms (Davis, 1982).

Planktonic, epiphytic and benthic diatoms are probably not nutrient limited in Netarts Bay. Water column nitrogen was measured monthly from July to September 1981, during which time the concentration varied from 0.16 to 3.23 μM for NO_3^- - NO_2^- and from 0.56 to 2.78 μM for NH_4^+ . Over the same period, orthophosphate ranged from 0.34 to

0.48 μM (Davis, 1982). Although the microalgae are not nutrient limited, biological processes have a pronounced effect on nutrient concentration in the water column, especially in the vicinity of the large Zostera beds (EPA, 1979).

IV. MATERIALS AND METHODS

Sampling Strategy

Species composition and relative abundances of diatoms were examined in planktonic, epiphytic and benthic collections over a period of one year from February 1980 to March 1981. Sampling stations were established at sites A, B and C in Netarts Bay (Fig. 1), which represented different sediment and substrate types. Samples were collected once a month on dates that corresponded to favorable tide and weather conditions.

Three collections of planktonic diatoms were taken on each sampling date. One sample was taken from the bay water at low tide near site B. Another sample was obtained from ocean water at high tide near the mouth of the bay. To measure the penetration of marine plankton into the estuary and to examine the amount of mixing of estuarine and marine floras, a third sample was taken at high tide near site B.

Diatoms that were epiphytic on Zostera marina were collected from a single study area at site B. Three sampling stations were established along an intertidal gradient across a large Zostera bed. These stations were designated as EP1, EP2, EP3, and corresponded to sample stations that were also used for studies on Zostera phenology and production (Kentula, 1983). Station 1 was located at 1.1 m above MLLW. The middle station, station 2, was located 1.2 m

above MLLW. The high intertidal station, station 3, was located near the upper intertidal limits of Zostera marina, 1.4 m above MLLW. Each sample consisted of one Zostera shoot and its associated epiphytes, and only one sample was taken at each station on a particular sampling date. No replications were attempted, as the measurement of host-to-host variation was beyond the scope of this study. As each collection consisted of an entire Zostera shoot, both colonizing epiphytes and older established epiphytes were pooled in a single sample.

Benthic samples were collected from intertidal transects at sites A, B, and C. Each transect had four sampling stations, each at a different tidal height. These stations corresponded to stations used in a study of benthic algal production (Davis, 1982). Sites A, B, and C represented three sediment types. Site A was located in sandy sediment near the mouth of the bay and was designated as the Sand site (SA). Site B was adjacent to the Zostera bed and was designated as the Fine Sand site (FS). Site C was located on the eastern shore near the mouth of Whiskey Creek and was designated as the Silt site (SI). The sample stations along each transect were located at 0.5 m above MLLW (station 1), 1.0 m above MLLW (station 2), 1.5 m above MLLW (station 3), and at 2.0 m above MLLW (station 4). As with epiphyte samples, benthic samples were identified by both a site and station designation. For example, a sample from SA2 was located in sandy sediment near the bay mouth and was 1.0 m above

MLLW. As the euphotic zone in sediment usually consists of only the upper few mm (Harper, 1969), each sample was obtained from the top 1 cm of sediment.

Sampling Methods

1. Diatom Assemblages

Plankton samples were collected by pouring 10 l of water through a 10 μ m mesh plankton net. As diatom identification usually depends on the ability to observe the ornamentation of the silica frustule, diatom samples are usually treated with acid to remove organic materials that interfere with close examination of cell wall morphology. However, most planktonic diatoms are too lightly silicified for the valves to survive the acid digestion process. For this study, planktonic diatoms were cleared of pigments in an ethanol preservative, and sea salt and other dissolved solids were removed from the samples by successive washings in distilled water. After several washings, a subsample was taken of the diatom suspension, and this material was placed on a microscope coverslip and allowed to air dry. Dried coverslips were mounted on microscope slides with Cumarone resin (Holmes et al., 1981), an inexpensive resin of high refractive index. Duplicate slides were made for the Oregon State University diatom collection.

One shoot of Zostera marina and its associated epiphytes was collected from each of the three intertidal sampling stations at site

B. Epiphyte samples were placed in screw-top bottles and were transported to the laboratory for the preparation of microscope slides.

Benthic cores were collected from all three sediment types by pushing a 2.3 cm diameter plastic pipe into the sediment and extracting the upper few cm. Plastic caps were placed over the ends of the pipe to prevent loss of material. Cores were transported and frozen in a vertical position to minimize sediment mixing. In the laboratory, the upper 1.0 cm of each core was cut off with a knife, cleared of organic material, and the diatoms were mounted on glass cover slips for microscopic examination.

Organic materials in the epiphytic and benthic samples were oxidized with nitric acid using a Kjeldahl digestion apparatus. The acid-sample mixture was boiled for approximately one-half hour. Organic matter remaining after the acid digestion was oxidized by the addition of small amounts of potassium dichromate. Cleaned diatom frustules were allowed to settle in beakers for at least 4 hr, and then the acid supernatant was decanted. The small amount of acid remaining with the frustules was diluted with distilled water and allowed to settle again. Successive decantings of acid and dilution with water eventually isolated the frustules in distilled water. As with plankton samples, a subsample of the frustule suspension was dried on a microscope cover slips and mounted in Cumarone. Duplicate slides were contributed to the O.S.U. diatom collection.

Epiphytic and benthic diatoms were identified and counted with a Zeiss research microscope at 1200X magnification with bright field

illumination. Each valve encountered on transects across a microscope slide was uniquely identified either by a species name or a reference number. Approximately 500 valves were identified for each sample. From analysis of other data sets, McIntire and Overton (1971) found that community composition parameters (i.e., measures of species diversity, similarity and niche breadth) changed very little as sample size was increased above 300 individuals. For this reason, a sample size of 500 valves was selected for this investigation.

Epiphytic samples from all 12 months were counted. Of the 116 benthic samples collected, samples from every other month were counted. Although phytoplankton samples were not counted, species lists were prepared for those months when euplanktonic species were present.

2. Physical Variables

On each sampling date, incident light intensity was measured in $E \cdot m^{-2} \cdot hr^{-1}$ with a LI-COR Quantum meter (model LI-185B). Water and air temperatures also were recorded, while salinity was measured by an American Optical refractometer. Photoperiods were calculated from a Netarts Bay tide table.

Sediment properties were investigated by Davis (1982) in a study of the benthic algal production of Netarts Bay. These environmental measures were used to help interpret patterns in the diatom flora. Changes in sediment height from erosion or deposition were monitored by comparisons of marks made on wooden stakes placed at each sampling

station. Sediment cores were collected each month for analysis of algal biomass which was estimated by extractions of chlorophyll-a in the top cm of sediment according to the methods of Strickland and Parsons (1972). Chlorophyll concentration also was measured in a 1 cm segment of the cores from 4-5 cm beneath the surface. The ratio of chlorophyll in the top cm to that at 4-5 cm was used as an index of sediment mixing. Values near unity indicated a homogenization of sediments from such processes as water turbulence and animal activity. Values greater than unity indicated sediments with less vertical mixing and a concentration of algal biomass near the surface.

Sediment cores were collected bimonthly for analysis of particle size and for determination of organic content. The concentration of organic matter in the top cm of sediment was determined from dry weights before and after ashing in a muffle furnace at 450⁰ C for 24 hr. Particle size analysis was accomplished by wet-sieving the sand fraction (particles greater than 63 μ m) from the silt and clay particles (smaller than 63 μ m). The sand fraction was dried and sieved on an agitator using a series of US Standard sieve meshes (Krumbein and Pettijohn, 1938). The fine fraction was analyzed by pipetting subsamples of the suspension at certain time intervals, drying and weighing the sample, and using standard sedimentation rates for a particular particle size (Davis, 1982). A particle size distribution was calculated for each sample based on dry weights of each size fraction (Inman, 1952). Particle sizes were expressed in phi

units (ϕ), where $\phi = -\log_2$ (diameter in mm). In addition, sorting and skewness coefficients were calculated for each sediment sample (Inman, 1952). The sorting coefficient is an expression of the variance in grain size in a sample. Sediments that are well sorted have a relatively small variance in particle size and have a low value for the sorting coefficient. Skewness represents the degree of symmetry in particle distribution. If the mean particle size and the median particle size are the same, then the value is equal to zero. Negative values indicate that the median particle size is greater than the mean, and that smaller particles predominate.

Data Analysis

1. Community Composition Parameters

One aspect of the data analysis followed the general approach of McIntire and Overton (1971). Diatom samples were compared by the estimation of the community composition parameters (e.g., measures of species diversity) and by measures of niche breadth and similarity. Components of species diversity included species richness (i.e., the number of species present in a given sample), redundancy (the degree of species dominance in an assemblage), and heterogeneity (an expression of both species richness and redundancy).

The Shannon-Weaver index (H'') was used as a measure of heterogeneity. The value of H'' is largest when there are many species present and when individuals are evenly distributed among species

(i.e., when dominance or redundancy is low). H'' was calculated from the expression

$$H'' = - \sum_{i=1}^S p_i \log_2 p_i ,$$

where S is the number of species in a sample, and where p_i is the proportion of the total number of individuals (N) in a given sample that are represented by the individuals of species i (n_i), i.e., $p_i = n_i/N$. The value of H'' can range from $H''_{\min|S}$ to $H''_{\max|S}$, where

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

and

$$H''_{\min|S} = - \left\{ \frac{S-1}{N} \log_2 \frac{1}{N} + \frac{N-S+1}{N} \log_2 \frac{N-S+1}{N} \right\} .$$

The degree of dominance, or the redundancy of the sample (RED), was calculated from the expression

$$RED = \frac{\frac{H''_{\max|S}}{H''_{\max|S}} - \frac{H''_{\text{obs}}}{H''_{\min|S}}}{\frac{H''_{\max|S}}{H''_{\max|S}} - \frac{H''_{\min|S}}{H''_{\min|S}}} ,$$

where H''_{obs} was the observed value of H'' . RED ranges from zero (no dominance) when all species are equally common, to unity (maximum dominance) when all but one species is represented by one individual

and the rest of the individuals in a sample belong to a dominant species.

The distribution of each species among the samples was expressed by B_i , a measure of niche breadth. In this case, B_i is a measure of the degree to which the i -th species tends to be equally distributed among the samples. B_i was calculated from the expression

$$B_i = \exp \left\{ - \sum_{j=1}^k \frac{p_{ij}}{R_i} \log_e \frac{p_{ij}}{R_i} \right\} ,$$

where p_{ij} is the proportion of individuals of species i in the j -th sample, k is the total number of samples, and $R_i = \sum_{j=1}^k p_{ij}$. B_i ranges from 1.0 if a species is present in only one sample, to k when a species has equal relative abundance in all samples.

Differences among samples were examined with an index of similarity, which is calculated from the expression

$$\text{SIMI (1,2)} = \frac{\sum_{i=1}^s p_{1i} p_{2i}}{\sqrt{\sum_{i=1}^s p_{1i}^2} \sqrt{\sum_{i=1}^s p_{2i}^2}} ,$$

where SIMI is a measure of the similarity between sample 1 and sample 2, p_i is the proportional abundance of the i -th species in the samples, and where s is the total number of species in the pooled samples. The numerator represents the probability that one individual drawn at random from sample 1 and one individual selected at

random from sample 2 are the same species. The denominator scales SIMI from zero when the samples have no species in common, to 1.0 when both samples have the same species and relative abundances.

The Jaccard index (Clifford and Stephenson, 1975) is an index of similarity that requires data in binary form. In contrast to SIMI, which is calculated using the relative abundances of species, the Jaccard index (JAC) uses only presence-absence information and thereby does not weight species according to their relative abundance. JAC is calculated from the expression

$$JAC (1,2) = \frac{a}{a + b + c}$$

where a is the number of species that samples 1 and 2 have in common, b is the number of species found in the first sample only, and c is the number of species found in the second sample only. JAC X100 represents the percentage of species that two samples have in common.

2. Multivariate Analysis

Multivariate analyses were used to identify patterns in community composition and in species relative abundance and to relate these patterns to environmental variables. Four multivariate ordination procedures were used, namely Polar Ordination (PO), Principal Components Analysis (PCA), Reciprocal Averaging (RA), and Canonical Correlation (CC). Ordination analyses are a useful method of

processing large data sets. Information is summarized in an ordination space of reduced dimensionality, thereby facilitating interpretation (Gauch, 1982). All 64 benthic samples, along with 18 epiphyte samples from months that matched the benthic data, were used for ordination analyses. Seventy-two species of interest were chosen based on abundance or fidelity to a specific substrate. The relative abundances of species were log transformed to de-emphasize the importance of the most abundant taxa.

Polar Ordination is based on a matrix of dissimilarity coefficients (Gauch, 1982). The most dissimilar sites (or species) serve as end points of the ordination and all other observations are placed relative to their dissimilarity to the end points.

Principal Components Analysis considers observations as points in a multidimensional space with each measure (or "score") denoting a position on an axis. The PCA algorithm generates new, orthogonal axes from linear combinations of the original variables (Gauch, 1982). If the original variables are highly correlated among themselves, the PCA transformation will concentrate a large proportion of the variance (or information) in relatively few new variables (the "principal components"). One important limitation of this method is that the interpretation of the results is dependent on the ability of linear models to explain the data. The results of the analysis sometimes is improved by the standardization of the variables, where the standardized variable (z_{ij}) is given by the equation

$$z_{ij} = (y_{ij} - \bar{y}_i) / s_i ,$$

Here, y_{ij} is the log-transformed relative abundance of species i in the j -th sample, and s_i is the standard deviation of species i . PCA may be used as an ordination method, in which case it resembles Reciprocal Averaging (RA), but it often gives less satisfactory results than RA (Gauch, 1982). For the analysis of the Netarts Bay data sets, PCA was found to be more useful as a means to summarize and simplify environmental data, rather than for the ordination of species and samples. The principal components from an analysis of standardized environmental variables were correlated with the relative abundances of epiphytic and benthic taxa for autecological interpretations.

As an ordination method, Reciprocal Averaging often gives site ordinations that are similar to results obtained by standardized PCA (Hill, 1973). Reciprocal Averaging uses weighted averages of species scores to ordinate samples, and the weighted averages of sample scores to ordinate species (Gauch, 1982). Because of the two-way averaging procedure, RA produces ordinations which maximize the correspondence between species scores and sample scores. Environmental interpretations of species and site ordinations were achieved by correlations of environmental variables with the ordination axes.

Canonical Correlation differs from PO, PCA and RA in the simultaneous use of species distribution data and environmental data. The

algorithm finds linear combinations of variables that maximize the covariances between dependant and independant variables (Cooley and Lohnes, 1971). As with the other ordination methods, variables were log transformed and standardized. Interpretation of the canonical axes is based on correlations of taxa and environmental variables with the new, canonical variables. For the best results, the dependent and independent variable matrices should not be too disparate in size. For this reason, the benthic data set was scaled down to 36 taxa of interest; the epiphyte data set was not compatible with this analysis.

All data analyses were performed on the Control Data Corporation Cyber 170-720 computer system using programs stored at the Oregon State University Computer Center. Community composition parameters were calculated by the AIDONE and AIDNX programs; the multivariate procedures were performed with the ORDIFLEX, CORRELX, PARTL, and CANON programs.

V. RESULTS

Analysis of Environmental Data

1. Raw Data

The environmental data for this research were taken from a thesis by Davis (1982) that was concurrent with this study. The amount of light energy available for photosynthesis in Netarts Bay was strongly influenced by photoperiod, water depth, and cloud cover. Daylength varied from 12.2 hr in June to 6.0 hr in December. At one site in July, the incident light intensity on sediment surfaces ranged from a mean of $3.0 \text{ E} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ at station 1 to $5.0 \text{ E} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ at station 4 on a sunny day (Davis, 1982, Fig. 9). On a cloudy day in September, corresponding values at the same site were 0.8 and $1.5 \text{ E} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ at stations 1 and 4 respectively. Measurements of photoperiod, water depth and cloud cover indicated that the benthic and epiphytic diatoms may be light-limited during the many cloudy days from September through May. Though microalgae were exposed to light intensities below light saturation at times during the study, they nevertheless maintained high biomasses throughout the year.

The temperatures of the air, water and sediment were usually above 10°C . Air and sediment temperatures had the greatest range, from 0° to 24°C and from 2° to 19°C , respectively. The temperature

of the bay water was moderated by mixing with ocean water and ranged from 8° to 18°C .

Water column salinity likewise was moderated by the influence of seawater and by the relatively small freshwater input. Water salinity in the bay ranged from 28 to 34‰. The salinity of interstitial water from sediment samples generally ranged from 25 to 35‰. However, interstitial water at the high intertidal stations (2.0 m above MLLW) had salinities as low as 5‰ during heavy rains that coincided with exposure during low tides.

The net change in sediment height was relatively small during the study (Figure 2). The Silt site had the least change in sediment height, while station 2 at the Sand site (SA2) and stations 1 and 4 at the Fine Sand site (FS1 and FS4) had the greatest change.

Ratios of chlorophyll a in the top cm of sediment to that at a depth of 4-5 cm generally ranged from about 1.0 to 7.0. As chlorophyll near the surface was about $25 \text{ mg}\cdot\text{m}^{-2}$ at the Sand site and $100 \text{ mg}\cdot\text{m}^{-2}$ at the Fine Sand and Silt sites, low ratios indicated a high amount of mixing of the sediments. The stations with the highest chlorophyll ratios were primarily the high intertidal stations, especially stations SA3 and SA4 at the Sand Site (Figure 3). Also, these two stations accounted for most of the variation in the value for this ratio.

The concentration of organic matter in the top cm of sediment, expressed as ash-free dry weight, was related to sediment type. The mean concentration at the Sand site was about $100 \text{ g}\cdot\text{m}^{-2}$, while that

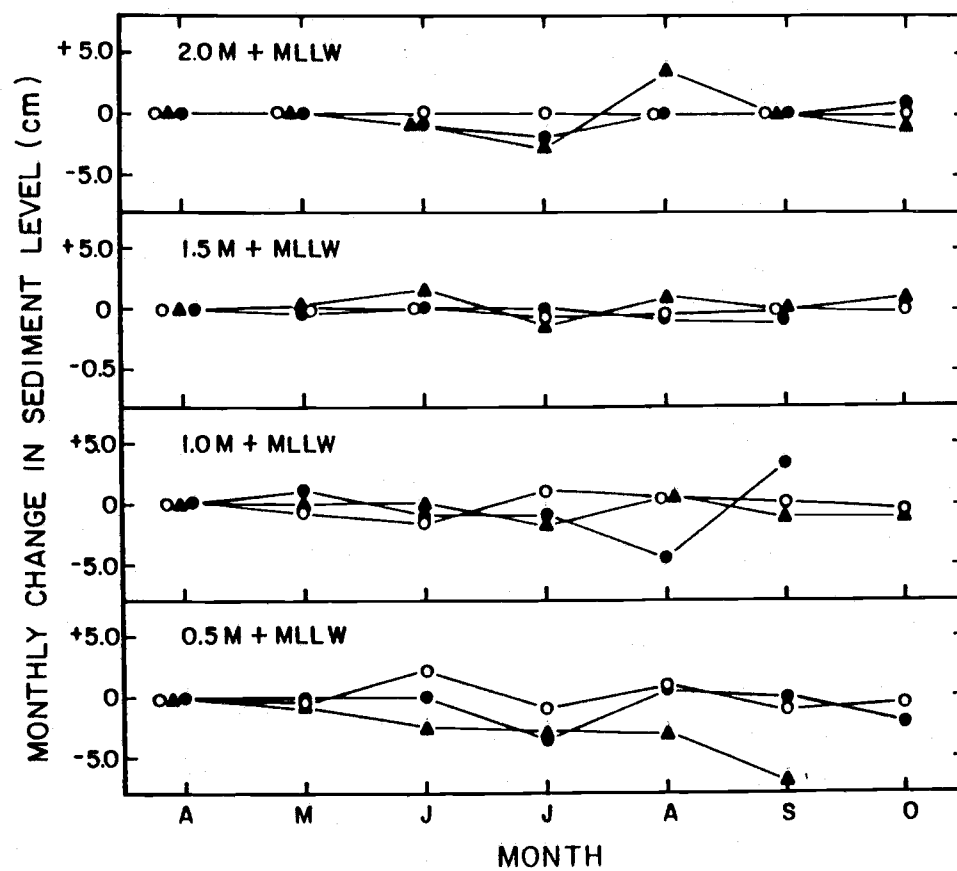


Figure 2. Monthly changes in sediment height at the intensive study sites in Netarts Bay. Sites include SAND (●), FINE SAND (▲) and SILT (○). (After Davis, 1982).

