SPATIAL AND TEMPORAL VARIATION IN THE DEVELOPMENT OF EPIPHYTIC DIATOM COMMUNITIES ON THE EELGRASS, *ZOSTERA MARINA* L.

by

TROY R. MUTCHLER

A THESIS

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Dr. Lynda Shapiro, Chair of the Examining Committee

Date

Committee in charge: Dr. Lynda Shapiro, Chair
Dr. Steven Rumrill
Dr. Alan Shanks

Accepted by:

Vice Provost and Dean of the Graduate School

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Approved: ______________________________
Dr. Lynda Shapiro

Variations in the physical conditions within an estuary may influence the dynamics of a given community. I followed development in epiphytic diatom communities on the eelgrass, *Zostera marina* L., throughout the 1996 growing season. Diatom assemblages were sampled at three locations in the South Slough National Estuarine Research Reserve (Charleston, Oregon). Samples were collected to document seasonal and short term temporal changes in community composition. An *in situ* manipulation was performed to establish community age without using an artificial substratum.

Mechanical removal of epiphytic diatoms did not effect diatom abundance or community composition. Analyses of community structure showed both spatial and temporal patterns in species abundances. Distinct communities existed at various locations along the estuarine gradient. In addition, the composition of the communities shifted as the season progressed. At the most landward site, variations in salinity and temperature were associated with changes in species abundances.

CURRICULUM VITAE

NAME OF AUTHOR: Troy Ronald Mutchler

GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:

University of Oregon
Pennsylvania State University

DEGREES AWARDED:

Master of Science in Biology, 1998, University of Oregon
Bachelor of Science in Biology, 1998, Pennsylvania State University

AREAS OF SPECIAL INTEREST:

Ecology
Phycology

PROFESSIONAL EXPERIENCE:

Phycology Laboratory Assistant, Oregon Institute of Marine Biology, Charleston, 1996-1997

Teaching Assistant, Oregon Institute of Marine Biology, Charleston, 1995

AWARDS AND HONORS:

Hoshaw Travel Award, 1997
Hannah T. Croasdale Award, 1996

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CHAPTER I

GENERAL INTRODUCTION

Over the last few decades diatom assemblages have been used to gain fundamental insight into community dynamics and relationships involving water quality issues. Several attributes of diatom communities are favorable for community analyses including: (1) short generation times; (2) sensitivity to physical and chemical changes; and (3) the relative ease with which the specimens may be handled. Freshwater ecologists have been particularly interested in the use of diatoms as indicators of water conditions (Hall and Smol 1992, Christie and Smol 1993, Lobo et al. 1995, Pan and Stevenson 1996). This application has proven quite effective in lakes and streams. Less attention, however, has been paid to diatom communities in marine and estuarine systems.

Estuaries are productive and dynamic environments which are often sites of extensive human development. Unfortunately, industrial and municipal pollution is frequently associated with this development. As a result, estuaries have historically been the recipients of substantial human impact. Given the successful use of diatoms as indicators of water quality in freshwater systems, the parallel application in estuaries is promising. In order for this practice to be effective, however, the community dynamics of estuarine diatoms must be well understood. Previous studies have documented the distribution of estuarine diatoms at various locations (Reyes-Vasquez 1970, McIntire and Overton 1971, Main and McIntire 1974, Sullivan 1977, 1979, McIntire 1978, Jacobs and Noten 1980, Medlin 1983), but there are methodological concerns regarding the use of artificial substrata or comparisons of communities of unknown ages. In particular, artificial substrata fail to reproduce host-epiphyte interactions, identical microscale hydrodynamics, as well as possible age-related changes in leaf characteristics.

The following chapters describe the temporal and spatial development of epiphytic diatom communities upon the natural substratum. An *in situ* manipulation (the removal of epiphytes) was utilized to provide uncolonized substratum for diatom growth. Chapter II describes an investigation of the community development of epiphytic diatoms on the eelgrass, *Zostera marina* L., at three locations within the South Slough Estuary (Charleston, Oregon). Ordination analysis, as well as community descriptors, were used to distinguish patterns in species composition at sites characterized by high, low, and intermediate salinity. In addition, differences between mechanically altered (treatment) and unaltered (control) eelgrass blades were examined. Chapter III provides a detailed analysis of epiphyte community dynamics at the low salinity site. The effect of the mechanical treatment on the overall diatom density, community composition, and diversity was analysed. In addition, species abundances were related to measurements of physical variables to determine the potential role of abiotic parameters in the development of community structure. Samples collected over shorter time intervals were used to investigate the development of diatom assemblages from 0 to 14 days of age.

CHAPTER II

SPATIAL DIFFERENCES IN THE DEVELOPMENT OF EPIPHYTIC DIATOM COMMUNITIES THROUGHOUT THE GROWING SEASON

INTRODUCTION

Estuaries are dynamic ecosystems that are characterized by tidal fluctuations and seasonal changes in a suite of physical parameters. Variability in physical forcing mechanisms may affect the community structure and development of the resident biota. Although environmental variations affect a large number of estuarine communities, some assemblages are more suited than others to studies of community responses. Epiphytic diatom communities are of particular interest as a result of their trophic position in the ecosystem as well as their use as biological indicators. Due to the important ecological role of epiphyton in food web dynamics, epiphyte-grazer interactions have been the focus of multiple studies (Kitting 1984, Mazzella and Russo 1989, Orth and van Montfrans 1984, van Montfrans et al. 1984). Additional consideration has been given to the influence of physical parameters on freshwater and estuarine epiphytic communities. For example, current velocities (Korte and Blinn 1983, Peterson 1987, Peterson and Stevenson 1989, Poff et. al. 1990, Steinman and McIntire 1986), nutrient loading (Coleman and Burkholder 1995, Coleman and Burkholder 1994, Neckles et. al. 1993, Neckles et. al. 1994, Williams and Ruckelshaus 1993) irradiance (Hudon and Bourget 1983, Steinman et. al. 1989), and salinity (Hargraves 1965, Martin 1970, McIntire 1978) have been shown to affect the growth and distribution of diatom communities.

The frequent use of diatoms as indicators of environmental conditions, particularly in freshwater systems, makes understanding diatom community development of critical importance. Diatoms are often employed as a model system due to their short generation times, their quick response to physical and chemical variables, and their suitability for long term preservation. In order to maximize the effectiveness of this model system, it is necessary to understand the biotic and abiotic factors that determine species abundances and distributions.

This study describes the community development of epiphytic diatom assemblages on the eelgrass, *Zostera marina* L., at three locations within the South Slough Estuary. Epiphyte communities were tracked throughout the course of the 1996 growing season, spanning a transition between the wet and dry seasons. In addition, an *in situ* manipulation of eelgrass blades was performed to insure that the diatom communities compared were of similar age and stage of development.

MATERIALS AND METHODS

Study sites. The field sites for the study were located in the South Slough National Estuarine Research Reserve (NERR) in Charleston, Oregon (Fig. 1). The climate of the area is characterized by a wet and dry season, and as a result, two physical regimes predominate in the estuary. During the wet season, from October to May, the area receives approximately 93% of its average annual rainfall (63.4 inches; courtesy of the North Bend Weather Station) and, therefore, freshwater runoff entering the South Slough is high. Conversely, little precipitation falls from June to September, greatly reducing the amount of freshwater input into the estuary. Total annual rainfall during 1996 was 84.57 inches.

Criteria that were considered in the selection of the study sites were the prevailing salinity regimes and the presence of dense *Zostera marina* L. assemblages. The sites that were selected represent portions of the salinity gradient that is characteristic of the South