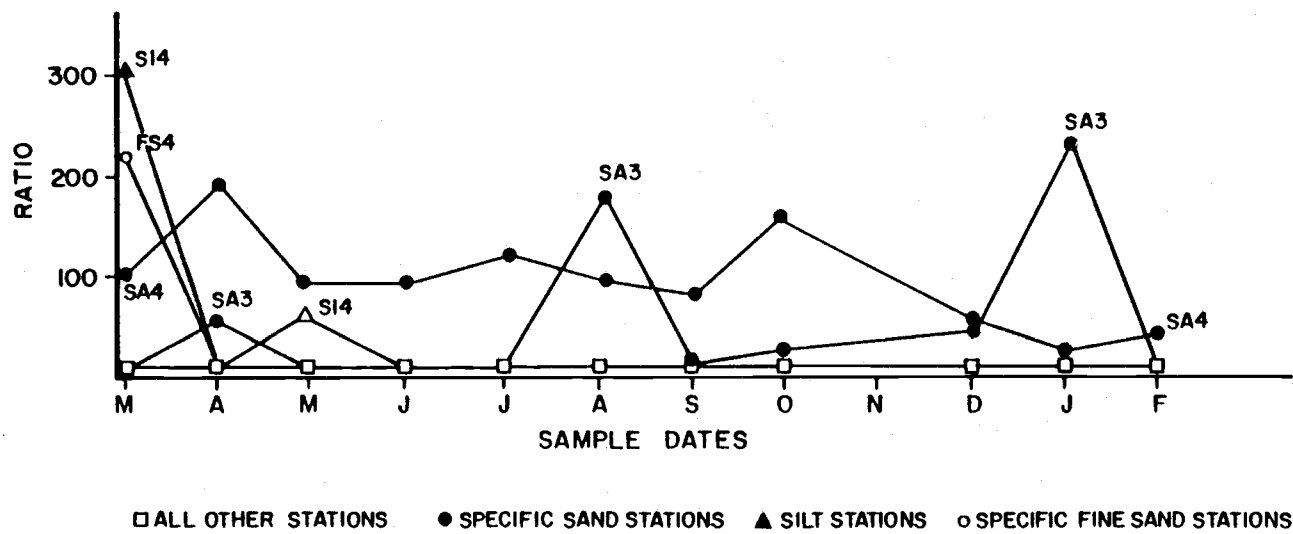


Figure 3. Monthly changes in the ratio of surface chlorophyll a to deep chlorophyll a (4 to 5 cm below the surface) at all benthic sampling stations.

at the Fine Sand site was usually about $200 \text{ g}\cdot\text{m}^{-2}$. The highest concentration of organic matter was found at the Silt site, usually ranging between 300 and $400 \text{ g}\cdot\text{m}^{-2}$.

Sediment particle size distributions, based on the coefficient of Inman (Table 1), were calculated for all sample stations. The Sand sites had a mean particle diameter of 0.21 mm (2.25 ϕ). Corresponding mean values for the sorting and skewness coefficient were 0.34 and 0.25, respectively. Therefore, the sediments at the Sand site were well sorted with a distribution slightly skewed toward the coarser particle sizes. The sediments at the Fine Sand site had a mean particle diameter of 0.16 mm (2.64 ϕ), and mean values for the sorting and skewness coefficients of 0.64 and 0.10, respectively. These sediments were moderately sorted, and the particle distribution was slightly skewed toward the coarser grain sizes. Mean values for sediment parameters at the Silt site were 0.07 mm (particle diameter), 1.13 (sorting), and -0.04 (skewness). At this site, the sediments were poorly sorted, and the distribution was nearly symmetrical with only a very slight skew toward finer particles.

2. Structure of the Environmental Data

Environmental variables were organized in two data sets, one with environmental variables corresponding to the epiphyte samples and another with variables corresponding to the benthic samples. The

TABLE 1

Conversions for sediment particle diameters
and Inman's phi coefficients.

Particle Diameter (in mm)	Phi (ϕ)	Particle Name
4.00-2.00	-2 - -1	granule
2.00-1.00	-1 - 0	very coarse sand
1.00-0.50	0 - 1	coarse sand
0.50-0.25	1 - 2	medium sand
0.25-0.125	2 - 3	fine sand
0.125-0.0625	3 - 4	very fine sand
0.0625-0.0312	4 - 5	coarse silt
0.0312-0.0156	5 - 6	medium silt
0.0156-0.0078	6 - 7	fine silt
0.0078-0.0039	7 - 8	very fine silt
< 0.0039	8+	clay

environmental data were matched with 18 samples of epiphytic diatoms and 64 samples of benthic diatoms.

Environmental variables related to the epiphyte samples included daylength, water temperature, and intertidal height represented by the three intertidal stations, daylength, and water temperature. The interrelationships among these variables were investigated by correlation analysis. The covariance of daylength and water temperature was high ($r = 0.82$). Daylength and water temperature were seasonal variables with largest values in summer and smallest values in winter.

Benthic environmental data consisted of nine variables, namely intertidal height (corresponding to four intertidal stations), surface chlorophyll a, surface organic matter (OM), the chlorophyll ratio, daylength, water temperature, mean particle size (PHI), and the sorting and skewness coefficients (SORT and SKEW). Covariances among the sediment properties PHI, SORT and OM were relatively high. Correlation coefficients for these variables were 0.67 (PHI-OM), 0.78 (SORT-OM), and 0.83 (PHI-SORT). Moreover, daylength and water temperature were closely correlated with each other ($r = 0.76$). The variables tidal height, surface chlorophyll, the chlorophyll ratio, and the skewness coefficient were not highly correlated with each other nor with other variables (correlation coefficients below 0.40).

The relatively large environmental data set associated with the benthic diatom samples was summarized by the concentration of variance into three principal components. The interpretation of the principal components was achieved by the examination of factor loadings. In this analysis, these were the correlation values between the components of interest and the original variables (Table 2). Relatively high correlations ($r > 0.8$) between the first principal component and OM, PHI and SORT indicated that this axis was an expression of sediment properties. The second axis was highly correlated ($r > 0.9$) with daylength (DAYL) and with water temperature (TEMP), and was interpreted as a seasonal component. The third axis was highly correlated ($r = 0.81$) with intertidal height (TIDE).

The relatively low communalities for surface chlorophyll (CHLA), the chlorophyll ratio (RATIO) and the skewness coefficient (SKEW) indicated that these measures were not expressed appreciably by the first three principal components. Eigenvalues indicated that the first three principal components accounted for 66% of the total variation in the environmental data, and 33% was expressed by the first PCA axis alone.

The Diatom Flora

Benthic, planktonic and epiphytic diatom samples contained a total of 336 taxa (species and varieties of species) from 68 genera (see Appendix A). Of these taxa, 50 were planktonic and 298 were

TABLE 2

Factor structure of the first three principal components generated from the environmental variables associated with benthic samples. Variables are intertidal height (TIDE), chlorophyll a concentration (CHLA), sediment organic matter (OM), chlorophyll ratio (RATIO), day-length (DAYL), water temperature (TEMP), mean sediment particle size (PHI), sorting coefficient (SORT), and the skewness coefficient (SKEW).

	PCA1 r_1	PCA2 r_2	PCA3 r_3	Communality
TIDE	-0.16	-0.18	0.81	0.72
CHLA	-0.50	-0.12	0.44	0.45
OM	-0.88	-0.10	0.07	0.78
RATIO	0.57	-0.07	0.40	0.48
DAYL	-0.03	0.93	0.13	0.88
TEMP	-0.00	0.93	0.13	0.88
PHI	-0.85	-0.03	-0.09	0.73
SORT	-0.91	-0.11	0.11	0.85
SKEW	-0.21	-0.03	0.38	0.15
Eigenvalues	2.94	1.80	1.12	
% of variance extracted	33%	20%	13%	

either benthic, epiphytic, or both. Only five taxa, namely Thalassiosira 1, Thalassiosira decipiens, Thalassiosira pacifica, Thalassionema nitzschioides and Skeletonema costatum, occurred among planktonic, benthic and epiphytic assemblages.

Approximately 53,850 diatom valves were identified and counted in 64 benthic samples and 36 epiphytic samples. Epiphyte samples collected monthly from three intertidal stations resulted in a count of 19,463 valves and the identification of 123 taxa. Benthic samples from every other month from all three sample sites, and along four intertidal stations resulted in the identification of 34,851 valves that represented 282 taxa. The overlap between benthic and epiphytic assemblages was 111 taxa, or 38% of the total for the two assemblages.

As is usually the case, most of the species within the assemblages were rare. Taxa represented by five or fewer valves accounted for 38% of the total number of taxa identified. These taxa contributed relatively little information to the analysis of distributional patterns, as their occurrence in a sample may represent allochthonous inputs, not a reflection of local environment. For this reason, specific taxa of interest were chosen for the multivariate analysis on the basis of their abundance, and the rarer taxa were eliminated. The 72 taxa chosen for ordination accounted for 95% of all epiphyte valves counted and 91% of all benthic valves counted. The 36 benthic taxa chosen for the regression and canonical correlation

analysis accounted for 79% of all benthic valves counted. The 22 epiphytic taxa chosen for a regression analysis with environmental variables accounted for 94% of all epiphytic valves.

In general, the taxa found in plankton samples were benthic or epiphytic taxa that were dislodged and suspended in the water column by tidal currents and turbulence. Common benthic species in these samples included Paralia sulcata, Anaulus balticus, Navicula digitoradiata, Navicula cancellata, Nitzschia socialis and Melosira moniliformis. Epiphytic taxa found as tychoplankton included Cocconeis scutellum, Cocconeis scutellum v. parva, Synedra fasciculata and Navicula directa. Euplanktonic species were abundant only in samples from February, March and August of 1980. In these samples, the species were typical of those found in the neritic plankton along the Oregon Coast during periods of peak off-shore production. The presence of marine plankton in Netarts Bay apparently was due to seawater transport into the bay by tidal fluxes.

Samples of plankton from the three months that had neritic floras are compared in Table 3. Although samples from February and March share fewer taxa (26%) than the February and August samples (38%), the February-March samples are dominated by the same species (e.g., Nitzschia seriata, Nitzschia pungens, Chaetoceros compressus, Skeletonema costatum, Thalassiosira decipiens, Thalassiosira 1 and Rhizosolenia setigera). August plankton samples were dominated by

TABLE 3

A list of planktonic species found in Netarts Bay during three months in 1980. Plus signs (+) indicate that a taxon was present.

	February	March	August
<u>Actinocyclus ehrenbergii</u>		+	
<u>Actinoptychus splendens</u>		+	
<u>Asterionella japonica</u>	+		+
<u>Bacteriastrum delicatulum</u>	+		+
<u>Bacteriastrum hyalinum</u>	+		
<u>Biddulphia longicuris</u>		+	
<u>Chaetoceros armatum</u>		+	
<u>Chaetoceros compressus</u>	+	+	+
<u>Chaetoceros constrictus</u>	+	+	+
<u>Chaetoceros curvisetus</u>			+
<u>Chaetoceros decipiens</u>	+		
<u>Chaetoceros didymus</u>	+		+
<u>Chaetoceros lacinosus</u>	+		
<u>Chaetoceros lorenzianus</u>	+		
<u>Chaetoceros radicans</u>	+		+
<u>Chaetoceros socialis</u>	+	+	+
<u>Chaetoceros vanheurcki</u>	+		
<u>Corethron hystrix</u>			+
<u>Coscinodiscus curvatulus</u>	+		
<u>Coscinodiscus eccentricus</u>	+		

Table 3
(Continued)

	February	March	August
<u>Coscinodiscus radiatus</u>		+	
<u>Coscinodiscus sublineatus</u>		+	
<u>Ditylum brightwellii</u>	+		
<u>Eucampia zodiacus</u>	+	+	+
<u>Hemiaulus hauckii</u>		+	
<u>Lauderia borialis</u>	+	+	
<u>Leptocylindrus danicus</u>	+		
<u>Lithodesmium undulatus</u>	+		
<u>Navicula complanatula</u>			+
<u>Navicula planamembranacea</u>	+		
<u>Nitzschia delicatissima</u>	+		
<u>Nitzschia pacifica</u>	+		+
<u>Nitzschia pungens</u>	+	+	
<u>Nitzschia seriata</u>	+	+	+
<u>Pleurosigma normanii</u>		+	
<u>Rhizosolenia alata</u>	+	+	
<u>Rhizosolenia hebatata v. semispinosa</u>	+		
<u>Rhizosolenia setigera</u>	+	+	

Table 3
(Continued)

	February	March	August
<u>Schroederella delicatula</u>	+	+	+
<u>Skeletonema costatum</u>	+	+	+
<u>Stephanopyxis nipponica</u>	+		
<u>Stephanopyxis palmeriana</u>	+		
<u>Thalassionema nitzschioides</u>	+	+	
<u>Thalassiosira 1</u>		+	
<u>Thalassiosira aestivalis</u>		+	
<u>Thalassiosira decipiens</u>	+	+	
<u>Thalassiosira nordenskiöldii</u>	+		+
<u>Thalassiosira pacifica</u>	+		+
<u>Thalassiosira rotula</u>			+
<u>Thalassiothrix longissima</u>	+		

several species of Chaetoceros, contained different species of Nitzschia and Thalassiosira than February-March samples, and lacked species of Rhizosolenia. Dominant species in the August samples included Chaetoceros compressus, Chaetoceros constrictus, Chaetoceros socialis, Nitzschia pacifica, Eucampia zodiacus, Thalassiosira nordenskiöldii and Thalassiosira pacifica.

The relative abundances and niche breadth values for 72 common benthic and epiphytic taxa are presented in Table 4. The most abundant epiphytes were Navicula salinicola, Navicula tripunctata v. schizonemoides, Navicula frustulum v. subsalina, and Synedra fasciculata; while the most abundant benthic taxa were Achnanthes hauckiana, and Opephora pacifica. In this case, niche breadth values may range from 1.0 if a species was present in only one sample, to 82 if equally abundant in all 82 samples. Although Paralia sulcata was not very abundant in the samples, it had a relatively high niche breadth value due to its presence in numerous sediment and epiphyte samples. In contrast, Opephora pacifica derived its large niche breadth value from its high relative abundance in numerous benthic samples.

Several species had low niche breadth values, indicating a restricted distribution, and yet made a substantial contribution to the samples in which they were found. Fragilaria striatula v. californica constituted approximately one-fifth of the total valves in two samples from SA2 in August and October. In all other samples,

TABLE 4

A list of 72 selected taxa, their total relative abundance (N_T), and their relative abundance in epiphyte (N_E) and benthic (N_B) samples. Also listed is the niche breadth values (B) for each taxon in relation to 82 epiphyte and benthic samples.

	N_T	N_E	N_B	B
<u>Achnanthes</u> 1	440	0	440	31.44
<u>Achnanthes</u> 11 B	918	0	918	20.26
<u>Achnanthes</u> <u>hauckiana</u>	3244	9	3235	30.86
<u>Achnanthes</u> <u>latestriata</u>	172	0	172	19.63
<u>Achnanthes</u> <u>lemmermanni</u>	621	2	619	36.51
<u>Amphora</u> 35	72	0	72	13.84
<u>Amphora</u> <u>coffeiformis</u>	441	4	437	43.20
<u>Amphora</u> <u>exigua</u>	349	2	347	19.87
<u>Amphora</u> <u>laevis</u> v. <u>perminuta</u>	155	0	155	14.99
<u>Amphora</u> <u>libyca</u>	148	0	148	22.65
<u>Amphora</u> <u>micrometra</u>	499	0	499	19.28
<u>Amphora</u> <u>proteus</u>	79	0	79	9.03
<u>Amphora</u> <u>sabyii</u>	1695	7	1688	41.31
<u>Amphora</u> <u>tenerrima</u>	678	104	574	38.48
<u>Anorthoneis</u> <u>eurystoma</u>	118	1	117	8.32
<u>Bacillaria</u> <u>paradoxa</u>	192	171	21	7.44
<u>Berkeleya</u> <u>rutilans</u>	473	373	100	9.32
<u>Cocconeis</u> 11 A	1649	2	1647	40.87
<u>Cocconeis</u> 11 C	336	2	334	32.89

TABLE 4
(Continued)

	N _T	N _E	N _B	B
<u>Cocconeis J</u>	991	11	980	28.39
<u>Cocconeis costata</u>	460	390	70	14.40
<u>Cocconeis placentula v.</u> <u>euglypta</u>	1365	38	1327	42.48
<u>Cocconeis scutellum</u>	798	585	213	19.92
<u>Cocconeis scutellum v.</u> <u>parva</u>	529	481	48	9.91
<u>Cymbellonitzschia</u> <u>hossamedinii</u>	1117	0	1117	21.64
<u>Fragilaria pinnata</u>	96	0	96	10.04
<u>Fragilaria striatula v.</u> <u>californica</u>	212	2	210	2.54
<u>Gomphonema oceanicum</u>	458	413	45	9.55
<u>Gyrosigma prolongum</u>	42	1	41	3.97
<u>Hantzschia 1</u>	38	0	38	6.44
<u>Hantzschia marina</u>	62	0	62	6.58
<u>Melosira moniliformis</u>	278	37	241	6.18
<u>Melosira nummuloides</u>	82	17	65	4.54
<u>Navicula 3</u>	71	2	69	3.36
<u>Navicula 16</u>	206	0	206	3.14
<u>Navicula 109</u>	460	16	444	24.27
<u>Navicula 150</u>	201	129	72	14.93
<u>Navicula 199</u>	1100	0	1100	17.30

TABLE 4
(Continued)

	N _T	N _E	N _B	B
<u>Navicula ammophila</u> v. <u>minuta</u>	144	0	144	16.84
<u>Navicula directa</u>	542	535	7	6.90
<u>Navicula disertata</u>	340	0	340	41.91
<u>Navicula diversistriata</u>	332	2	330	15.86
<u>Navicula forcipata</u>	120	0	120	15.01
<u>Navicula gottlandica</u>	162	0	162	9.06
<u>Navicula gregaria</u>	857	4	853	32.34
<u>Navicula groschopfi</u>	76	0	76	5.47
<u>Navicula patrickae</u>	214	1	213	20.18
<u>Navicula salina</u>	48	0	48	9.66
<u>Navicula salinicola</u>	3665	1760	1905	41.12
<u>Navicula tripunctata</u>	69	0	69	2.49
<u>Navicula tripunctata</u> v. <u>schizonemoides</u>	1229	930	299	24.86
<u>Nitzschia 2</u>	82	0	82	16.51
<u>Nitzschia 5</u>	100	62	38	19.64
<u>Nitzschia 37</u>	117	0	117	3.18
<u>Nitzschia 171</u>	223	202	21	3.72
<u>Nitzschia brevirostris</u>	78	78	0	3.08
<u>Nitzschia dissipata</u> v. <u>media</u>	314	207	107	29.97
<u>Nitzschia frustulum</u>	41	0	41	12.92

TABLE 4
(Continued)

	N _T	N _E	N _B	B
<u>Nitzschia frustulum v. subsalina</u>	2456	1060	1396	37.13
<u>Nitzschia fundi</u>	1524	472	1052	42.75
<u>Nitzschia pseudohybrida</u>	274	191	83	13.86
<u>Nitzschia punctata</u>	21	0	21	16.23
<u>Nitzschia rostellata</u>	232	191	41	8.54
<u>Opephora pacifica</u>	3503	6	3497	54.23
<u>Opephora perminuta</u>	262	1	261	15.80
<u>Opephora schultzi</u>	237	3	234	34.15
<u>Paralia sulcata</u>	565	18	546	45.06
<u>Rhoicosphenia curvata</u>	56	49	7	11.60
<u>Rhopalodia musculus</u>	65	3	62	8.51
<u>Synedra fasciculata</u>	851	803	48	15.14
<u>Thalassiosira 1</u>	1037	119	918	42.65
<u>Trachysphenia australis</u>	246	2	244	11.62

this taxon was absent or rare. Navicula 3 was abundant only in February in samples SA3 and SA4. Although Navicula 16 was found only in sand samples and was usually rare, this diatom represented about two-fifths of all the valves identified from SA4 in April. Nitzschia 171 and Nitzschia breviostris were epiphytic taxa with restricted distributions. Nitzschia breviostris was abundant only in the three epiphyte samples from October (EP1-3). Nitzschia 171 was abundant in the September epiphyte samples where it was found in the colonial mucilage of Bacillaria paradoxa.