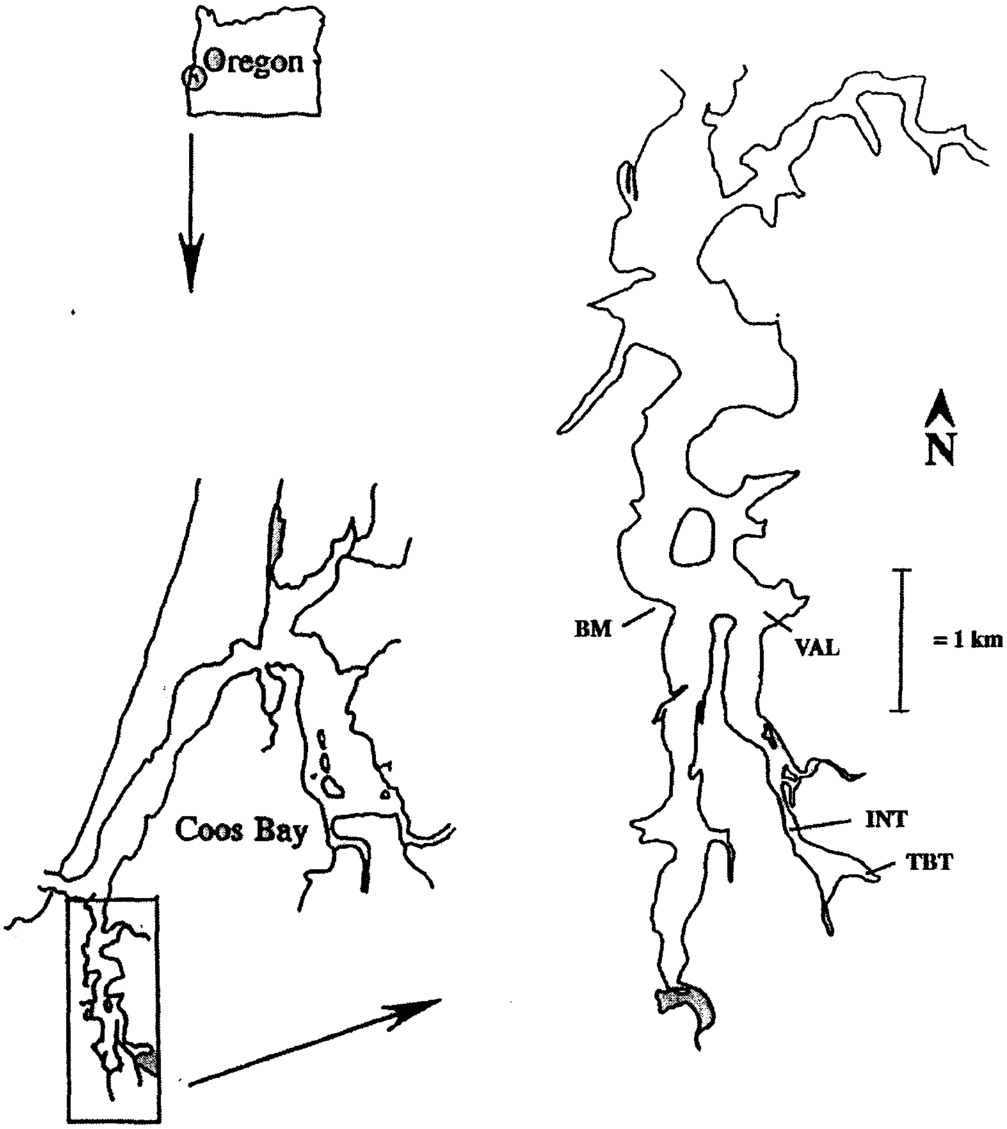


Fig. 1. Sampling locations in the South Slough Estuary. A) Map of Oregon showing the location of the greater Coos Bay area. B) Map of the Coos Bay area highlighting the South Slough. C) Detailed map of the South Slough showing the TBT site, the INT site, the VAL site, and the benchmark (BM) at Ferrie Ranch. Scale bar represents one kilometer. (Adapted from Miner 1993).

Slough Estuary. The first site was located in the lower estuary near Valino Island (VAL site). Salinity at this site was heavily influenced by seawater throughout the year. During the period from April to June 1996, the mean salinity for lower low tides was 14.58 ppt (SD = 4.66). From July to September, the mean lower low tide salinity was 29.3 ppt (SD = 3.29). The second site (INT site) located in the intermediate region of the Sengstacken arm of the slough had intermediate salinity levels. From April to June, the lower low tide mean salinities were 1.17 ppt (SD = 1.53). From July to September, the mean lower low tide salinity was 14.9 ppt (SD = 2.23). The third site at Talbot Creek (TBT site), characterized by the lowest salinities, was located in the upper portion of the Sengstacken arm. The mean salinity for lower low tides at this site from April to June was 0.5 ppt (SD = 0.80). From July to September, the lower low tide mean salinity was 8.8 ppt (SD = 1.93). Thus, the salinity at the sites ranged from virtually freshwater to nearly seawater.

Tidal elevations of the three sites were surveyed in relation to an established benchmark in the Ferrie Ranch portion of the South Slough NERR. The Valino Island site was -0.88 m below North American Vertical Datum (NAVD). The intermediate site was -0.30 m below NAVD, and the TBT site was located at 0.595 m above NAVD. The lag period of the tide reaching the TBT site (in reference to an established NOAA tide recording station in Charleston, OR) was calculated with a cross-correlation to be +1 hour in May and June, and +2 hours in August and September.