The abundance of 36 dominant benthic taxa at the Sand, Fine Sand, and Silt sites are presented in Table 5. These taxa were also used for regression and canonical correlation analyses. Cocconeis placentula v. euglypta, Cocconeis J, Navicula 199, Opephora pacifica and Thalassiosira 1 were common in the samples from the Sand site. Achnanthes hauckiana and Opephora pacifica dominated the Fine Sand site, while Achnanthes hauckiana, Achnanthes 11B, Navicula salinicola and Opephora pacifica were common at the Silt site.

Most species were much more common in certain sediments than in others. For example, Achnanthes latestriata, Amphora exigua, Amphora laevis v. perminuta, Amphora libyca, Amphora proteus, Anorthoneis eurytoma, Cocconeis J, Navicula 199, Navicula ammophila v. minuta, Navicula 16, and Navicula diversistriata had more than two-thirds of their total number of valves in samples from sand. Cymbellonitzschia hossamedinii, Melosira moniliformis, and Trachysphenia australis

TABLE 5

A list of 36 selected benthic taxa with their total abundances in samples from the Sand (N_{SA}), Fine Sand (N_{FS}), and Silt (N_{SI}) sites.

	N_{SA}	N_{FS}	N_{SI}
<u>Achnanthes</u> 1	6	177	247
<u>Achnanthes</u> 11 B	6	53	859
<u>Achnanthes</u> hauckiana	214	1514	1507
<u>Achnanthes</u> latestriata	144	18	10
<u>Achnanthes</u> lemmermanni	363	152	104
<u>Amphora</u> exigua	268	56	23
<u>Amphora</u> laevis v. <u>perminuta</u>	127	6	22
<u>Amphora</u> libyca	166	7	25
<u>Amphora</u> micrometra	10	8	481
<u>Amphora</u> proteus	77	1	1
<u>Amphora</u> sabyii	377	845	466
<u>Amphora</u> tenerrima	352	76	146
<u>Anorthoneis</u> eurystoma	155	0	2
<u>Cocconeis</u> 11 A	336	800	511
<u>Cocconeis</u> J	708	258	14
<u>Cocconeis</u> placentula v. <u>euglypta</u>	734	398	195
<u>Cymbellonitzschia</u> <u>hossamedinii</u>	486	626	5
<u>Melosira</u> moniliformis	153	79	9
<u>Navicula</u> 3	65	1	3

TABLE 5
(Continued)

	N _{SA}	N _{FS}	N _{SI}
<u>Navicula</u> 16	205	0	1
<u>Navicula</u> 109	83	78	283
<u>Navicula</u> 199	800	59	241
<u>Navicula ammophila</u> v. <u>minuta</u> 128	12	4	
<u>Navicula diversistriata</u>	292	35	3
<u>Navicula gottlandica</u>	0	11	151
<u>Navicula gregaria</u>	474	69	310
<u>Navicula groschopfi</u>	0	2	74
<u>Navicula salinicola</u>	293	509	1103
<u>Nitzschia</u> 37	0	46	71
<u>Nitzschia frustulum</u> v. <u>subsalina</u>	117	795	484
<u>Nitzschia fundi</u>	280	262	510
<u>Opephora pacifica</u>	991	1152	1354
<u>Opephora perminuta</u>	73	128	60
<u>Opephora schultzi</u>	28	43	163
<u>Thalassiosira</u> 1	583	97	238
<u>Trachysphenia australis</u>	128	113	3

occurred almost exclusively at the Sand and Fine Sand sites. None of the 36 taxa investigated had a strong preference (two-thirds or more of their total occurrences) in fine sand. Achnanthes 1, Achnanthes hauckiana, and Nitzschia 37 occurred almost exclusively in the samples from the Fine Sand and Silt sites. Achnanthes 11 B, Amphora micrometra, Navicula gottlandica, Navicula groschopfi, and Opephora schultzi had two-thirds of their total number of valves in Silt samples.

Autecological relationships were examined by regressing the abundances of selected epiphytic taxa against the environmental data. The coefficient of determination for these regressions (R^2) ranged from 0.02 for Cocconeis scutellum to 0.81 for Nitzschia fundi (Table 6). Nine of 22 taxa had R^2 values of 0.50 or greater. Therefore, a large amount of the variation in the relative abundances of many epiphyte taxa was related to the environmental variables tidal height, daylength and water temperature. Also, nine of 22 epiphytic taxa had correlation coefficients greater than 0.50 relative to daylength and water temperature (Table 6). Of these species, Navicula tripunctata v. schizonemiodos, Nitzschia frustulum v. subsalina, and Nitzschia fundi were abundant throughout the year, but had a distinct maximum occurrence during winter, spring, or summer, respectively. Cocconeis scutellum v. parva and Berkeleya rutilans were absent or rare in the summer or fall, but were common during winter and spring. Several species of Nitzschia were common in the October

TABLE 6

The relationship between 22 selected epiphytic taxa and three environmental variables: intertidal height (TIDE), daylength (DAYL), and water temperature (TEMP). Correlation coefficients are given for each taxon as well as the coefficient of determination (R^2) for the multiple regression of the abundance of each taxon against the three variables.

	TIDE	DAYL	TEMP	R^2
<u>Amphora tenerrima</u>	0.19	0.48	0.37	0.27
<u>Bacillaria paradoxa</u>	0.02	0.11	-0.14	0.17
<u>Berkeleya rutilans</u>	0.11	0.53	0.42	0.30
<u>Cocconeis costata</u>	0.08	0.34	0.12	0.20
<u>Cocconeis scutellum</u>	-0.08	-0.01	0.05	0.02
<u>Cocconeis scutellum v. parva</u>	0.30	0.70	0.58	0.58
<u>Gomphonema oceanicum</u>	-0.16	-0.07	-0.43	0.44
<u>Navicula 150</u>	0.07	0.50	0.28	0.30
<u>Navicula directa</u>	-0.01	-0.46	-0.39	0.22
<u>Navicula salinicola</u>	0.24	-0.38	0.03	0.52
<u>Navicula tripunctata v. schizonemoides</u>	-0.23	-0.74	-0.57	0.61
<u>Nitzschia 5</u>	0.03	-0.22	-0.49	0.32
<u>Nitzschia 171</u>	0.05	0.12	-0.03	0.07
<u>Nitzschia brevirostris</u>	0.05	-0.24	-0.58	0.53
<u>Nitzschia dissipata v. media</u>	-0.09	-0.14	-0.57	0.66
<u>Nitzschia frustulum v. subsalina</u>	0.18	0.81	0.68	0.69

TABLE 6
(Continued)

	TIDE	DAYL	TEMP	R ²
<u>Nitzschia fundi</u>	0.09	0.89	0.81	0.81
<u>Nitzschia pseudohybrida</u>	0.02	-0.50	-0.70	0.50
<u>Nitzschia rostellata</u>	-0.08	-0.10	-0.37	0.27
<u>Rhoicosphenia curvata</u>	-0.21	0.23	0.08	0.12
<u>Synedra fasciculata</u>	-0.06	0.06	-0.37	0.55
<u>Thalassiosira 1</u>	0.13	0.10	0.05	0.03

samples, namely N. brevirostris, N. dissipata v. media, N. pseudohybrida, N. rostellata and Nitzschia 5. Nitzschia 171 was present only in September samples, and therefore had a distinct seasonality in spite of its low correlations with daylength and water temperature. This discrepancy is accounted for by the non-linearity of the data, i.e., temperature and daylength were near their mean values during the only month this taxon was present. Correlations of the same taxa with tidal height were relatively weak. Of the 22 epiphyte taxa under consideration, only Cocconeis scutellum v. parva exhibited a weak relationship with intertidal positions ($r = 0.30$); this taxon was found primarily at EP2 and EP3.

An autecological analysis of selected benthic taxa is presented in Table 7. Twenty-two of the 36 taxa of interest were at least weakly associated ($r \geq 0.38$) with the first principal component of the environmental data matrix, and 13 taxa had correlation coefficients of 0.50 or greater. This component expressed sediment properties, especially OM, PHI, and SORT (Table 2). Negative correlation coefficients for Achnanthes 1, Achnanthes 11B, Amphora micrometra, Navicula gottlandica, and Opephora schultzi indicated that these taxa were associated with sediments that were composed of finer particles, were poorly sorted, and had a high concentration of organic matter. Relatively high positive correlations with Achnanthes latestriata, Amphora proteus, Anorthoneis eurystoma, Cocconeis J, Cymbello-nitzschia hossamedinii, Navicula ammophila v. minuta, Navicula 16,

TABLE 7

The relationship between 36 selected benthic taxa and the first three principal components of the environmental data matrix. Correlation coefficients (r_1 , r_2 and r_3) are given for each component. R_f^2 is the coefficient of determination for the regression of the species variables against the first three components, where $R_f^2 = r_1^2 + r_2^2 + r_3^2$ and R^2 is the coefficient of determination for the multiple regression of species abundance against all environmental variables.

	PCA1 r_1	PCA2 r_2	PCA3 r_3	R_f^2	R^2
<u>Achnanthes</u> 1	-0.67	0.06	0.02	0.46	0.48
<u>Achnanthes</u> 11 B	-0.74	-0.03	-0.07	0.55	0.66
<u>Achnanthes</u> <u>hauckiana</u>	-0.47	-0.24	0.40	0.44	0.61
<u>Achnanthes</u> <u>latestriata</u>	0.55	-0.21	-0.18	0.39	0.43
<u>Achnanthes</u> <u>lemmermanni</u>	0.44	0.12	0.40	0.36	0.46
<u>Amphora</u> <u>exigua</u>	0.49	-0.26	-0.07	0.32	0.48
<u>Amphora</u> <u>laevis</u> v. <u>perminuta</u>	0.39	0.28	-0.05	0.23	0.33
<u>Amphora</u> <u>libyca</u>	0.39	-0.01	-0.18	0.19	0.29
<u>Amphora</u> <u>micrometra</u>	-0.74	-0.07	-0.00	0.55	0.64
<u>Amphora</u> <u>proteus</u>	0.59	-0.11	0.28	0.44	0.79
<u>Amphora</u> <u>sabyii</u>	-0.20	0.00	-0.42	0.22	0.34
<u>Amphora</u> <u>tenerrima</u>	0.29	0.18	-0.17	0.14	0.22
<u>Anorthoneis</u> <u>eurystoma</u>	0.58	-0.07	0.25	0.40	0.58
<u>Cocconeis</u> 11 A	-0.20	-0.02	-0.36	0.17	0.24
<u>Cocconeis</u> J	0.68	0.10	-0.19	0.52	0.67
<u>Cocconeis</u> <u>placentula</u> v. <u>euglypta</u>	0.28	0.13	-0.46	0.29	0.47
<u>Cymbellonitzschia</u> <u>hossamedinii</u>	-0.54	0.03	-0.39	0.45	0.62

TABLE 7
(Continued)

	PCA1 r_1	PCA2 r_2	PCA3 r_3	R_F^2	R^2
<u>Melosira moniliformis</u>	-0.05	0.17	-0.10	0.04	0.12
<u>Navicula 3</u>	0.26	-0.20	0.12	0.12	0.22
<u>Navicula 16</u>	0.53	-0.01	0.20	0.32	0.41
<u>Navicula 109</u>	-0.22	0.59	-0.26	0.46	0.55
<u>Navicula 199</u>	0.18	-0.32	0.00	0.13	0.32
<u>Navicula ammophila v. minuta</u>	0.58	0.02	0.04	0.34	0.41
<u>Navicula diversistriata</u>	0.57	-0.13	-0.32	0.45	0.56
<u>Navicula gottlandica</u>	-0.52	-0.02	-0.12	0.28	0.43
<u>Navicula gregaria</u>	0.01	0.20	0.20	0.08	0.29
<u>Navicula groschopfi</u>	-0.44	-0.00	0.44	0.39	0.51
<u>Navicula salinicola</u>	-0.44	-0.29	0.04	0.27	0.34
<u>Nitzschia 37</u>	-0.24	-0.32	0.32	0.28	0.32
<u>Nitzschia frustulum v. subsalina</u>	-0.39	0.05	-0.27	0.23	0.31
<u>Nitzschia fundi</u>	-0.41	0.49	0.17	0.44	0.54
<u>Opephora pacifica</u>	-0.34	-0.16	-0.05	0.15	0.25
<u>Opephora perminuta</u>	-0.09	0.34	0.16	0.15	0.30
<u>Opephora schultzi</u>	-0.62	-0.32	0.03	0.48	0.61
<u>Thalassiosira 1</u>	0.13	0.24	-0.45	0.28	0.48
<u>Trachysphenia australis</u>	0.32	-0.00	0.14	0.12	0.25

and Navicula diversistriata indicated that these taxa were associated with sandy, well-sorted sediments with low organic content. A comparison of the taxa listed above with Table 5 demonstrates the limits of linear models. For example, Amphora exigua, Amphora laevis v. perminuta and Amphora libyca have from 77% to 82% of their total occurrences at the Sand site and yet have weak correlations with the first factor ($r = 0.39$ to 0.49). Melosira moniliformis is an extreme case, with 63% of its valves in sand and 96% of its valves in sand and fine sand together, yet its correlation with the sediment factor was only -0.05 .

The second principal component is correlated with daylength and temperature, variables that express seasonal changes. In general, species correlations with this axis were weak except for Navicula 109 and Nitzschia fundi. These taxa were most common in the summer.

The third principal component was an expression of intertidal height. Species correlations with this component also were weak, with no correlation coefficient greater than 0.50 and most values less than 0.30 . Achnanthes hauckiana, Achnanthes lemmermanni, and Navicula groschopfi had a positive correlation with this component (r values between 0.40 and 0.44); while Amphora sabyii, Cocconeis placentula v. euglypta, Cymbellonitzschia hossamedinii and Thalassiosira 1 had negative correlations with this component (r values between -0.39 and -0.46). The former group of species was associated with high intertidal stations, whereas the latter group was associated with the lower stations.

Taxa mentioned above that were associated with factors 1, 2, or 3 had R^2 values ranging from 0.22 to 0.55 for the multiple regression of relative abundance against the first three principal components of the environmental data. The total R^2 for the multiple regression of each of these taxa against all nine environmental variables ranged from 0.34 to 0.79.

Community Organization

1. Community Composition Parameters

The diversity of epiphytic assemblages (H'') ranged from 1.61 in January at EP1 to 4.10 in October at EP2 (Table 8). The mean H'' value was 2.89 for 36 epiphyte samples. Low values of H'' observed in May and June were due mainly to low species richness (S), as the dominance (RED) in these samples remained approximately the same. The lowest H'' values were found for samples taken from November through January and were the result of a decrease in richness and a concurrent increase in dominance. The transition from the highest diversity values in October to a period of relatively low values in November through January was remarkably abrupt. An analysis of variance indicated that there was a significant difference among the monthly mean values of H'' for the epiphyte samples (Table 9). However, there was no significant difference among the mean H'' values associated with the three tidal heights.

TABLE 8

Sample size (N), species richness (S), redundancy (RED), and species diversity (H'') for 36 samples of epiphytic diatoms.

Month	Tidal Height	Acronym	N	S	RED	H''
Feb	1	EP1	501	16	0.36	2.68
Feb	2	EP2	553	27	0.35	3.24
Feb	3	EP3	536	38	0.36	3.62
Mar	1	EP1	536	20	0.33	3.00
Mar	2	EP2	530	20	0.37	2.86
Mar	3	EP3	546	19	0.31	3.02
Apr	1	EP1	596	28	0.30	3.51
Apr	2	EP2	563	32	0.36	3.41
Apr	3	EP3	610	29	0.28	3.62
May	1	EP1	518	18	0.28	3.08
May	2	EP1	512	12	0.46	2.05
May	3	EP3	517	13	0.56	1.77
Jun	1	EP1	622	19	0.32	2.98
Jun	2	EP2	526	13	0.37	2.41
Jun	3	EP3	530	12	0.32	2.52
Jul	1	EP1	562	32	0.39	3.29
Jul	2	EP2	544	20	0.38	2.83
Jul	3	EP3	567	18	0.37	2.73
Aug	1	EP1	500	32	0.32	3.61
Aug	2	EP2	537	36	0.35	3.60

TABLE 8
(Continued)

Month	Tidal Height	Acronym	N	S	RED	H"
Aug	3	EP3	612	40	0.26	4.09
Sep	1	EP1	562	34	0.29	3.81
Sep	2	EP2	568	33	0.29	3.75
Sep	3	EP3	589	29	0.30	3.56
Oct	1	EP1	552	27	0.23	3.76
Oct	2	EP2	511	37	0.25	4.10
Oct	3	EP3	620	34	0.24	3.98
Nov	1	EP1	605	20	0.66	1.70
Nov	2	EP2	597	26	0.61	2.11
Nov	3	EP3	574	23	0.58	2.14
Dec	1	EP1	517	14	0.61	1.64
Dec	2	EP2	530	15	0.58	1.80
Dec	3	EP3	556	18	0.62	1.80
Jan	1	EP1	578	17	0.65	1.61
Jan	2	EP2	540	15	0.58	1.78
Jan	3	EP3	581	19	0.43	2.54
Mean				36.00	0.40	2.89
Standard Deviation				8.41	0.13	0.78

TABLE 9

Mean species diversity (\bar{H}'') and standard error ($S_{\bar{H}''}$) for epiphyte samples relative to sample date and to tidal height. Significant differences among means are indicated by the F statistic.

Main Effects	\bar{H}''	$S_{\bar{H}''}$	F
Date:			15.67 (P < 0.005)
Feb	3.18	0.27	
Mar	2.96	0.05	
Apr	3.51	0.06	
May	2.30	0.40	
Jun	2.64	0.17	
Jul	2.95	0.17	
Aug	3.77	0.16	
Sep	3.71	0.08	
Oct	3.95	0.10	
Nov	1.98	0.14	
Dec	1.75	0.05	
Jan	1.98	0.29	
Tidal level:			0.07 (P > 0.25)
EP1	2.89	0.24	
EP2	2.83	0.23	
EP3	2.95	0.24	

Species diversity (H') for benthic samples ranged from 2.38 in February at FS4 to 5.34 in June SA3 (Tables 10-12). In contrast with epiphyte samples, an analysis of variance indicated that there were no significant differences among mean H' values relative to season (Table 13). However, significant differences were found among mean H' values relative to tidal height and to sediment type. Of the four intertidal stations, the upper stations (station 4) had the lowest mean species diversity. The Fine Sand site had the lowest mean diversity among the sediment types.

The mean species diversity (H') for all benthic samples taken together was 4.23, in comparison to a mean of 2.89 for all epiphyte samples. An unpaired t-test indicated that these mean values were significantly different ($P < 0.005$). In general, the benthic diatom assemblages had higher species richness and lower dominance than the epiphytic assemblages. Mean species richness for the epiphytic and benthic samples was 36.00 and 51.11 respectively, while corresponding mean values for redundancy were 0.40 and 0.32.

Both Jaccard and SIMI indices of similarity were used to compare the species composition of epiphytic and benthic assemblages (Table 14). The Jaccard index indicated that the epiphyte samples had from 32% to 35% of their taxa in common with samples from the Sand, Fine Sand, or Silt sites. Benthic samples from these three sediments shared a greater percentage of taxa among themselves, in this case from 52% to 59%. In contrast to the Jaccard index, SIMI reflects the

TABLE 10

Sample size (N), species richness (S), redundancy (RED), and species diversity (H'') for the 22 samples of benthic diatoms from the Sand site.