Diatom analysis. The epiphytic diatom community was sampled throughout the 1996 growing season. Four sampling dates were chosen from June to September. Each sampling effort was preceded by the removal of the epiphytic diatom community from three randomly selected eelgrass blades at each of the three sites within the South Slough Estuary. Epiphyte communities were removed by drawing the eelgrass blades between two glass slides. The use of mechanical means to remove the epiphytic diatom community from eelgrass blades has been shown by Borum (1987) to be greater than 90% effective. The technique was modified to be performed in the field by construction of a device that contained two glass slides between which an eelgrass blade was drawn. Each eelgrass blade was then marked by a pattern of small holes punched with a 22 gauge syringe needle at the base of the leaf. To identify each plant, a cable tie was used to secure a strip of colored flagging tape to the stem.

Three treated blades from each site, along with three unaltered blades chosen according to their position on the eelgrass shoot (Sand-Jensen 1975), were collected 14 days after the initial removal of epiphytes. New eelgrass blades emerge from a central location within the shoot and move laterally as they age. The position of the eelgrass blade within the shoot was used to estimate the age of the control blades. A 10 cm square segment located 5 cm from the distal end of the blade was collected and placed into a test tube for transport to the lab. Thus, on each sampling day, three blades were collected from each treatment at each site. During collection of the blades, the distance of the marked pattern from the basal meristem was measured. This measurement served as an estimator of blade elongation and growth. In addition, the salinity and temperature of the water was measured in the primary tidal channel at each site on each sampling day. All samples were collected at low tide for the easiest access to the eelgrass bed.

In the laboratory, the individual blades and resident diatoms were rinsed and cleaned with potassium permanganate and concentrated hydrochloric acid (Hasle and Fryxell, 1970). One milliliter subsamples of the cleaned diatoms from each portion of eelgrass blade were then mounted onto separate slides with Cumar (a high refractive mounting medium). Diatom preparations were observed and enumerated at 1250X on a Zeiss Universal microscope. Transects across the diameter of the cover slip were counted for each slide until at least 500 diatom valves were counted for each sample. The area of the transects and volume of the subsample were then used to calculate diatom abundance x cm^{-2}

of eelgrass blade. Taxonomic identification followed keys by Krammer and Lange-Bertalot (1986, 1988, 1991a, b) Patrick and Reimer (1966, 1975) and Cleve-Euler (1951).

Chemical and physical measurement. Chemical and physical properties of the water in the estuarine tidal channels were recorded at the uppermost site in the Sengstacken arm of the South Slough NERR by a YSI 6000 automated data logger. The YSI 6000 measured water depth, pH, turbidity, conductivity, salinity, temperature, and dissolved oxygen at intervals of 30 minutes. In addition to the data collected by the YSI 6000 data logger, salinity and temperature measurements were taken on sample days and on several dates prior to sampling. These measurements were collected only at lower low tide using a refractometer and thermometer.

Data analysis. Bhattacharyya's (1946) Similarity Index was used to measure relative changes in community composition between sites and treatments. This index

$$Sij = \sum (PikPjk)^{1/2}$$

utilizes the proportional abundances of species. P*ik* and P*jk* refer to the proportion of species *k* for replicates *i* and *j*, respectively.

For measurements of the community diversity between sites and treatments, the Shannon Index

$$H = -\sum (Pi*\ln Pi)$$

was used (Shannon 1948). Here P*i* represents the proportion of the *i*th species.

Correspondence Analysis (CA) was performed on the relative abundances using the computer program CANOCO v.3.1 (ter Braak 1990). CA was used to distinguish the primary patterns in the distribution of species and samples. The axes derived through CA are "theoretical variables" that can best explain the variation within the diatom species data. Only species with mean relative abundances of greater than 1% or maximum relative abundance greater than 5% were included in the CA.

RESULTS

Physical characteristics. The physical conditions recorded at the TBT site (Fig. 1) during 1996 showed a transition from a regime in which freshwater inputs are relatively high, to one in which they are negligible. May, 1996 was characterized by low temperatures and salinities whereas August and September were associated with higher values for each of these parameters (Figs. 2 and 3). The months of June and July appeared to be the transition between the two regimes. Both maximum and minimum salinity increased over the course of the growing season. The initial salinity maximum was 21.2 PSU (1 PSU = 1 ppt) in May, but it had risen to 31.1 PSU by September. Similarly, the salinity minimum increased from 0.1 PSU at the inception of the study to 4.9 PSU by its conclusion in September. Thus, the physical conditions at the TBT site changed across the growing season.

The seasonal increase in salinity was also reflected in the lower low tide salinity measurements taken at each of the three sites (Fig. 4). As previously noted, there were substantial differences in salinity between sites. The VAL site had significantly higher values for lower low tide salinity than both the TBT and INT sites ($P < 0.05$). In May and June, lower low tide salinity was not significantly different between the TBT and INT sites. During August and September, however, the salinity at the TBT site was significantly ($P < 0.05$) lower than the lower low tide salinity at the INT site. In addition, the lower low tide salinity at the INT site during August and September was not significantly different from the salinity at the VAL site in May and June. There were no significant differences in temperature.

Treatment effects. Similarities between the mechanical removal treatment and the control samples were high at all three sites. At the TBT site, similarity indices between the treatment and the control eelgrass blades averaged 0.934 (SD = 0.057). Treatment

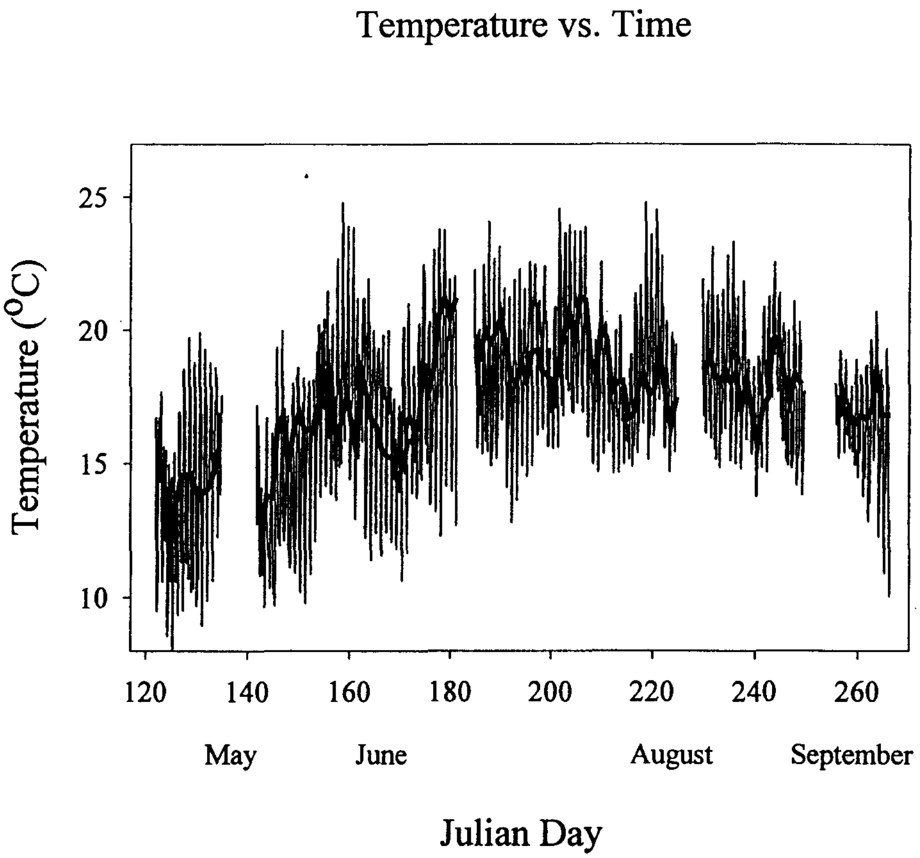


Fig. 2. Temperature (°C) recorded at the TBT site between 2 May and 23 September, 1996. The bold line represents the semidiurnal moving average.