Month	Tidal Height	Acronym	N	S	RED	H''
Apr	1	SA1	526	54	0.21	4.77
Apr	2	SA2	544	61	0.22	4.89
Apr	3	SA3	638	59	0.21	4.83
Apr	4	SA4	763	71	0.30	4.61
Jun	1	SA1	524	55	0.26	4.56
Jun	2	SA2	527	49	0.31	4.14
Jun	3	SA3	527	72	0.17	5.34
Jun	4	SA4	521	31	0.33	3.49
Aug	1	SA1	534	56	0.23	4.73
Aug	2	SA2	516	50	0.28	4.36
Aug	3	SA3	511	58	0.16	5.12
Aug	4	SA4	524	24	0.51	2.49
Oct	1	SA1	538	56	0.31	4.34
Oct	2	SA2	537	47	0.39	3.72
Oct	3	SA3	533	67	0.23	4.98
Oct	4	SA4	543	50	0.23	4.57
Dec	2	SA2	539	50	0.26	4.41
Dec	4	SA4	538	59	0.27	4.61
Feb	1	SA1	544	61	0.28	4.59

TABLE 10
(Continued)

Tidal						
Month	Height	Acronym	N	S	RED	H"
Feb	2	SA2	520	49	0.33	4.09
Feb	3	SA3	540	65	0.24	4.89
Feb	4	SA4	548	62	0.17	5.14
Mean				54.82	0.27	4.49
Standard Deviation				11.34	0.08	0.63

TABLE 11

Sample size (N), species richness (S), redundancy (RED), and species diversity (H'') for the 19 samples of benthic diatoms from the Fine Sand site.

Month	Tidal Height	Acronym	N	S	RED	H''
Apr	1	FS1	529	51	0.67	3.80
Apr	2	FS2	516	51	0.77	4.37
Apr	3	FS3	555	52	0.80	4.54
Apr	4	FS4	562	33	0.62	3.15
Jun	2	FS2	515	47	0.25	4.38
Jun	3	FS3	519	47	0.26	4.36
Jun	4	FS4	511	29	0.54	2.53
Aug	1	FS1	533	56	0.30	4.39
Aug	2	FS2	534	53	0.32	4.23
Aug	3	FS3	523	40	0.39	3.57
Aug	4	FS4	532	25	0.46	2.71
Oct	2	FS2	552	60	0.27	4.60
Oct	3	FS3	525	40	0.32	3.88
Oct	4	FS4	551	28	0.49	2.68
Dec	2	FS2	509	54	0.35	4.11
Dec	3	FS3	530	58	0.25	4.66

TABLE 11
(Continued)

Tidal						
Month	Height	Acronym	N	S	RED	H"
Dec	4	FS4	533	44	0.47	3.29
Feb	3	FS3	526	53	0.35	4.06
Feb	4	FS4	521	30	0.58	2.38
Mean				40.76	0.45	3.77
Standard Deviation				16.80	0.18	0.76

TABLE 12

Sample size (N), species richness (S), redundancy (RED), and species diversity (H'') for the 23 samples of benthic diatoms from the Silt site.

Month	Tidal Height	Acronym	N	S	RED	H''
Apr	1	SI1	519	65	0.21	5.03
Apr	2	SI2	498	53	0.31	4.28
Apr	3	SI3	516	43	0.28	4.15
Apr	4	SI4	552	60	0.41	3.95
Jun	1	SI1	516	49	0.21	4.62
Jun	2	SI2	519	49	0.22	4.60
Jun	3	SI3	534	38	0.26	4.80
Jun	4	SI4	513	50	0.32	4.16
Aug	1	SI1	540	61	0.20	5.03
Aug	2	SI2	536	54	0.20	4.82
Aug	3	SI3	544	45	0.22	4.45
Aug	4	SI4	541	48	0.35	3.96
Oct	1	SI1	550	63	0.22	4.91
Oct	2	SI2	526	61	0.21	4.92
Oct	3	SI3	532	51	0.26	4.46
Oct	4	SI4	535	55	0.32	4.26
Dec	2	SI2	551	57	0.21	4.84
Dec	3	SI3	540	51	0.26	4.45
Dec	4	SI4	524	38	0.58	2.62

TABLE 12
(Continued)

Tidal						
Month	Height	Acronym	N	S	RED	H"
Feb	1	SI1	525	78	0.24	5.12
Feb	2	SI2	527	52	0.23	4.60
Feb	3	SI3	502	45	0.24	4.38
Feb	4	SI4	633	48	0.37	3.80
Mean				52.78	0.28	4.41
Standard Deviation				9.16	0.09	0.54

TABLE 13

Mean species diversity (\bar{H}'') and standard error ($S_{\bar{x}}$) for benthic samples relative to sample data, tidal height and sediment type. Significant differences among means are indicated by the F statistic.

Main Effects	\bar{H}''	$S_{\bar{x}}$	F
Date:			0.33 (P > 0.25)
Apr	4.36	0.16	
Jun	4.21	0.22	
Aug	4.16	0.25	
Oct	4.03	0.37	
Dec	3.96	0.29	
Feb	4.31	0.26	
Tidal level:			11.75 (P < 0.005)
Sta. 1	4.66	0.11	
Sta. 2	4.43	0.08	
Sta. 3	4.48	0.11	
Sta. 4	3.58	0.21	
Sediment Type:			7.39 (P < 0.005)
Sand	4.48	0.13	
Fine Sand	3.77	0.17	
Silt	4.41	0.11	

Table 14

A comparison of the similarity of pooled epiphytic and benthic samples using SIMI and Jaccard indices. SIMI compares the presence and relative abundance of species among samples and is found in the lower left half of the table. The Jaccard index uses only presence-absence data and form the upper right half of the table. The pooled samples are epiphytes (EP) and the assemblages from the Sand (SA), Fine Sand (FS) and Silt (SI) sites.

	EP	SA	FS	SI
EP	1.00	0.35	0.32	0.32
SA	0.18	1.00	0.54	0.52
FS	0.29	0.62	1.00	0.59
SI	0.40	0.56	0.84	1.00

relative abundances of species as well as their joint occurrences in samples. SIMI values ranged from 0.18 to 0.84 and emphasized the differences between the epiphyte samples and the benthic samples (SIMI = 0.18 to 0.40) as well as the similarities among benthic samples (SIMI = 0.56 to 0.84). Epiphytic samples were more similar to samples from the Silt site than to samples from the Sand or Fine Sand sites, while assemblages from sand were more similar to those from fine sand than from silt.

2. Ordination Analyses

Species and samples were ordinated along axes by three ordination methods: Polar Ordination (PO), Principal Components Analysis (PCA) and Reciprocal Averaging (RA). Of these methods, the PO axes were the least interpretable. PCA produced sample ordinations that were virtually identical to those obtained by RA, however species ordinations by RA were easier to interpret than corresponding results from PCA. RA analysis maximized correspondence between sample and species ordinations, and was the preferred method for the analysis of the species abundance data from Netarts Bay. Consequently, only RA ordinations are presented in this section.

Figure 4 illustrates relationships among 82 epiphytic and benthic samples as represented by reciprocal averaging. The first axis separates all 18 epiphytic samples from all 64 benthic samples. The second axis represents a continuum relative to sediment type with

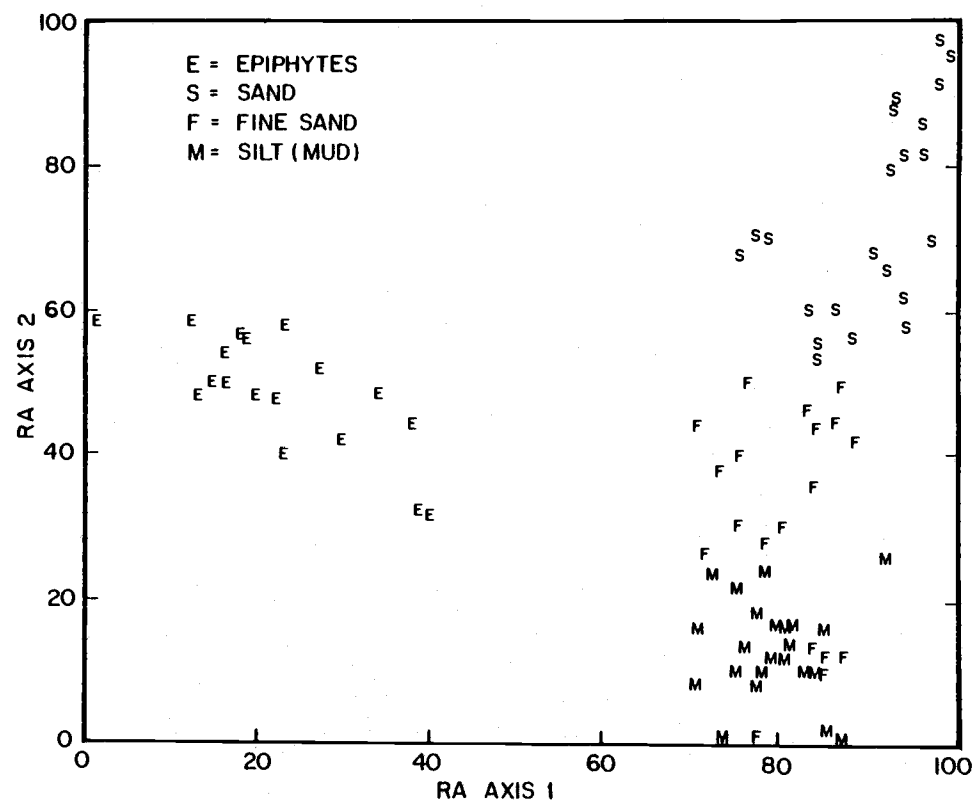


Figure 4. Reciprocal Averaging ordination of 82 benthic and epiphytic samples. Letters correspond to epiphyte samples (E), sand sample (S), fine sand samples (F), and silt samples (M).

samples from the Sand site at the top right, those from the Fine Sand site at the center right, and assemblages from the Silt site at the bottom right. High intertidal sand samples (SA3-4) are found in the upper right-hand corner of the diagram with scores greater than 0.80 on RA2. Below these are the low intertidal Sand samples (SA1-2), and the low and mid intertidal Fine Sand samples (FS1-3). On the lower right edge of the diagram, all Silt samples (SI1-4) are mixed with the high intertidal samples from the Fine Sand site (FS4).

The correspondence of site and species ordinations can be examined by a comparison of Figure 4 with Figure 5. Epiphytic species are found on the left side of Figure 5 (group 1). These species were Nitzschia brevirostris, Rhoicosphenia curvata, Navicula directa, Gomphonema oceanicum, Synedra fasciculata, Bacillaria paradoxa, Cocconeis costata, Cocconeis scutellum v. parva, Nitzschia 5, Navicula tripunctata v. schizonemoides, Nitzschia dissipata v. media, Nitzschia psuedohybrida, Nitzschia rostellata, Nitzschia 171, Navicula 150 and Cocconeis scutellum. Benthic species are found on the right side of the diagram, with species from sand on the top, species from fine sand in the center, and species from silt on the bottom. Taxa that were abundant in all sediment types (group 8) are in the center near the right margin of the figure. These taxa are found mixed with species that had greater fidelity to specific substrates (mainly groups 5 and 6). Species that were found in benthic as well as epiphytic samples are in the center of the figure

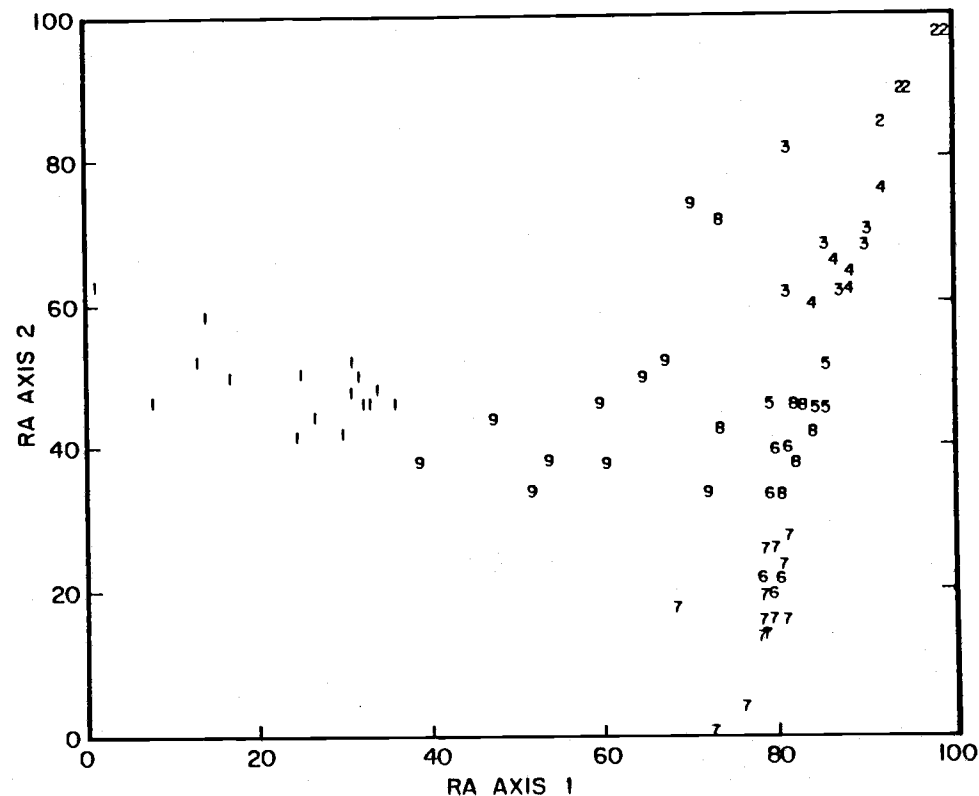


Figure 5. Reciprocal Averaging ordination of 72 benthic and epiphytic species. Numbers correspond to groups of taxa mentioned in text (see pp. 84-88). Specifically, they are epiphytes (1), species found in high intertidal sand (2), mid intertidal sand species (3), low intertidal sand species (5), species found generally throughout sand samples (4), species found in fine sand (6), species found in silt (7), species found generally throughout all three sediment types (8), and species found in both epiphyte and sediment samples (9).

(group 9). These taxa were Navicula salinicola, Navicula 109, Navicula 3, Nitzschia frustulum v. subsalina, Nitzschia fundi, Melosira nummuloides, Melosira moniliformis, Thalassiosira 1, Berkeleya rutilans, and Amphora tenerrima.

A group of five species that were virtually restricted to the upper intertidal stations at the Sand site (SA4) are found in the upper right-hand corner of Figure 5 (group 2). These taxa were Hantzschia marina, Hantzschia 1, Anortheoneis eurystoma, Amphora proteus and Navicula 16. The two Hantzschia species were always present at SA4 but were never very abundant. However; their large size made these species very conspicuous members of this assemblage.

Taxa that were most abundant at the mid-intertidal stations at the Sand site are labeled as group 3. These taxa were Gyrosigma prolongum, Achnanthes latestriata, Navicula forcipata, Amphora exigua, Cocconeis J, and Navicula diversistriata. Another member of this group, Navicula 3, was also found in epiphyte samples; therefore, this taxon was classified in group 9 and was displaced toward epiphyte species to the left of other members of group 3.

Interspersed with members of group 3 were taxa that were found in the sand samples, at all tidal heights. These species (group 4) included Navicula ammophila v. minuta, Amphora laevis v. perminuta, Amphora libyca, Trachysphenia australis and Cymbellonitzschia hossamedinii.

Near the right-center of the figure, there are species that were common in the low intertidal region at the Sand site. These taxa (group 5) also were common at the mid and low intertidal stations at the Fine Sand site (FS1-3). These taxa included Amphora tenerrima, Thalassiosira 1, Navicula 199, Achnanthes lemmermanni, Navicula diserta, and Cocconeis placentula v. euglypta. Two other species were closely related to this group, but were classified as members of group 9 because they were also common epiphytes. These taxa were Amphora tenerrima and Thalassiosira 1.

Several taxa that were common at stations FS1-3 were also common in samples from the Silt site. These taxa (group 6) were Amphora sabyii, Cocconeis 11A, Achnanthes hauckiana, Achnanthes 1, Navicula patrickae and Nitzschia punctata. Four other taxa were associated with this group but were classified as members of group 9 because they were also epiphytic species. These taxa included Navicula salinicola, Navicula 109, Nitzschia fundi, and Nitzschia frustulum v. subsalina.

Taxa that were most abundant in the samples from the Silt site are found at the lower right of Figure 5. These taxa, classified as group 7, were Navicula tripunctata, Opephora schultzi, Amphora 35, Nitzschia frustulum, Nitzschia 2, Navicula gottlandica, Achnanthes 11B, Amphora micrometra, Navicula salina, Navicula groschopfi, Rhopalodia musculus, Fragilaria pinnata, and Nitzschia 37.

Species that were common in all three sediments were placed in group 8 and included Opephora pacifica, Opephora perminuta, Amphora coffeiformis, Paralia sulcata, Cocconeis 11C, Navicula gregaria, and Fragilaria striatula v. californica.

To obtain better resolution in the ordinations and to relate the sample ordinations to patterns in the environmental data set, the data matrix was divided into the epiphyte samples and the benthic samples, and an RA ordination was performed separately on each data subset.

A plot of epiphyte samples relative to the first and second RA axes is presented in Figure 6. The samples from winter and spring are found on the lower left of the diagram. There was a change in community structure in June that caused most of the June samples to be oriented in the upper left of the figure. The epiphyte samples from August and October are located on the right end of RA axis 1, an orientation that also illustrated temporal changes and discontinuities in species composition and relative abundance.

An RA ordination of epiphytic taxa corresponded closely with the pattern of sample ordinations in Figure 6 and helped to elucidate the seasonal changes in community composition (Figure 7). The taxa on the lower left, identified by four-letter acronyms, are Navicula directa, Gomphonema oceanicum, Paralia sulcata, Rhoicosphenia curvata, Cocconeis scutellum, and Cocconeis costata. These taxa were spring and winter species that had a maximum relative abundance in

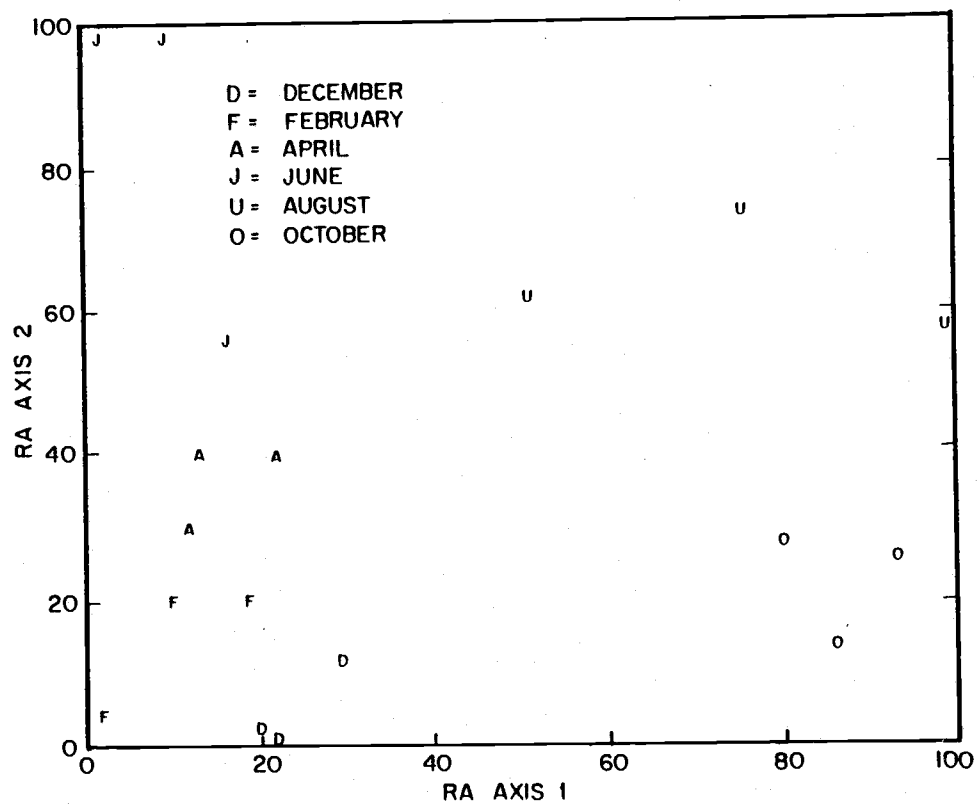


Figure 6. Reciprocal Averaging ordination of epiphyte samples. Letters correspond to months in which samples were taken, where D is December, F is February, A is April, J is June, U is August, and O is October.