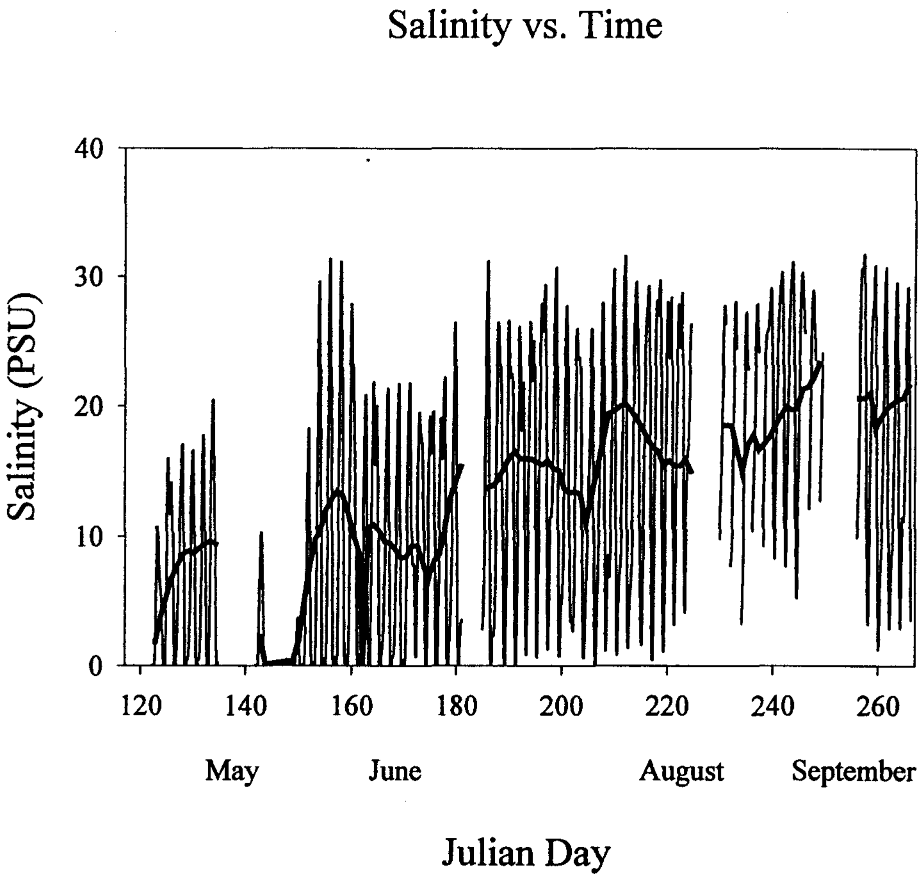


Fig. 3. Salinity (PSU) recorded at the TBT site between 2 May and 23 September, 1996. The bold line represents the semidiurnal moving average.

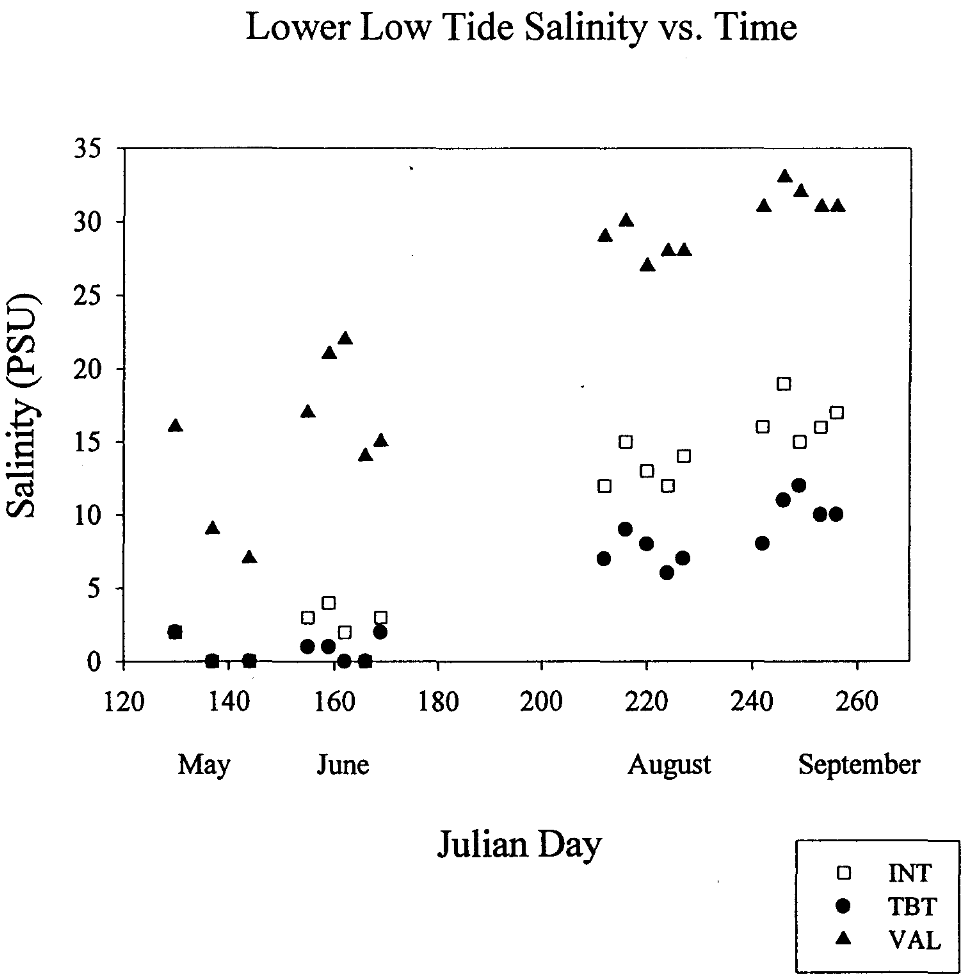


Fig. 4. Lower low tide salinity measurements taken on and 4 days prior to the sampling dates at the TBT, INT, and VAL sites.

comparisons at the VAL site yielded a comparable result, 0.927 (SD = 0.031), and the mean similarity value for the INT treatments was 0.934 (SD = 0.025). The overall mean similarity value was 0.932 (SD = 0.037). Thus, there was no difference in the community composition between the treatment and control groups.

Results of the analysis of variance on the overall sample densities are shown in Table 1 and in Fig. 5. The three way analysis of variance (site, date, and treatment), indicated a significant effect of both site and date ($P < 0.05$). No significant effect of treatment alone was shown. There were, however, two significant interaction effects in which treatment was involved. The site/treatment interaction was significant as well as the date/site/treatment interaction ($P < 0.05$). A two-way ANOVA of site and treatment by individual dates indicated site was a significant factor ($P < 0.05$) but treatment was not on the May sampling date. Once again, there was a significant ($P < 0.05$) interaction effect. For both the June and August sampling dates, no significant effect was found for site, treatment, or their interaction. In September, site was found to be significant ($P < 0.05$), but treatment and the interaction were not. When treatment was analyzed independent of site or date, the result was not significant. Thus, treatment alone had no real affect on the square root of sample density. Significant interaction terms were more likely the result of site and/or date effects than of treatment effects. The absence of significant differences in the community composition and diatom densities between the treatment and control groups demonstrates that the mechanical removal of epiphytes can be used to standardize community age and the stage of development without affecting the ultimate community composition.