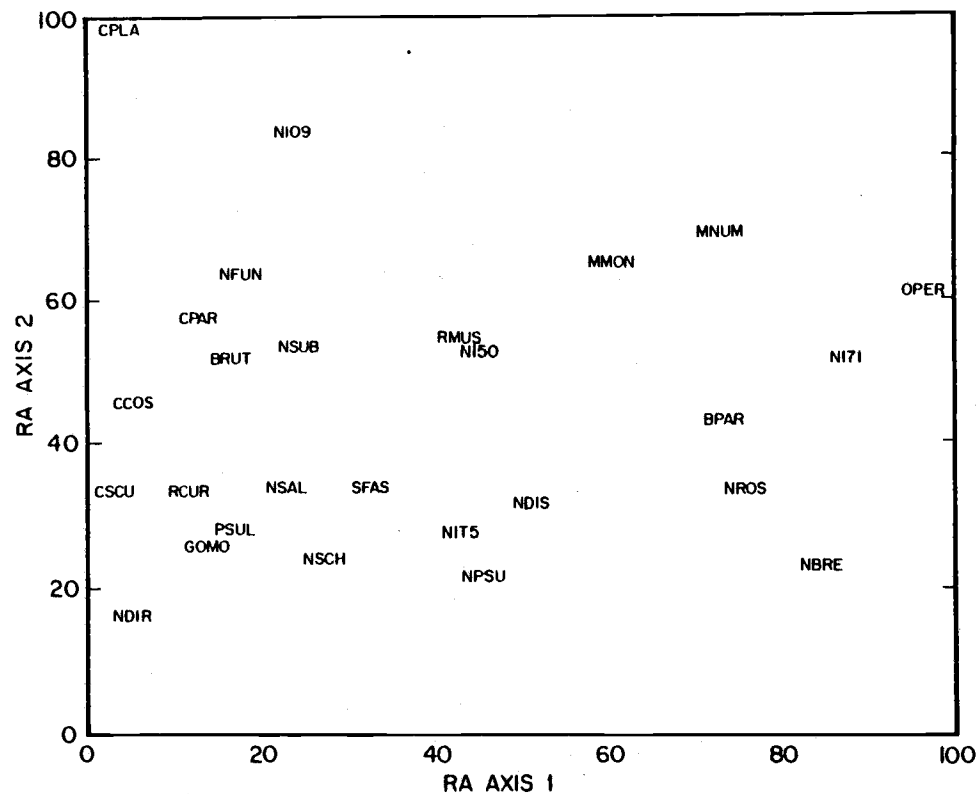


Figure 7. Reciprocal Averaging ordination of dominant epiphyte species. The taxa are: *Navicula directa* (NDIR), *Gomphonema oceanicum* (GOMO), *Paralia sulcata* (PSUL), *Cocconeis scutellum* (CSCU), *Rhizosolenia curvata* (RCUR), *Navicula salinicola* (NSAL), *Cocconeis costata* (CCOS), *Berkeleya rutilans* (BRUT), *Nitzschia frustulum* v. *subsalina* (NSUB), *Cocconeis scutellum* v. *parva* (NPAR), *Nitzschia fundi* (NFUN), *Navicula 109* (NIO9), *Cocconeis placentula* v. *euglypta* (CPLA), *Rhopalodia musculus* (RMUS), *Navicula 150* (N150), *Melosira moniliformis* (MMON), *Melosira nummuloides* (MNUM), *Nitzschia 171* (N171), *Opephora perminuta* (OPER), *Bacillaria paradoxa* (BPAR), *Nitzschia rostellate* (NROS), *Nitzschia brevirostris* (NBRE), *Nitzschia dissipata* v. *media* (NDIS), *Nitzschia pseudohybrida* (NPSU), *Nitzschia 5* (NIT5), *Synedra fasciculata* (SFAS), and *Navicula tripunctata* v. *schizonemoides* (NSCH).

February or March. Taxa that were abundant in spring and summer are found in the upper left of the figure. These taxa, Berkeleya rutilans, Nitzschia frustulum v. subsalina, Cocconeis scutellum v. parva, Nitzschia fundi, Navicula 109, and Cocconeis placentuala v. euglypta, were abundant from April through August and had maximum relative abundances from May through July. Taxa that were common from August through October are found in the center of the diagram and to the far right. Rhopalodia musculus, Navicula 150, Melosira moniliformis, Melosira nummuloides, Bacillaria paradoxa, Nitzschia 171, Opephora perminuta, and Nitzschia rostellata were most abundant in October. Synedra fasciculata, Navicula salinicola, and Navicula tripunctata v. schizonemoides are found just below and to the left of the center of the diagram and were abundant during all seasons.

An RA ordination of benthic samples and species resulted in a distributional continuum that was related to sediment type. The relative positions of benthic samples and species were similar to the ordinations of the entire data set (Figures 4 and 5). High intertidal sand samples (SA4) were found at one end of the first axis, mid intertidal sand samples were next (SA3), followed by the lower intertidal sand samples (a mixture of SA1 and SA2). Mid and low intertidal samples from fine sand were found near the center of the axis, and all samples from silt and from high intertidal fine sand (FS4) were intermingled on the other end of the axis. The species ordination followed the same pattern, with high intertidal

sand species at one end of the axis and the silt associated flora on the other end. The second axis ordered sand and silt samples and species at one end of the axis, fine sand samples and species at the other end, and a mixture of all three sediments in the center.

3. Community Structure Relative to Environmental Data

In order to interpret the distributions of samples and taxa in relationship to the physical environment, RA axes from the sample ordinations were correlated with environmental variables. Canonical correlation also was used as a separate analysis for the same purpose.

Two RA axes generated from an ordination of epiphyte samples were correlated with tidal height, daylength, and water temperature (Table 15). The highest correlations were between the second RA axis and daylength ($r = 0.90$) and between this same axis and temperature ($r = 0.85$). The first RA axis is weakly correlated with the same variables ($r < 0.25$). Therefore, the second axis is an expression of seasonal variation in the epiphytic flora while the first axis is uninterpretable relative to these environmental variables.

The examination of pattern in the benthic samples relative to the physical environment also was investigated by correlation analysis (Table 16). The first RA axis for the benthic samples was highly correlated with sediment properties, as $r = -0.75$, -0.68 , -0.77 for correlations between this axis and organic matter, mean particle size, and the sorting coefficient, respectively. The first

TABLE 15

Correlations between environmental variables and two RA axes generated from an analysis of epiphyte data. The environmental variables are intertidal height (TIDE), daylength (DAYL), and water temperature (TEMP). The coefficient of determination (R^2) is given for the multiple regression of each RA axis against the three environmental variables.

Variable	Correlation Coefficients	
	RA1	RA2
TIDE	-0.04	0.25
DAYL	-0.05	0.90
TEMP	-0.24	0.85
R^2	0.13	0.90

TABLE 16

Correlations between environmental variables and two RA axes generated from an analysis of benthic data. The environmental variables are intertidal height (TIDE), surface chlorophyll a (CHLA), organic matter (OM), chlorophyll ratio (RATIO), daylength (DAYL), water temperature (TEMP), mean sediment particle size (PHI), the sorting coefficient (SORT), and the skewness coefficient (SKEW). The coefficient of determination (R^2) is given for the multiple regression of each RA axis against the nine environmental variables.

Variable	Correlation Coefficients	
	RA1	RA2
TIDE	-0.01	-0.45
CHLA	-0.41	-0.15
OM	-0.75	-0.11
RATIO	0.52	-0.37
DAYL	0.03	-0.01
TEMP	-0.02	-0.03
PHI	-0.68	-0.23
SORT	-0.77	-0.25
SKEW	-0.07	-0.01
R^2	0.76	0.46

RA axis was correlated to a lesser degree with the chlorophyll ratio ($r = 0.53$). Therefore, this axis contrasts assemblages associated with fine sediments that were poorly sorted, high in organic content, and with low chlorophyll ratios, with assemblages associated with coarse, well sorted sediments that were low in organic content and had high chlorophyll ratios. The stations with high chlorophyll ratios were the high intertidal stations, especially SA3 and SA4. The second RA axis is weakly associated with tidal height ($r = -0.45$) and the chlorophyll ratio ($r = -0.37$). This axis contrasts low intertidal stations which had relatively low chlorophyll ratios with the high intertidal stations.

A multiple regression analysis indicated that 76% of the variation in the benthic sample scores for the first RA axis was associated with the nine environmental variables. Approximately 46% of the variation in sample scores for the second RA axis was associated with the same environmental variables. However, weak correlations of this axis with environmental variables made the interpretation of this axis ambiguous.

Canonical correlation analysis also was used to find structure in the species-abundance matrix of the benthic samples relative to structure in the corresponding environmental data matrix. Interpretation of this analysis was based on correlations between linear combinations of variables, the canonical variables, and the original variables in each data matrix (Table 17). The first canonical

TABLE 17

Correlations between environmental variables, 36 selected benthic taxa, and the first three canonical variables from a canonical correlation analysis of the benthic data. The table includes canonical correlation coefficients (R_c) and the redundancy in the species data, given the environmental data, for each axis. The environmental variables are intertidal height (TIDE), surface chlorophyll a (CHLA), organic matter (OM), chlorophyll ratio (RATIO), daylength (DAYL), water temperature (TEMP), mean sediment particle size (PHI), the sorting coefficient (SORT), and the skewness coefficient (SKEW).

Variables	CV1	CV2	CV3
Environmental:			
TIDE	0.36	-0.56	0.60
CHLA	0.33	0.09	0.08
OM	0.71	0.42	-0.03
RATIO	-0.31	-0.44	0.44
RAYL	-0.41	0.58	0.57
TEMP	-0.30	0.59	0.41
PHI	0.69	0.60	-0.04
SORT	0.77	0.77	-0.07
SKEW	0.13	0.10	0.37
Taxa:			
<u>Achnanthes 1</u>	0.53	0.42	-0.02
<u>Achnanthes 11 B</u>	0.65	0.46	-0.12
<u>Achnanthes haukiana</u>	0.71	-0.13	0.16
<u>Achnanthes latestriata</u>	-0.43	-0.42	-0.21

Table 17
(Continued)

	CV1	CV2	CV3
<u>Achnanthes lemmermanni</u>	-0.15	-0.34	0.51
<u>Amphora exigua</u>	-0.33	-0.41	-0.12
<u>Amphora laevis</u> v. <u>perminuta</u>	-0.47	0.01	0.24
<u>Amphora libyca</u>	-0.38	-0.21	-0.08
<u>Amphora micrometra</u>	0.61	0.47	-0.06
<u>Amphora proteus</u>	-0.33	-0.44	0.37
<u>Amphora sabyii</u>	-0.05	0.27	-0.39
<u>Amphora tenerrima</u>	-0.37	0.04	0.06
<u>Anorthoneis eurystoma</u>	-0.30	-0.42	0.36
<u>Cocconeis</u> 11 A	0.06	0.19	-0.37
<u>Cocconeis</u> J	-0.76	-0.26	-0.10
<u>Cocconeis placentula</u> v. <u>euglypta</u>	-0.46	0.04	-0.43
<u>Cymbellonitzschia</u> <u>hossamedinii</u>	-0.65	-0.18	-0.33
<u>Melosira moniliformis</u>	-0.10	0.19	-0.07
<u>Navicula</u> 3	-0.12	-0.35	0.03
<u>Navicula</u> 16	-0.29	-0.37	0.30
<u>Navicula</u> 109	-0.12	0.64	0.05
<u>Navicula</u> 199	0.13	-0.34	-0.06

Table 17
(Continued)

	CV1	CV2	CV3
<u>Navicula ammophila v. minuta</u>	-0.49	-0.29	0.16
<u>Navicula diversistriata</u>	-0.54	-0.34	-0.38
<u>Navicula gottlandica</u>	0.36	0.42	-0.16
<u>Navicula gregaria</u>	-0.02	0.12	0.41
<u>Navicula groschopfi</u>	0.47	-0.01	0.26
<u>Navicula salinicola</u>	0.44	0.12	-0.15
<u>Nitzschia 37</u>	0.40	-0.23	0.01
<u>Nitzschia frustulum v. subsalina</u>	0.18	0.29	-0.34
<u>Nitzschia fundi</u>	0.09	0.58	0.41
<u>Opephora pacifica</u>	0.38	0.02	-0.23
<u>Opephora perminuta</u>	-0.18	0.30	0.25
<u>Opephora schultzi</u>	0.74	0.13	-0.22
<u>Thalassiosira 1</u>	-0.46	0.29	-0.24
<u>Trachysphenia australis</u>	-0.30	-0.17	0.19
 R_c	 0.979	 0.966	 0.914
 Redundancy	 0.166	 0.094	 0.055

variable contrasts poorly sorted fine sediments containing a high concentration of organic matter, with coarse sediments that are well sorted and low in organic matter. The correlations of 36 selected benthic taxa with the first canonical variable range from 0.02 for Navicula gregaria to -0.76 for Cocconeis J. In general, the taxa with the highest correlations with the variable are the same taxa with high correlations with the first PCA-generated axis in Table 7. The second canonical variable is correlated with tidal height ($r = -0.56$), daylength ($r = 0.58$), water temperature ($r = 0.59$), and mean sediment particle size ($r = 0.60$). The variable represents a complex interaction among seasonal changes such as daylength and water temperature with tidal height and sediment particle size. Samples from the lower intertidal region in the summer are contrasted with samples obtained from the high intertidal region in the winter. Although ten taxa are at least weakly correlated with this canonical variable ($r > 0.40$), only Navicula 109 and Nitzschia fundi are strongly associated with this axis. The third canonical variable is correlated with tidal height ($r = 0.60$) and daylength ($r = 0.57$), suggesting seasonal variations along intertidal gradients. Only one species, Achnanthes lemmermanni, is strongly correlated with this axis ($r = 0.51$).

The canonical correlation analysis also indicated that the total redundancy in the species abundance data given the environmental data was 42.6%. The redundancies associated with CV1, CV2 and CV3 were

16.6%, 9.4% and 5.5% respectively, or a total of 31.5% for the first three canonical variables. In general, canonical correlation analysis emphasized the same species and environmental interactions discussed in relation to the reciprocal averaging analysis; however, the interactions are somewhat more complex and the species correlations are slightly lower.

VI. DISCUSSION

The investigation of the diatom flora of Netarts Bay included five assemblages: a marine planktonic assemblage, the epiphytes of Zostera marina, and the benthic floras from sand, fine sand, and silty sediments. Attempts to describe floristic patterns in these assemblages and to associate the patterns with environmental conditions led to the following conclusions:

1. Tychoplankton predominate in samples from the water column throughout most of the year. Marine neritic plankton may be brought into the bay by flood tides, especially during periods of offshore enrichment and the development of coastal plankton blooms.
2. Diatom taxa that were epiphytic on Zostera marina formed an assemblage that was distinct from the benthic assemblages. Only a few taxa, mainly species of Navicula, Nitzschia and Melosira, were common in both epiphytic and benthic samples.
3. The species composition of epiphyte samples demonstrated a seasonal pattern, with a winter-spring flora (November-July) that was dominated by species of Cocconeis, Gomphonema, Rhiocosphenia, Synedra and Navicula directa, and a late summer-early fall flora (August-October) dominated by a diverse group of Navicula and Nitzschia species.
4. The distribution of the most common epiphyte taxa was found

to be virtually unaffected by intertidal gradients, but was related to seasonal changes in temperature and daylength.

5. In contrast to epiphytic taxa, the species composition of benthic samples demonstrated little seasonal variation.
6. Although most benthic taxa exhibited maximal occurrences in either sand or silt, and certain taxa were virtually restricted to the high intertidal sand, many benthic taxa tended to be broadly distributed across different sediment types and across the intertidal gradient.
7. The physical properties of the sediment, especially mean particle size, the organic content, and the degree of sediment sorting, were primarily associated with patterns in the distribution and relative abundance of benthic taxa.

Because of the chemically inert nature of diatom frustules and the ease with which they are transported by water turbulence, the contamination of living assemblages by dead cells is an important concern. Owen et al. (1978) demonstrated that diatom assemblages may consist of between 2-75% dead cells. A living diatom may be used as an indicator of a set of physical and biological conditions that allowed it to survive. Contamination from other areas, or from cells that were alive at a different successional stage, may inhibit meaningful interpretations of floristic structure relative to environmental patterns (Round, 1971). Direct inspection of preserved material using wet-mount slides may be used to determine ratios of

living cells to dead cells (Owen et al., 1978), but this procedure is usually inadequate for species identification. Holmes et al. (1981) suggested that cells may be cleared of pigments in organic solvents and permanently mounted in resins for microscopic observation under an oil-immersion lens. The presence of organic matter in diatom frustules is indicative of cells that were alive at the time of collection. While this approach is attractive in many respects, it is not practical for processing large numbers of samples. McIntire and Moore (1977) pointed out that the choice of methods used in diatom ecology involves a trade off between complex procedures that would be appropriate for the detailed analysis of a few samples to simple procedures that are more appropriate for broad surveys involving many samples. Also, the determination of whether or not a cell is alive at the time of collection does not answer the original question of whether or not a cell is endemic to a specific place at a certain time or is merely a contaminant. It is clear that living as well as dead cells are commonly transported in estuarine water (Baillie and Welsh, 1980).

The existence of distinct patterns in the diatom flora of Netarts Bay indicates that cell transport is not sufficient to homogenize diatom associations. The diatom flora of a given area is likely to be composed primarily of cells that were living and reproducing in that area. Contaminants are usually less abundant than the established flora, and if not suited to that particular habitat,

often are overwhelmed by more productive taxa. The frustules of diatoms that are not able to survive may be rapidly buried or destroyed by abrasion. In addition, Lewin (1961) has demonstrated that the dissolution of empty frustules in seawater can be very rapid, with most of the silica wall being lost in 3-4 weeks.

In this study, taxa found in the neritic plankton constituted the most distinct diatom association. These taxa were rare or absent in most epiphytic and benthic samples. The exceptions included epiphyte samples from February, March and August, months when neritic plankton were abundant and could have become entangled in the felt-like growths of epiphytes. Another exception was the presence of euplanktonic taxa in samples from the low intertidal transect at the Sand site. As was the case with the epiphyte samples, planktonic contaminants were most common during months when these organisms were abundant in the water column. Part of the explanation for this distribution may be that the transect at the Sand site was near the bay mouth and therefore was closest to the source of neritic plankton. This data set does not provide enough information to indicate why plankton were more likely to be stranded in the low intertidal region at the Sand site than at the upper stations of this site.

The preservation of the planktonic frustules in epiphyte and sediment samples was very selective. The only planktonic taxa found in non-planktonic samples were Thalassiosira 1, Thalassiosira

deciens, Thalassiosira pacifica, Thalassionema nitzschioides, and Skeletonema costata. Apparently, selection was not directly related to the degree of silicification, as Thalassiosira deciens and Thalassiosira pacifica were strongly silicified, while Thalassiosira 1 and Skeletonema costatum were not. The heavily silicified species of planktonic Pleurosigma and Nitzschia were abundant in the water column, and yet were absent in non-planktonic samples. It is possible that the planktonic contaminants of the benthic samples were taxa that commonly spend periods of their life history in the sediment.

Although samples of epiphytic and benthic assemblages shared approximately one-third of their taxa, these assemblages were very distinct. Virtually all the abundant taxa were found almost exclusively in either epiphytic or benthic samples (Table 4). The few taxa that were abundant in both assemblages were probably endemic to both assemblages. Rare occurrences in an assemblage probably represent contamination which helps explain why one-third of the species are found in both benthic and epiphytic samples. For this reason, SIMI was a more suitable index of similarity than the Jaccard index, as SIMI weights species relative to their abundance and the Jaccard index weights all species the same.

The large number of taxa found in common among samples from sand, fine sand and silty sediments probably represented a real tolerance of benthic taxa for a variety of sediment types. In general,

the common benthic taxa were abundant and broadly distributed in all three sediments, although they often exhibited their maximum relative abundance in either sand or silt (Table 5).

The development of a planktonic flora is partially related to the amount of available light, e.g., relatively open reservoirs, lakes, and large rivers tend to have euplanktonic organisms while narrow shaded streams do not. The residence time of water within the system also contributes to the development of a planktonic flora. Euplanktonic organisms are typically absent from small fast flowing water courses, but may develop in impoundments, sloughs and in the lower reaches of large rivers (Whitford, 1956). A lack of a resident phytoplankton in small estuaries might be expected if water has a short residence time in the bay before it is flushed into the ocean. However, the unusual hydrologic features of Netarts Bay that promote long retention times of bay water for some reason do not promote a resident planktonic diatom flora.

Except for the studies of Lewin dealing with the phytoplankton of the surf zone (Lewin, 1974; Lewin and Norris, 1970; Lewin, 1977), the plankton of the coastal water of the Pacific Northwest have received little floristic and community analysis. In winter and spring on the Oregon coast phytoplankton blooms are correlated with available solar radiation (Small et al., 1972), i.e., peak phytoplankton biomass occurs when clear weather and reduced water turbulence allow accumulation of large standing crops. Summer phyto-

plankton blooms are associated with upwelling and clear weather. The species lists from Netarts Bay samples from February, March and August (Table 3) suggested that there might be different floras that develop in winter and spring compared to periods of summer upwelling. Experiments with phytoplankton cultures have demonstrated that different nutrient requirements and competitive interactions influence the temporal distribution of planktonic species off the Oregon coast (Frey and Small, 1980).

The seasonal variation in epiphyte floristic structure in Netarts Bay was probably related to a combination of the effects of environmental variables on the epiphytes directly as well as the effects of environmental variables on the growth dynamics of the host plant, Zostera marina. The development of high epiphyte biomass in the spring coincided with an increase in water temperature and available light at this time of year (Kentula, 1983). During this period, the leaves of Zostera marina were larger and were retained longer than at any other time of the year. However, there was little change in the species composition of the epiphytes as biomass increased. The change in species composition and the relatively low biomass in the late summer and early fall corresponded to the warmest water temperatures and to a reduction in the life span of the average Zostera leaf (Kentula, 1983). At the same time, a large biomass of Enteromorpha prolifera accumulated on the mudflats and within the Zostera beds. Large entangled mats of this alga smothered patches of

Zostera and apparently had a significant impact on the production and biomass of Zostera during this time of the year (Kentula, 1983). The reappearance of the winter-spring epiphyte flora occurred with the onset of cooler temperatures, shorter days, and a sloughing of the large summer-type leaves during the first winter storms in October and November. Epiphyte biomass and species diversity were at a minimum at this time, roughly from November through February. After the sloughing of the summer epiphyte flora with the summer leaves of Zostera, epiphyte biomass was maintained at a low level by scouring during winter storms and by slow growth rates that resulted from short photoperiods and overcast skies.

In general, intertidal gradients between 1.1 and 1.4 m above MLLW were found to exert little influence on the distribution and relative abundance of epiphytic diatoms on Zostera marina. Diatom mucilage may have provided some protection against desiccation, or possibly desiccation was not a problem at these tidal heights. Zostera marina has little or no leaf cuticle and usually grows in the subtidal and lower intertidal regions, or else in depressions in the mud-flats where water is retained after low tide (Kentula, 1983; Phillips, 1972). It seems likely that desiccation gradients in the mid-intertidal regions may influence epiphyte distributions more by controlling the distributions of the host plants than by direct effects on the diatoms themselves.

Apparently epiphyte and benthic assemblages are not always as

distinct as the assemblages found in Netarts Bay. McIntire and Overton (1971) found that many of the epiphytic diatoms in Yaquina Bay were also common on other substrates. Sullivan (1977) found that 37 of 57 taxa that were epiphytic on Ruppia maritima, including the 6 dominant taxa, were also found in benthic samples. Sullivan concluded that the benthic environment may serve as the primary source of colonizing diatoms in a New Jersey salt marsh. Perhaps this is true only of salt marshes, or possibly Ruppia is too small or too ephemeral to support growths of Gomphonema, Licmophora, Synedra, Rhoicosphenia, Navicula directa, Cocconeis scutellum and Cocconeis costata. These taxa dominated the Netarts epiphyte flora and were never found growing on sediments.

The suggestion that the growth dynamics of Zostera marina, especially the turnover time of the leaves, may act as a regulator of epiphyte biomass and species composition concurs with other studies of host-epiphyte interactions. Main and McIntire (1974) and Sullivan (1977) concluded that leaf senescence and host die-back can influence species composition and species diversity in epiphyte assemblages. Godward (1934) found that younger leaves had lower epiphyte biomass than older leaves and that senescent leaves generally had senescent algal epiphytes.

In a review of the ecology of marine littoral diatoms, McIntire and Moore (1977) concluded that the distribution of epiphytic diatoms is thought to be determined by horizontal salinity gradients up the

estuary and by vertical desiccation and insolation gradients. Temporal variation is also thought to be important, and is probably related to temperature, photoperiod, and other variables with seasonal fluctuations. While seasonal variation was important in the epiphyte assemblages in Netarts Bay, the single Zostera bed examined in this study did not afford an opportunity to investigate large salinity gradients.

Another topic of interest to the study of epiphyte ecology is the question of host specificity. This study investigated only the epiphytes of Zostera marina, but other studies indicate that epiphytes in a given physical and chemical milieu tend to be uniformly distributed over the available host macrophytes (Main and McIntire, 1974; Sullivan, 1979; Ballantine, 1972; Tuchman and Blinn, 1979). This is especially true of vascular plant hosts and is less true of algal hosts (Craigie and McLachlan, 1964; Edsbacke, 1966; Conover and Sieburth, 1966; Ballantine, 1979). Sometimes epiphyte assemblages are dominated by a single taxon (Round, 1971; McIntire and Moore, 1977). A good example is the virtually unialgal stands of Isthmia nervosa that develop on Rhodomela larix on the Oregon coast. This was not the case in Netarts Bay, where epiphyte diversity (species richness and H') was relatively high and was similar to the epiphyte flora studied in Yaquina Bay (Main and McIntire, 1974).

In contrast to freshwater diatoms, the benthic diatoms found in estuaries often have affinities for specific sediment types (Round,

1960; Hendey, 1964; Colijn and Koeman, 1975; Amspoker and McIntire, 1978; Dexter, 1979). In Netarts Bay, a few taxa were almost equally abundant on all sediment types, but most species were found to have their maximum relative abundances in a specific sediment type. The physical characteristics of the sediment that were most related to distributions of benthic diatoms were organic content, mean grain size and the degree of sediment sorting. These characteristics are closely related to water movements and turbulence. Sandy sediments are usually found in areas where the action of waves and currents wash away finer sediments and organic matter that might otherwise have been deposited. Fine sediments are deposited in more quiescent water and accumulate more organic matter.

The mean particle size, the degree of sorting, and the organic content of a sediment will influence the sediment's physical and chemical characteristics. Water retention capacity may be enhanced by organic matter and may protect benthic organisms from rapid changes in salinity. In addition, larger grains of sediment provide more fractures and other concavities where most epipsammic diatoms are found (Meadows and Anderson, 1966). In poorly sorted sediments, the mixture of different particle sizes reduces the amount of interstitial space, thereby reducing sediment porosity and the variance of interstitial water salinity. Moreover, poorly sorted sediments tend to accumulate organic matter which may limit light penetration and support anaerobic decomposition. Therefore, fine and

coarse sediments probably offer very different physical and chemical environments for benthic microalgae.

While the benthic algal production in Netarts Bay had a seasonal pattern (Davis, 1982), the taxonomic structure of benthic diatom assemblages did not. The lack of seasonal variation in benthic diatom floristics might be related to the low light requirements of these taxa. Also, the physical characteristics of the sediment were probably relatively stable in comparison to the environment of the epiphytic assemblages.

The interaction between intertidal height and sediment characteristics can be seen from the results of the ordination procedures. The first Reciprocal Averaging axis was highly correlated with the chlorophyll ratio, a variable that expressed a high intertidal environment (see Figure 3) and was also correlated with the sediment properties OM, PHI and SORT. An interaction between tidal height and sediment characteristics was likewise expressed in the Canonical Correlation analysis by high correlations with the variables TIDE and PHI.

High intertidal stations were exposed for longer periods of time during low tides and therefore may have had more infiltration of freshwater from rain or from marsh areas. This would be less true of poorly sorted sediments, as the mixture of different grain sizes and the predominance of small grains would make this substrate less porous. This may explain in part why the silt flora was so homo-

geneous and why the intertidal gradient was such an important determinant of the sand floristics. Desiccation and differential grazing may have also contributed to this pattern. However, desiccation is probably less of an influence on organisms that live in sediment than to those that live on solid substrates. Estuarine sediments retain water in interstitial spaces and rarely appear dry. In addition, epipellic taxa can migrate to escape exposure at the sediment surface.

The ordination of all high intertidal samples from fine sand (FS4) with samples from silty sediment, instead of with other fine sand samples, cannot be explained with the present data set. Amspoker (1977) found intertidal gradients in the distribution of benthic diatoms that on closer inspection turned out to be related to finer grain sizes predominating at high intertidal stations, rather than to exposure gradients. This was not the case in Netarts Bay. The sediment at FS4 had a mean grain size that was intermediate within the range of grain sizes for the Fine Sand transect. One variable that was shared by these sampling stations was a proximity to a freshwater source, i.e., the marsh fringe at the Fine Sand site and Whiskey Creek at the Silt site. However, neither salinity measures (Davis, 1982) nor diatom floristics reflect a strong freshwater influence. Freshwater taxa were virtually absent from these samples and the taxa that were present were found at all other sampling stations.

The importance of sediment properties in determining floristic composition has been recognized by many researchers. Brockman (1950) felt that there were distinct floras associated with sand, silty sand, and silt. This plant sociological approach to classification of benthic systems may be more appropriate for benthic assemblages than for epiphytic ones (McIntire and Moore, 1977). Round (1971) used two different classification systems, e.g. a desiccation gradient (supratidal, intertidal, and subtidal) and a sediment-type system (epipellic and epipsammic). Epipsammic floras are generally found on sand, especially where water turbulence washes away non-attached forms or causes them to be crushed by particle abrasion. Epipsammic taxa are generally small and are either araphid and therefore non-mobile, or else they are raphid but not actively mobile. Common epipsammic taxa include species of Opephora, Plagiogramma, Raphoneis, Dimmerogramma, Cymatosira, Campylosira, Achnanthes, Cocconeis and Amphora. The epipellic flora is characterized by species that are generally larger and actively mobile, and are predominant on silty sediments. When present in sand, an epipellic flora is often dominated by a few taxa, mostly large species of Hantzschia, Nitzschia and Navicula. The benthic diatoms of Netarts Bay can generally be characterized as sand-associated or as silt-associated. No taxa could be identified as being specifically associated with silty sand as suggested by Brockman (1950). Also, individual taxa could often be identified as epipsammic or epipellic, although any given collec-

tion had diatoms of both categories present. The epipsammic-epipellic distinction is therefore more appropriate for characterizing specific taxa rather than whole assemblages. All diatom samples from Netarts Bay sediments contained only a few taxa that were both common and were epipsammic (e.g., species of Opephora, and small species of Cocconeis, Navicula and Achnanthes). Other common epipsammic genera such as Plagiogramma, Dimmerogramma, Cymatosira and Campylosira were either absent or very rare in benthic collections regardless of sediment type. Possibly the sand-bar areas, not included in this study and representing the more unstable sediments within the estuary, would have had more epipsammic taxa.

A review of benthic diatom ecology by McIntire and Moore (1977) concluded that benthic assemblages represent a patchy mosaic whose species composition is determined by local discontinuities in sediment type and by the more continuously variable gradients such as salinity, temperature and intertidal exposure. The benthic diatoms of Netarts Bay demonstrated very little variability in species composition in relationship to such seasonal variables as salinity, temperature or daylength. This agrees with the findings of some other researchers who found that benthic diatom taxa tend to be present year around with little change in assemblage species composition (e.g., Round, 1960; Cox, 1977; Baillie and Welsh, 1980). On the other hand, some researchers have found seasonal variability in species composition attributed to changes in temperature or salinity

(Admiraal and Peletier, 1980; Edsbagge, 1966; Sullivan, 1975). Sullivan (1977) regards many benthic species from marsh sediments to be opportunistic, in that they are prevalent only when certain environmental conditions prevail. Apparently, the physical nature of the estuary must be accounted for in making such generalizations. For instance, water depth and the degree of fluvial influence are important differences in comparing marshes and estuaries, and would also be important in comparing estuaries with each other.

Round's classification scheme based on desiccation gradients separates diatom assemblages into supratidal, intertidal, and subtidal groups, each with its own distinctive species composition (Round, 1971). The supratidal is characterized by certain pennate taxa, and is located above the high water mark on the shore. The intertidal zone is characterized by a different group of predominantly pennate species, which at least in temperate parts of the world seem to have a cosmopolitan distribution. This species list conforms well with the list of taxa that dominated the Netarts Bay diatom flora. The upper subtidal is similar to the intertidal with many of the same species, but the lower subtidal is dominated by a group of centric species.

In summary, benthic taxa seem to be distributed mainly by sediment type, and sometimes by exposure, salinity, light and temperature gradients. Most estuarine diatoms are tolerant of wide differences in salinity, but salinities above 5‰ will exclude most freshwater

taxa. Exposure is most important where it is most extreme, i.e., on solid substrates that do not retain water well, and the upper intertidal or supratidal zones. The effects of light and temperature on the distribution of estuarine diatoms are still unclear, as these effects are confounded in other variables which have seasonal variation. The attenuation of light by water depth or turbidity is clearly an important factor. Hopefully, interest in estuarine ecology will continue to attract scientific investigation and will lead to an even better understanding of these relationships.

BIBLIOGRAPHY

- Admiraal, W. 1977a. Influence of light and temperature on the growth rate of estuarine benthic diatoms in culture. *Mar. Biol.* 39:1-9.
- Admiraal, W. 1977b. Salinity tolerances of benthic estuarine diatoms as tested with a rapid polarographic measurement of photosynthesis. *Mar. Biol.* 39:11-18.
- Admiraal, W. 1977c. Experiments with mixed populations of benthic estuarine diatoms in laboratory microecosystems. *Bot. Mar.* 20:479-485.
- Admiraal, W., and H. Peletier. 1979a. Influences of organic compounds and light limitation on the growth rate of estuarine benthic diatoms. *Br. phycol. J.* 14:197-206.
- Admiraal, W., and H. Peletier. 1979b. Sulphide tolerance of benthic diatoms in relation to their distribution in an estuary. *Br. phycol. J.* 14:185-196.
- Admiraal, W., and H. Peletier. 1980. Distribution of diatom species on an estuarine mudflat and experimental analysis of the selective effect of stress. *J. Exp. Mar. Biol. Ecol.* 46:157-175.
- Aleem, A. A. 1950a. Distribution and ecology of British marine littoral diatoms. *J. Ecol.* 38:75-106.
- Aleem, A. A. 1950b. The diatom community inhabiting the mud-flats at Whitstable, Kent. *New Phytol.* 49:174-188.
- Aleem, A. A. 1973. Contribution to the study of littoral diatoms on the west coast of Sweden. *Bot. Mar.* 16:193-200.
- Amspoker, M. C. 1977. The distribution of intertidal epipsammic diatoms on Scripps Beach, La Jolla, California, U.S.A. *Bot. Mar.* 20:227-232.
- Amspoker, M. C., and C. D. McIntire. 1978. Distribution of intertidal diatoms associated with sediments in Yaquina Estuary, Oregon. *J. Phycol.* 14:387-395.
- Anderson, F. E. 1973. Observation of some sedimentary processes acting on a tidal flat. *Mar. Geol.* 14:101-116.

- Aykulu, G. 1982. The epipellic algal flora of the River Avon. Br. phycol. J. 17:27-38.
- Bacon, G. B., and A. R. A. Taylor. 1976. Succession and stratification in benthic diatom communities colonizing plastic collectors in a Prince Edward Island estuary. Bot. Mar. 19:231-240.
- Baillie, P. W., and B. L. Welsh. 1980. The effect of tidal resuspension on the distribution of intertidal epipellic algae in an estuary. Est. Coast. Mar. Sci. 10:165-180.
- Ballantine, D. L. 1972. Epiphytes of four Florida seagrass species in the Anclote Anchorage, Tarpon Springs, Florida. M. A. thesis, University of Southern Florida, Tampa, 87p.
- Ballantine, D. L. 1979. The distribution of algal epiphytes on macrophyte hosts offshore from La Parguera, Puerto Rico. Bot. Mar. 22:107-111.
- Beardall, J., D. Mukerjee, J. E. Glover and I. Morris. 1976. The path of carbon in photosynthesis by marine phytoplankton. J. Phycol. 12:409-417.
- Branch, G. M., and M. L. Branch. 1980. Competition in Bembicium auratum and its effect on microbial standing stock in mangrove mudflats. Oecologia 46:106-114.
- Brockman, C. 1950. Die Watt-Diatomeen der schleswig-holsteinischen Westküste. Abh. senckenberg. naturf. Ges. 478:1-26.
- Bruno, S. F., R. D. Staker and G. M. Sharma. 1980. Dynamics of phytoplankton production in the Peconic Bay Estuary, Long Island. Est. Coast. Mar. Sci. 10:247-263.
- Castenholz, R. W. 1967. Seasonal ecology of non-planktonic marine diatoms on the western coast of Norway. Sarsia 29:237-256.
- Cattano, A. 1978. The microdistribution of epiphytes on the leaves of natural and artificial macrophytes. Br. phycol. J. 13:183-188.
- Cattano, A., and J. Kalff. 1979. Primary production of algae growing on natural and artificial aquatic plants: A study of interactions between epiphytes and their substrates. Limnol. Oceanogr. 24(6):1031-1037.

- Clifford, H. T., and W. Stephenson. 1975. An Introduction to Numerical Classification. Academic Press, N.Y., p. 54.
- Colijn, F., and R. Koeman. 1975. Das Mikrophytobenthos der Watten, Strände und Riffe um den hohen Knechtsand in der Wesermündung. Forschungsstelle für Insel-und Küstenschutz der Niedersächsischen Wasserwirtschaftsverwaltung 26:53-83.
- Conover, J. T., and J. McN. Sieburth. 1966. Effects of tannins from Phaeophyta on planktonic animal survival in tidepools. In: proceedings of the Fifth International Seaweed Symposium, E. Gordon Young and J. L. McLachlan (eds.). Pergamon Press, N.Y. pp. 99-100.
- Cook, L. L., and S. A. Whipple. 1982. The distribution of edaphic diatoms along environmental gradients of a Louisiana salt marsh. J. Phycol. 18:64-71.
- Cooley, W. W., and P. R. Lohnes. 1971. Multivariate Data Analysis. John Wiley and Sons, N.Y., 364p.
- Cox, E. J. 1977. The tube-dwelling diatom flora at two sites in the Severn Estuary. Bot. Mar. 20:111-119.
- Craigie, J. S., and J. McLachlan. 1964. Excretion of colored U.V.-absorbing substances by marine algae. Can. J. Bot. 42:23.
- Cupp, E. E. 1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Oceanogr., Tech. Ser. 5:1-238.
- Cushing, D. H. 1964. The work of grazing in the sea. In: Grazing in Terrestrial and Marine Environments, D. J. Crisp (ed.). Blackwell Sci. Publ., Oxford, pp. 207-225.
- Darley, W. M., C. L. Montague, F. G. Plumley, W. W. Sage and A. T. Psalidas. 1981. Factors limiting edaphic algal biomass and production in a Georgia salt marsh. J. Phycol. 17:122-128.
- Davis, M. W. 1982. Production dynamics of sediment-associated algae in two Oregon estuaries. Ph.D. thesis, Oregon State University, Corvallis, Oregon. 135p.
- Dexter, D. M. 1979. Community structure and seasonal variation in intertidal Panamanian sandy beaches. Est. Coast. Mar. Sci. 9(5):543-558.

- Drum, R. W., and E. W. Webber. 1966. Diatoms from a Massachusetts salt marsh. *Bot. Mar.* 9:70-77.
- Edsbagge, H. 1966. Some problems in the relationship between diatoms and seaweeds. *Bot. Mar.* 11:64-67.
- Edsbagge, H. 1968. Zur Ökologie der Marinen Angehefteten Diatomeen. *Botanica Gothoburgensia* 6:1-153.
- EPA. 1979. Unpublished data, Wetlands Research Program, Corvallis, Oregon.
- Estrada, M., I. Valiela and J. M. Teal. 1974. Concentration and distribution of chlorophyll in fertilized plots in a Massachusetts salt marsh. *J. exp. mar. Biol. Ecol.* 14:47-56.
- Fitzgerald, G. P. 1969. Some factors in the competition or antagonism among bacteria, algae and aquatic weeds. *J. Phycol.* 5:351-359.
- Fox, W. T., and R. A. Davis, Jr. 1979. Surf zone dynamics during upwelling on the Oregon coast. *Est. Coast. Mar. Sci.* 9:683-697.
- Frey, B. E., and L. F. Small. 1980. Effects of micro-nutrients and major nutrients on natural phytoplankton populations. *J. Plankton Res.* 2(1):1-22.
- Frostick, L. E., and I. N. McCave. 1979. Seasonal shifts of sediment within an estuary mediated by algal growth. *Est. Coast. Mar. Sci.* 9:569-576.
- Gale, W. F., A. J. Gurzynski and R. L. Lowe. 1979. Colonization and standing crops of epilithic algae in the Susquehanna River, Pennsylvania. *J. Phycol.* 15:117-123.
- Gauch, H. G. 1982. *Multivariate Analysis in Community Ecology.* Cambridge University Press, Cambridge, 298 p.
- Godward, M. B. 1934. An investigation of the causal distribution of algal epiphytes. *Beih. zum Bot. Centralblatt* 52:506-539.
- Gran, H. H., and E. C. Angst. 1931. Plankton diatoms of Puget Sound. *Publ. Puget Sound Mar. Biol. Stn.* 7:417-519.
- Guillard, R. R. L., and P. Kilham. 1977. The ecology of marine planktonic diatoms. In: *The Biology of Diatoms*, D. Werner (ed.). University of California Press, pp. 372-467.

- Gunter, G. 1979. Notes on sea beach ecology. Food sources on sandy beaches and localized diatom blooms bordering Gulf beaches. *Gulf Res. Reports* 6(3):305-307.
- Harper, M. A. 1969. Movement and migration of diatoms on sand grains. *Br. phycol. J.* 4:97-103.
- Harper, M. A. 1977. Diatom movements. In: *The Biology of Diatoms*, D. Werner (ed.). University of California Press, pp. 224-249.
- Hartwig, E. O. 1978. Factors effecting respiration and photosynthesis by the benthic community of a subtidal siliceous sediment. *Mar. Biol.* 46:283-293.
- Hellebust, J. A., and J. Lewin. 1977. Heterotrophic nutrition. In: *The Biology of Diatoms*, D. Werner (ed.). University of California Press, pp.169-197.
- Hendey, N. I. 1964. An introductory account of the smaller algae of British coastal waters. Part V. Bacillariophyceae (Diatoms). *Fish. Invest. Ser. 4*, 317p.
- Hill, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61:237-249.
- Holmes, R. W., C. J. Wilson and M. C. Amspoker. 1981. Techniques for preparing permanent preparations of cleaned and uncleaned diatoms using Cumar R-9, a cumarone-indene resin. *Bacillaria* 4:21-27.
- Hustedt, F. 1939. Die Diatomeenflora des Küstengesbietes der Nordsee vom Dollart bis zur Elbemündung. *Naturwissenschaftlicher Verein zu Bremen* 31:572-677.
- Hustedt, F. 1955. Marine littoral diatoms of Beaufort, North Carolina. *Duke Univ. Mar. Stat. Bull.* 6:1-67.
- Hustedt, F., and A. A. Aleem. 1951. Littoral diatoms from the Salstone near Plymouth. *J. Mar. Biol. Assoc. U. K.* 30:177-196.
- Inman, D. L. 1952. Measures for describing the size distribution of sediments. *J. Sed. Petrol.* 22(3):125-145.
- Jacobs, R. P. W. M., and T. M. P. A. Noten. 1980. The annual pattern of the diatoms in the epiphyton of eelgrass (Zostera marina) at Roscoff, France. *Aquat. Bot.* 8:355-370.

- Joint, I. R. 1978. Microbial production of an estuarine mudflat. *Est. Coast. Mar. Sci.* 7:185-195.
- Jones, J. A. 1968. Primary productivity by the tropical marine turtlegrass Thalassia testudinum and its epiphytes. Ph.D. thesis, University of Miami, Coral Gables, 196 p.
- Josselyn, M. N., and A. C. Mathieson. 1980. Seasonal influx and decomposition of autochthonous macrophyte litter in a north temperate estuary. *Hydrobiol.* 71:197-208.
- Karentz, D. 1975. The distribution of planktonic diatoms in the Yaquina Estuary, Oregon. M.S. thesis, Oregon State University, Corvallis, Oregon, 137 p.
- Kentula, M. E. 1983. Production dynamics of a Zostera marina bed in Netarts Bay, Oregon. Ph.D. thesis, Oregon State University, Corvallis, Oregon, 158 p.
- Khfaji, A. K., and A. D. Boney. 1979. Antibiotic effects of crustose germlings of the red alga Chondrus crispus on benthic diatoms. *Ann. Bot.* 43:231-232.
- Krumbein, W. C., and F. J. Pettijohn. 1938. *Manual of Sedimentary Petrology*. Appleton-Century-Crofts, N.Y., 549 p.
- Lee, J. J., M. E. McEnery and J. R. Garrison. 1980. Experimental studies of larger Foraminifera and their symbionts from the Gulf of Elat on the Red Sea. *J. Foram. Res.* 10(1):31-47.
- Lewin, J. 1961. The dissolution of silica from diatom walls. *Geochim. Cosmochim. Acta* 21:182-198.
- Lewin, J. 1974. Blooms of surf-zone diatoms along the coast of the Olympic Peninsula, Washington. III. Changes in the species composition of the blooms since 1925. *Nova Hedw. Beih.* 45:251-257.
- Lewin, J. 1977. Persistent blooms of surf diatoms along the Northwest coast. In: *The Marine Plant Biomass of the Pacific Northwest Coast*, R. Kraus (ed.). Oregon State University Press. pp. 81-92.
- Lewin, J., and R. E. Norris. 1970. Surf-zone diatoms of the coasts of Washington and New Zealand (Chaetoceros armatum and Asterionella sp.). *Phycologia* 9:143-149.

- Loftus, M. E., D. V. S. Rao and H. H. Seliger. 1972. Growth and dissipation of phytoplankton in Chesapeake Bay. I. Response to a large pulse of rainfall. *Ches. Sci.* 13(4):282-299.
- Main, S. P., and C. D. McIntire. 1974. The distribution of epiphytic diatoms in the Yaquina Estuary, Oregon. *Bot. Mar.* 17:88-99.
- Mann, K. H. 1974. Comparisons of freshwater and marine systems: The direct and indirect effects of solar energy on primary and secondary production. In: *Proc. First Internat. Congr. Ecology*, pp. 168-173.
- Marshall, N., C. A. Oviatt and D. M. Skauen. 1971. Productivity of the benthic microflora of shoal estuarine environments in southern New England. *Int. Rev. ges Hydrobiol.* 56:947-956.
- McIntire, C. D. 1978. The distribution of estuarine diatoms along environmental gradients: A canonical correlation. *Est. Coast. Mar. Sci.* 6:447-457.
- McIntire, C. D., and W. W. Moore. 1977. Marine littoral diatoms: Ecological considerations. In: *The Biology of Diatoms*, D. Werner (ed.). University of California Press, pp. 333-371.
- McIntire, C. D., and W. S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecology* 52:758-777.
- McIntire, C. D. and B. L. Wulff. 1969. A laboratory method for the study of marine benthic diatoms. *Limnol. Oceanogr.* 14:667-678.
- McLean, R. O., J. Corrigan and J. Webster. 1981. Heterotrophic nutrition in Melosira nummuloides, a possible role in affecting distribution in the Clyde Estuary. *Br. phycol. J.* 16:95-106.
- McRoy, C. P., and J. J. Goering. 1974. Nutritional transfer between the seagrass Zostera marina and its epiphytes. *Nature* 248:173-174.
- Meadows, P. S., and J. G. Anderson. 1966. Microorganisms attached to marine and freshwater sandgrains. *Nature* 212:1059-1060.
- Moore, W. W., and C. D. McIntire. 1977. Spatial and seasonal distribution of littoral diatoms in the Yaquina Estuary, Oregon. *Bot. Mar.* 20:99-109.

- Moss, B. 1981. The composition and ecology of periphyton communities in freshwaters. II. Inter-relationships between water chemistry and phytoplankton populations in a shallow lake and associated experimental reservoirs. *Br. phycol. J.* 16:59-76.
- Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. *Ecology* 58:1020-1032.
- Odum, E. P. 1971. *Fundamentals of Ecology*. W. B. Saunders Co., Philadelphia, pp. 352-362.
- Owen, B. B., M. Afzal and W. R. Cody. 1978. Staining preparations for phytoplankton and periphyton. *Br. phycol. J.* 13:155-160.
- Patrick, R. 1977. Ecology of freshwater diatoms. In: *The Biology of Diatoms*, D. Werner (ed.). University California Press, pp. 284-332.
- Patrick, R. 1978. Effects of trace metals on the aquatic ecosystem. *Amer. Sci.* 66:185-191.
- Penhale, P. A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (Zostera marina) community. *J. exp. mar. Biol. Ecol.* 26:211-224.
- Phillips, R. C. 1972. Ecological life history of Zostera marina L. (Eelgrass) in Puget Sound, Washington. Ph.D. thesis, University of Washington, 154 p.
- Phillips, R. C., D. Eminson and B. Moss. 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4:103-126.
- Pritchard, D. W. 1967. What is an estuary?: Physical viewpoint. In: *Estuaries*, G. F. Lauff (ed.). Amer. Assoc. Adv. Sci. Publ. no. 83, Washington, D. C., pp. 3-5.
- Ragothaman, G., and V. N. R. Rao. 1978. Diatom abundance in the near shores of the Bay of Bengal off Madras. *Indian J. of Mar. Sci.* 7(1):1-2.
- Ramm, G. 1977. Structure of epiphytic diatom populations of the phytol of the Kiel Bight (west Baltic). *Nova Hedw., Beih.* 54:379-387.
- Riznyk, R. Z. 1973. Interstitial diatoms from two tidal flats in Yaquina Estuary, Oregon. *Bot. Mar.* 16:113-138.

- Riznyk, R. Z., and H. K. Phinney. 1972. The distribution of intertidal phytosammon in an Oregon estuary. *Mar. Biol.* 13:318-324.
- Round, F. E. 1960. The diatom flora of a salt marsh on the River Dee. *New Phytol.* 59:332-348.
- Round, F. E. 1971. Benthic marine diatoms. *Oceanogr. Mar. Biol. Ann. Rev.* 9:83-139.
- Round, F. E., and C. M. Haphey. 1965. Persistent vertical migration rhythms in benthic microflora. IV. A diurnal rhythm of the epipellic diatom association in non-tidal flowing water. *Br. phycol. J.* 2:463-471.
- Saks, N. M., and E. G. Kahn. 1979. Substrate competition between a salt marsh diatom and a bacterial population. *J. Phycol.* 15:17-21.
- Samuels, W. B., R. Nuzzi and A. Uzzo. 1979. Phytoplankton ecology and physiochemical factors in a coastal salt pond. *Nova Hedw.* 31:391-406.
- Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3:55-63.
- Sieburth, J. McN., and J. L. Tootle. 1981. Seasonality of microbial fouling on Ascophyllum nodosum, Fucus vesiculosus, Polysiphonia lanosa and Chondrus crispus. *J. Phycol.* 17:57-64.
- Siver, P. A. 1978. Development of diatom communities on Potamogeton robbinsonii. *Rhodora* 80, 823:417-430.
- Small, L. F., H. Curl, Jr. and W. A. Glooschenko. 1972. Effects of solar radiation and upwelling on daily primary production off Oregon. *J. Fish. Res. Bd. Can.* 29(9):1269-1275.
- Sorsa, K. 1979. Primary production of epipellic algae in Lake Suomunjärvi, Finnish North Karelia. *Ann. Bot. Fennici* 16:351-366.
- Strickland, J. D. H., and T. R. Parsons. 1972. A practical handbook of seawater analysis. *Fish. Res. Bd. Can., Bull. no. 167* (second ed.) 310 p.
- Sullivan, M. J. 1975. Diatom communities from a Delaware salt marsh. *J. Phycol.* 11:384-390.

- Sullivan, M. J. 1977. Structural characteristics of a diatom community epiphytic on Ruppia maritima. *Hydrobiol.* 53:81-86.
- Sullivan, M. J. 1978. Diatom community structure: Taxonomic and statistical analysis of a Mississippi salt marsh. *J. Phycol.* 14:468-475.
- Sullivan, M. J. 1979. Epiphytic diatoms of three seagrasses in Mississippi Sound. *Bull. Mar. Sci.* 29(4):459-464.
- Sullivan, M. J. 1982. Distribution of edaphic diatoms in a Mississippi salt marsh: A canonical correlation analysis. *J. Phycol.* 18:130-133.
- Taasen, J. P. 1972. Observations on Navicula endophytica (Bacillariophyceae). *Sarsia* 51:67-82.
- Taasen, J. P. 1974. Remarks on the epiphytic diatom flora of Dumontia incrassata (Rhodophyceae). *Sarsia* 55:129-132.
- Thomas, W. H., A. N. Dodson and F. M. H. Reid. 1978. Diatom production compared to other algae in natural marine phytoplankton assemblages. *J. Phycol.* 14:250-253.
- Tuchman, M., and D. Blinn. 1979. Comparison of attached algal communities on natural and artificial substrates along a thermal gradient. *Br. phycol. J.* 14:243-254.
- Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. *Fish. Bull.* 77(2):339-357.
- Welsh, E. B., R. M. Emery, R. I. Matsuda and W. A. Dawson. 1972. The relationship of periphytic and planktonic algal growth in an estuary to hydrographic factors. *Limnol. Oceanogr.* 17(5):731-737.
- Whitford, L. A. 1956. The communities of algae in the springs and spring streams of Florida. *Ecology* 37(3):433-442.
- Wood, E. J. F. 1963. A study of the diatom flora of fresh sediments of the south Texas bays and adjacent waters. *Publ. Inst. Mar. Sci. Univ. Texas* 9:237-310.
- Zimmerman, R., R. Gilson and J. Harrington. 1979. Herbivory and detritivory among Gammarid amphipods from a Florida seagrass community. *Mar. Biol.* 54:41-47.

APPENDIX

APPENDIX**TABLE 1**

**DIATOM TAXA IDENTIFIED IN SAMPLES FOR BENTHIC (B),
EPIPHYTIC (E) AND PHYTOPLANKTON (P) SAMPLES IN
NETARTS BAY, OREGON.**

APPENDIX TABLE 1

Diatom taxa identified in samples from benthic (B), epiphytic (E) and phytoplankton (P) samples in Netarts Bay, Oregon. Taxa are listed alphabetically and benthic and epiphytic taxa are ranked in abundance classes according to their total occurrences in samples from each substrate. The abundance classes are: A (absent), R (rare, 1-5 total occurrences), P (present but not common, 6-50 occurrences), C (common, 51-500 occurrences) and D (dominant, over 500 occurrences). Plankton samples were not enumerated and presence in these samples is indicated with a plus sign (+).

TAXON	B	E	P
<u>Achnanthes</u> 1	C	A	-
<u>Achnanthes</u> 11 B	D	A	-
<u>Achnanthes</u> 16	P	A	-
<u>Achnanthes</u> 23	C	A	-
<u>Achnanthes</u> 25	A	R	-
<u>Achnanthes</u> <u>brevipes</u> Ag.	R	A	-
<u>Achnanthes</u> <u>dependita</u> Giff.	R	A	-
<u>Achnanthes</u> <u>groenlandica</u> v. <u>phinneyii</u> McIntire and Reim.	P	A	-
<u>Achnanthes</u> <u>hauckiana</u> Grun.	D	A	-
<u>Achnanthes</u> <u>hauckiana</u> v. <u>rostrata</u> Schultz	P	A	-
<u>Achnanthes</u> <u>hustedtii</u> Bílý	C	R	-
<u>Achnanthes</u> <u>intermedia</u> Kütz.	R	R	-
<u>Achnanthes</u> (Bréb.) Grun.	P	P	-
<u>Achnanthes</u> <u>latestriata</u> Riznyk	C	A	-
<u>Achnanthes</u> <u>lemmermanni</u> Hust.	D	R	-
<u>Achnanthes</u> <u>tenera</u> Hust.	R	A	-
<u>Actinocyclus</u> <u>ehrenbergii</u> Ralfs	A	A	+
<u>Actinoptychus</u> <u>splendens</u> (Shadb.) Ralfs	A	A	+
<u>Actinoptychus</u> <u>undulatus</u> (Bail.) Ralfs	R	A	-
<u>Amphora</u> 16	P	A	-
<u>Amphora</u> 22	R	A	-
<u>Amphora</u> 29	R	A	-
<u>Amphora</u> 33	P	A	-
<u>Amphora</u> 35	C	A	-
<u>Amphora</u> 40	P	A	-
<u>Amphora</u> 41	P	A	-
<u>Amphora</u> 42	P	A	-
<u>Amphora</u> 43	R	A	-
<u>Amphora</u> 154	C	A	-
<u>Amphora</u> 206	R	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Amphora angustata</u> v. <u>ventricosa</u> (Greg.) Cl.	P	P	-
<u>Amphora arenicola</u> (Grun.) Cl.	P	A	-
<u>Amphora coffeiformis</u> (Ag.) Kütz.	C	R	-
<u>Amphora coffeiformis</u> v. <u>purpusilla</u> Grun.	P	A	-
<u>Amphora crassa</u> Greg.	P	A	-
<u>Amphora exigua</u> Greg.	C	R	-
<u>Amphora griffeana</u> Hendey	R	A	-
<u>Amphora holsatica</u> Hust.	P	A	-
<u>Amphora laevis</u> Greg.	R	R	-
<u>Amphora laevis</u> v. <u>perminuta</u> (Grun.) Cl.	C	A	-
<u>Amphora libyca</u> . (<u>A. ovalis</u> v. <u>pediculus</u> (Kütz.) V.H.)	C	A	-
<u>Amphora lineolata</u> Ehr.	R	A	-
<u>Amphora tonga</u> Hust.	P	A	-
<u>Amphora micrometra</u> Giff.	C	A	-
<u>Amphora ovalis</u> (Kütz.) Kütz.	R	R	-
<u>Amphora polita</u> Krasske	P	A	-
<u>Amphora proteus</u> Greg.	C	A	-
<u>Amphora pulchella</u> Per.	P	A	-
<u>Amphora sabyii</u> Salah	D	P	-
<u>Amphora tennerrima</u> Aleem and Hust.	D	C	-
<u>Amphora turgida</u> Greg.	P	A	-
<u>Anaulus balticus</u> Simon.	P	P	-
<u>Anorthoneis eurystoma</u> Cl.	C	R	-
<u>Asterionella japonica</u> Cl.	R	A	+
<u>Aulacodiscus oregonus</u> Harv. and Bail.	A	R	-
<u>Bacillaria paradoxa</u> Gmel.	P	C	-
<u>Bacteriastrium delicatulum</u> Cl.	A	A	+
<u>Bacteriastrium hyalinum</u> Laud.	A	A	+
<u>Berkeleya rutilans</u> (Trent.) Grun.	C	C	-
<u>Biddulphia aurita</u> (Lyngb.) Bréb. and Godey	P	R	-
<u>Biddulphia longicuris</u> Grev.	A	A	+
<u>Caloneis brevis</u> (Greg.) Cl.	R	A	-
<u>Caloneis westii</u> (W. Sm.) Hendey	R	A	-
<u>Campylosira</u> 1	P	P	-
<u>Cerataulus turgidus</u> (Ehr.) Ehr.	R	A	-
<u>Chaetoceros armatum</u> West	A	A	+
<u>Chaetoceros compressus</u> Laud.	A	A	+

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Chaetoceros constrictus</u> Gran	R	A	+
<u>Chaetoceros curvisetus</u> Cl.	A	A	+
<u>Chaetoceros decipiens</u> Cl.	R	A	+
<u>Chaetoceros didymus</u> Ehr.	A	A	+
<u>Chaetoceros lacinosus</u> Schütt	A	A	+
<u>Chaetoceros lorentzianus</u> Grun.	A	A	+
<u>Chaetoceros radicans</u> Schütt	R	A	+
<u>Chaetoceros socialis</u> Laud.	A	A	+
<u>Chaetoceros vanheurckii</u> Gran	A	A	+
<u>Cocconeis</u> 8	P	A	-
<u>Cocconeis</u> 11 A	D	R	-
<u>Cocconeis</u> 11 C	C	R	-
<u>Cocconeis</u> 13	P	A	-
<u>Cocconeis</u> J	D	P	-
<u>Cocconeis amydrophyllum</u> Riznyk	R	A	-
<u>Cocconeis californica</u> (Grun.) Grun.	P	R	-
<u>Cocconeis clandestinata</u> A. S.	P	A	-
<u>Cocconeis costata</u> Greg.	C	C	-
<u>Cocconeis costata</u> v. <u>pacifica</u> Grun.	R	A	-
<u>Cocconeis decipiens</u> Cl.	R	A	-
<u>Cocconeis discrepans</u> A. S.	P	A	-
<u>Cocconeis diminuta</u> Pant.	P	A	-
<u>Cocconeis disculus</u> (Schumann) Cl.	P	A	-
<u>Cocconeis distans</u> Greg.	C	A	-
<u>Cocconeis pediculus</u> Ehr.	R	P	-
<u>Cocconeis placentula</u> v. <u>euglypta</u> (Ehr.) Grun.	D	P	-
<u>Cocconeis psammicola</u> Riznyk	P	R	-
<u>Cocconeis pseudomarginata</u> Greg.	P	A	-
<u>Cocconeis scutellum</u> Ehr.	C	D	-
<u>Cocconeis scutellum</u> v. <u>parva</u> (Grun.) Cl.	P	C	-
<u>Corethron hystrix</u> Hensen	A	A	+
<u>Coscinodiscus curvatulus</u> Grun.	A	A	+
<u>Coscinodiscus eccentricus</u> Ehr.	A	A	+
<u>Coscinodiscus lineatus</u> Ehr.	R	A	-
<u>Coscinodiscus marginatus</u> Ehr.	R	A	-
<u>Coscinodiscus radiatus</u> Ehr.	A	A	+
<u>Coscinodiscus sublineatus</u> (Grun.) Rattr.	R	A	+

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Cyclotella meneghiniana</u> Kütz.	P	R	-
<u>Cylindrotheca closterium</u> (Ehr.) Reiman and Lewin	R	A	-
<u>Cymbellonitzschia hossamedinii</u> Salah	D	A	-
<u>Denticula subtilis</u> Grun.	R	A	-
<u>Dimmerogramma minor</u> (Greg.) Ralfs	R	A	-
<u>Dimmerogramma minor</u> v. <u>nanna</u> (Greg.) V. H.	R	A	-
<u>Diploneis bombus</u> Ehr.	R	A	-
<u>Diploneis didyma</u> (Ehr.) Ehr.	R	A	-
<u>Diploneis interrupta</u> (Kütz.) Cl.	R	A	-
<u>Diploneis papula</u> A. S.	P	A	-
<u>Diploneis smithii</u> (Bréb.) Cl.	R	A	-
<u>Ditylum brightwellii</u> (West) Grun.	A	A	+
<u>Donkinia recta</u> (Donk.) Grun.	R	A	-
<u>Donkinia reticulata</u> Norman	R	A	-
<u>Entomoeneis alata</u> (Ehr.) Ehr.	R	A	-
<u>Entomoeneis alata</u> f. <u>minor</u> Ehr.	R	A	-
<u>Entomoeneis hyalina</u> Grev.	R	P	-
<u>Entomoeneis sulcata</u> O'Meara	R	A	-
<u>Eucampia zodiacus</u> Ehr.	R	A	+
<u>Eunotia incisa</u> Greg.	R	A	-
<u>Eunotia pectinalis</u> (Dillw.) Rabh.	R	A	-
<u>Eunotia perpusilla</u> Grun.	R	A	-
<u>Eunotogramma laeve</u> Grun.	P	A	-
<u>Eunotogramma marina</u> (W. Sm.)	P	R	-
<u>Fragilaria</u> 1	A	R	-
<u>Fragilaria brevistriata</u> Grun.	R	A	-
<u>Fragilaria construens</u> v. <u>venter</u> (Ehr.) Grun.	R	A	-
<u>Fragilaria crotonensis</u> Kitt.	R	A	-
<u>Fragilaria pinnata</u> Ehr.	C	A	-
<u>Fragilaria striatula</u> v. <u>californica</u> Grun.	C	R	-
<u>Frustulia linkei</u> Hust.	R	A	-
<u>Gomphonema</u> 2	A	R	-
<u>Gomphonema kamschaticum</u> Grun.	R	P	-
<u>Gomphonema oceanicum</u> Chol.	P	C	-
<u>Gomphonema valentinica</u> Kikolajev	R	A	-
<u>Gyrosigma eximium</u> (Thw.) Boyer	R	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Gyrosigma fasciola</u> (Ehr.) Griff.	P	A	-
<u>Gyrosigma pallidum</u> Riznyk	R	A	-
<u>Gyrosigma peisonis</u> (Grun.) Hust.	R	A	-
<u>Gyrosigma prolongatum</u> (W. Sm.) Griff.	P	R	-
<u>Gyrosigma spenceri</u> (W. Sm.) Griff.	P	A	-
<u>Gyrosigma spenceri</u> v. <u>curvula</u> (Grun.) Reim.	P	A	-
<u>Gyrosigma wansbeckii</u> (Donk.) Cl.	A	R	-
<u>Hantzschia</u> 1	P	A	-
<u>Hantzschia marina</u> (Donk.) Grun.	C	A	-
<u>Hantzschia petitiana</u> Grun.	P	A	-
<u>Hemiaulus hauckii</u> Grun.	A	A	+
<u>Lauderia borialis</u> Gran	A	A	+
<u>Leptocylindrus danicus</u> Cl.	A	A	+
<u>Licmophora gracilis</u> (Ehr.) Grun.	A	R	-
<u>Licmophora paradoxa</u> (Lyngb.) Ag.	A	P	-
<u>Lithodesmium undulatum</u> Ehr.	A	A	+
<u>Mastogloia</u> 1	P	A	-
<u>Mastogloia exigua</u> Lewis	P	A	-
<u>Melosira</u> 1	R	A	-
<u>Melosira dubia</u> Kütz.	R	A	-
<u>Melosira granulata</u> (Ehr.) Ralfs	R	A	-
<u>Melosira jurgensii</u> Ag.	R	P	-
<u>Melosira moniliformis</u> O. F. Müll.	C	P	-
<u>Melosira nummuloides</u> (Dillw.) Ag.	C	P	-
<u>Navicula</u> 2	P	A	-
<u>Navicula</u> 3	C	R	-
<u>Navicula</u> 6	A	R	-
<u>Navicula</u> 14	P	A	-
<u>Navicula</u> 15	R	A	-
<u>Navicula</u> 16	C	A	-
<u>Navicula</u> 26	C	P	-
<u>Navicula</u> 43	R	A	-
<u>Navicula</u> 61	R	R	-
<u>Navicula</u> 74	P	A	-
<u>Navicula</u> 81	A	R	-
<u>Navicula</u> 85	R	A	-
<u>Navicula</u> 86	P	A	-
<u>Navicula</u> 87	R	A	-
<u>Navicula</u> 88	R	A	-
<u>Navicula</u> 90	C	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Navicula</u> 109	C	C	-
<u>Navicula</u> 150	C	C	-
<u>Navicula</u> 199	D	A	-
<u>Navicula</u> <u>abunda</u> Hust.	P	P	-
<u>Navicula</u> <u>ammophila</u> Grun.	P	A	-
<u>Navicula</u> <u>ammophila</u> v. <u>minuta</u> (Grun.) Ostr.	C	A	-
<u>Navicula</u> <u>cancellata</u> Donk.	P	R	-
<u>Navicula</u> <u>cincta</u> (Ehr.) Ralfs	P	R	-
<u>Navicula</u> <u>circumtexta</u> Meist.	R	R	-
<u>Navicula</u> <u>comoides</u> (Dillw.) Per.	R	A	-
<u>Navicula</u> <u>complanatoides</u> Hust.	R	A	-
<u>Navicula</u> <u>complanatula</u> Hust.	P	P	+
<u>Navicula</u> <u>crucigera</u> (W. Sm.) Cl.	R	P	-
<u>Navicula</u> <u>cryptocephala</u> v. <u>veneta</u> (Kütz.) Grun.	C	A	-
<u>Navicula</u> <u>digitoradiata</u> (Greg.) Ralfs	P	A	-
<u>Navicula</u> <u>directa</u> (W. Sm.) Ralfs	P	D	-
<u>Navicula</u> <u>diserta</u> Hust.	C	A	-
<u>Navicula</u> <u>diversistriata</u> Hust.	C	R	-
<u>Navicula</u> <u>exima</u> Greg.	R	A	-
<u>Navicula</u> <u>finmarchica</u> (Cl. and Grun.) Cl.	P	R	-
<u>Navicula</u> <u>flanatica</u> Grun.	R	A	-
<u>Navicula</u> <u>forcipata</u> Grev.	C	A	-
<u>Navicula</u> <u>gottlandica</u> Grun.	C	A	-
<u>Navicula</u> <u>gregaria</u> Donk.	D	R	-
<u>Navicula</u> <u>groschopfi</u> Hust.	C	A	-
<u>Navicula</u> <u>grevellei</u> (Ag.) Heib.	A	R	-
<u>Navicula</u> <u>hamulifera</u> Grun.	R	A	-
<u>Navicula</u> <u>inattigens</u> Simon.	P	R	-
<u>Navicula</u> <u>incomposita</u> Hagelst.	R	A	-
<u>Navicula</u> <u>jamalensis</u> Cl.	P	A	-
<u>Navicula</u> <u>lanceolata</u> (Ag.) Kütz.	R	A	-
<u>Navicula</u> <u>litoricola</u> Hust.	C	A	-
<u>Navicula</u> <u>lyra</u> f. <u>denudata</u> (Grun.) Hust.	R	A	-
<u>Navicula</u> <u>mutica</u> Kütz.	R	A	-
<u>Navicula</u> <u>normalis</u> Hust.	R	R	-
<u>Navicula</u> <u>nyella</u> Hust.	P	R	-
<u>Navicula</u> <u>oculiformis</u> Bréb.	A	R	-
<u>Navicula</u> <u>ostrearia</u> (Gaill.) Bory	R	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<i>Navicula palpebralis</i> Bréb.	R	A	-
<i>Navicula patrickae</i> Hust.	C	R	-
<i>Navicula phyllepta</i> Kütz.	R	A	-
<i>Navicula planamembranacea</i> Hendey	A	A	+
<i>Navicula protracta</i> (Grun.) Cl.	R	A	-
<i>Navicula pseudoforcipata</i> Hust.	R	A	-
<i>Navicula pseudony</i> Hust.	P	A	-
<i>Navicula radiosa</i> Kütz.	R	A	-
<i>Navicula rhynchocephala</i> Kütz.	R	A	-
<i>Navicula salinarum</i> Grun.	P	A	-
<i>Navicula salinicola</i> Hust.	D	D	-
<i>Navicula subinflatooides</i> Hust.	P	A	-
<i>Navicula tripunctata</i> (O. F. Müll.) Bory	C	A	-
<i>Navicula tripunctata</i> v. <i>schizonemoides</i> (V. H.) Patr.	C	D	-
<i>Navicula viridula</i> (Kütz.) Ehr.	R	A	-
<i>Nitzschia</i> 1	A	P	-
<i>Nitzschia</i> 2	A	P	-
<i>Nitzschia</i> 5	P	P	-
<i>Nitzschia</i> 12	C	A	-
<i>Nitzschia</i> 23	P	A	-
<i>Nitzschia</i> 24	R	A	-
<i>Nitzschia</i> 37	R	A	-
<i>Nitzschia</i> 56	R	A	-
<i>Nitzschia</i> 73	P	A	-
<i>Nitzschia</i> 75	C	A	-
<i>Nitzschia</i> 76	R	A	-
<i>Nitzschia</i> 171	P	C	-
<i>Nitzschia acuminata</i> (W. Sm.)	P	A	-
<i>Nitzschia admissa</i> Hust.	A	R	-
<i>Nitzschia admissoides</i> Chol.	R	P	-
<i>Nitzschia angularis</i> W. Sm.	A	P	-
<i>Nitzschia apiculata</i> (Greg.) Grun.	R	A	-
<i>Nitzschia cursoria</i> (Donk.) Grun.	P	A	-
<i>Nitzschia cylindrus</i> (Grun.) Krieger	R	A	-
<i>Nitzschia delicatissima</i> Cl.	A	A	+
<i>Nitzschia dissipata</i> (Kütz.) Grun.	R	R	-
<i>Nitzschia dissipata</i> v. <i>media</i> (Hantz.) Grun.	C	C	-
<i>Nitzschia dubia</i> W. Sm.	R	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<i>Nitzschia dubiiformis</i> Hust.	A	R	-
<i>Nitzschia frustulum</i> (Kütz.) Grun.	P	A	-
<i>Nitzschia frustulum</i> v. <i>perminuta</i> Grun.	R	A	-
<i>Nitzschia frustulum</i> v. <i>subsalina</i> Hust.	D	D	-
<i>Nitzschia fundi</i> Chol.	D	D	-
<i>Nitzschia granulata</i> Grun.	R	A	-
<i>Nitzschia hungarica</i> Grun.	P	A	-
<i>Nitzschia littoralis</i> v. <i>delawarensis</i> Grun.	R	A	-
<i>Nitzschia longissima</i> Ralfs	P	R	-
<i>Nitzschia longissima</i> v. <i>parva</i> V. H.	R	C	-
<i>Nitzschia marginulata</i> f. <i>minuta</i> Grun.	R	A	-
<i>Nitzschia obtusa</i> W. Sm.	R	A	-
<i>Nitzschia pacifica</i> Cupp	A	A	+
<i>Nitzschia pseudohybrida</i> Hust.	C	C	-
<i>Nitzschia punctata</i> (W. Sm.) Grun.	R	A	-
<i>Nitzschia punctata</i> v. <i>coarctata</i> Grun.	P	R	-
<i>Nitzschia pungens</i> Grun.	A	A	+
<i>Nitzschia rostellata</i> Hust.	P	C	-
<i>Nitzschia seriata</i> Cl.	A	A	+
<i>Nitzschia sigma</i> (Kütz.) W. Sm.	P	A	-
<i>Nitzschia sigma</i> v. <i>rigida</i> (Kütz.) Grun.	A	R	-
<i>Nitzschia sigma</i> v. <i>sigmatella</i> Grun.	R	A	-
<i>Nitzschia socialis</i> Greg.	A	P	-
<i>Nitzschia spathulata</i> Greb.	R	A	-
<i>Nitzschia subhybrida</i> Hust.	R	A	-
<i>Nitzschia valdestriata</i> Aleem and Hust.	P	A	-
<i>Nitzschia vexans</i> Grun.	P	A	-
<i>Opephora marina</i> (Greg.) Petit	C	R	-
<i>Opephora pacifica</i> (Grun.) Petit	D	P	-
<i>Opephora perminuta</i> Grun.	C	R	-
<i>Opephora schultzi</i> (Brock.) Simon.	C	A	-
<i>Pinnularia ambigua</i> Cl.	P	A	-
<i>Pinnularia minuta</i> (Öster.) Cl.	P	A	-
<i>Pinnularia traveliana</i> (Donk.) Rabh.	R	A	-
<i>Paralia sulcata</i> (Ehr.) Cl.	P	C	-
<i>Plagiogramma brockmanni</i> Hust.	R	A	-
<i>Plagiogramma staurophorum</i> (Greg.) Heib.	P	A	-

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Plagiogramma vanheurckii</u> Grun.	R	A	-
<u>Plagiotropis elegans</u> (W. Sm.) Reim.	A	R	-
<u>Plagiotropis lepidoptera</u> (Cl.) Reim.	R	A	-
<u>Plagiotropis vanheurckii</u> (Cl.) Reim.	C	P	-
<u>Pleurosigma angulatum</u> (Quek.) W. Sm.	R	A	-
<u>Pleurosigma intermedium</u> W. Sm.	A	R	-
<u>Pleurosigma normanii</u> Ralfs	A	A	+
<u>Pleurosigma stuxbergii</u> v. <u>rhombioides</u> Cl.	R	A	-
<u>Pseudoeunotia doliolus</u> (Wall.) Grun.	R	A	-
<u>Rhaphoneis</u> 7	R	R	-
<u>Rhaphoneis surirella</u> (Ehr.) Grun.	C	R	-
<u>Rhizosolenia alata</u> Brightw.	A	A	+
<u>Rhizosolenia hebatata</u> v. <u>semispinosa</u> (Hensen) Gran	A	R	+
<u>Rhizosolenia setigera</u> Brightw.	A	A	+
<u>Rhoicosphenia curvata</u> (Kütz.) Grun.	P	P	-
<u>Rhopalodia musculus</u> O. Müll.	C	R	-
<u>Schroderella delicatula</u> (Per.) Pav.	A	A	+
<u>Skeletonema costatum</u> Grev.	C	P	+
<u>Stauroneis</u> 3	P	A	-
<u>Stauroneis decipiens</u> Hust.	P	P	-
<u>Stauroneis marina</u> Hust.	R	A	-
<u>Stephanodiscus hantzschia</u> Grun.	R	A	-
<u>Stephanopyxis nipponica</u> Gran and Yendo	A	A	+
<u>Stephanopyxis palmeriana</u> (Grev.) Grun.	A	A	+
<u>Stephanopyxis turris</u> Grev.	R	A	-
<u>Surirella</u> A	R	A	-
<u>Surirella fastuosa</u> v. <u>cuneata</u> Witt	R	A	-
<u>Surirella gemma</u> Ehr.	P	A	-
<u>Surirella ovata</u> Kütz.	R	A	-
<u>Synedra fasciculata</u> (Ag.) Kütz.	P	D	-
<u>Synedra fasciculata</u> v. <u>truncata</u> (Grev.) Patr.	R	A	-
<u>Synedra tabulata</u> v. <u>parva</u> Kütz.	P	A	-
<u>Thalassionema nitzschioides</u> Grun.	P	R	+
<u>Thalassiosira</u> 1	D	C	+
<u>Thalassiosira</u> 2	R	A	-
<u>Thalassiosira aestivalis</u> Gran and Angst	A	A	+
<u>Thalassiosira decipiens</u> (Grun.) Jørg.	R	R	+
<u>Thalassiosira nordenskiöldii</u> Cl.	A	A	+

APPENDIX TABLE 1

(Continued)

TAXON	B	E	P
<u>Thalassiosira pacifica</u> Grun.	C	R	+
<u>Thalassiosira rotula</u> Meun.	A	A	+
<u>Thalassiothrix longissima</u> Cl. and Grun.	A	A	+
<u>Trachyneis aspera</u> Ehr.	R	A	-
<u>Trachysphenia australis</u> Petit	C	R	-