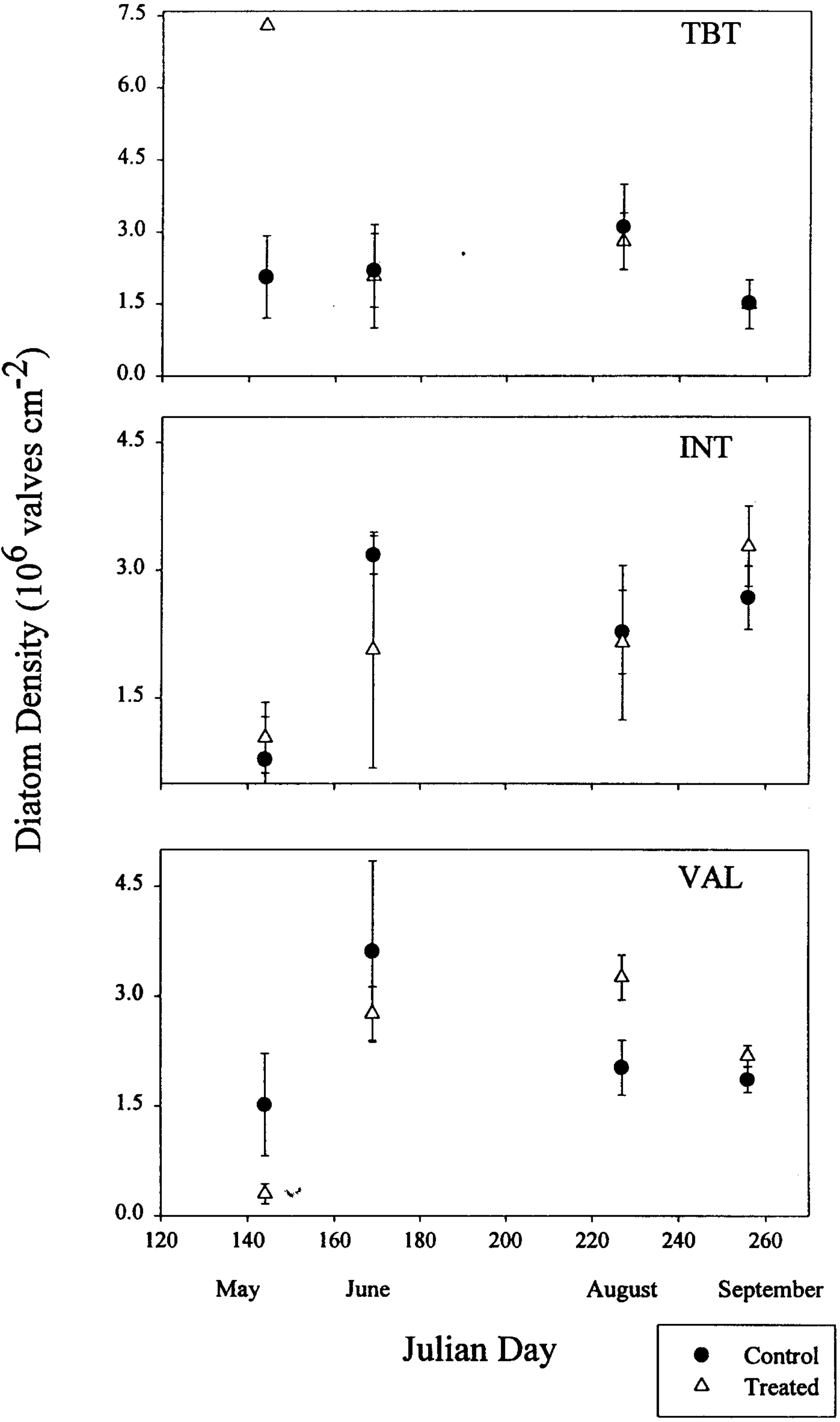
Community indices. The values for Bhattacharyya's Similarity Index (Bhattacharyya 1946) calculated between samples within a site were high. Similarity indices were 0.899 (SD = 0.095), 0.915 (SD = 0.041), and 0.924 (SD = 0.020) for the TBT, INT, and VAL sites, respectively.

Table 1. *ANOVA results for square-root transformed diatom density.*

Three way ANOVA		Factor	df	P-value
		Date	3	0.003
		Site	2	0.028
		Treatment	1	0.413
		Date*Site	6	0.000
		Date*Treatment	3	0.055
		Site*Treatment	2	0.036
		Date*Site*Treatment	6	0.000
Two way ANOVA				
	May	Site	2	0.000
		Treatment	1	0.112
		Site*Treatment	2	0.002
	June	Site	2	0.266
		Treatment	1	0.176
		Site*Treatment	2	0.681
	August	Site	2	0.207
		Treatment	1	0.465
		Site*Treatment	2	0.190
	September	Site	2	0.000
		Treatment	1	0.145
		Site*Treatment	2	0.375
One way ANOVA				
		Treatment	1	0.825

Fig. 5. Diatom density (10^6 valves x cm^{-2}) of 14 day old communities (treated and control samples) measured at the TBT, INT, and VAL sites throughout the 1996 growing season.

Diatom Density vs. Time



Bhattacharyya's Similarity Index between the three sites indicated that many species overlapped in their distributions. Figure 6 shows the similarity indices calculated using mean abundance values at the sites over the growing season. The similarity between the TBT and INT sites averaged 0.79 (SD = 0.06) and decreased over time. The similarity between the INT and VAL sites was 0.75 (SD = 0.04) but increased as the 1996 growing season progressed. The lowest inter-site similarity occurred between the TBT and VAL sites (mean = 0.65; SD = 0.04). The similarity between the TBT and VAL sites was significantly lower than those between both the INT and VAL sites as well the TBT and INT sites ($P< 0.05$). Thus, the greatest numerical difference in community composition existed between the sites most distant from each other (TBT + VAL).

As was noted earlier, the August and September lower low tide salinities at the INT site were not significantly different from the salinities at the VAL site in May and June. In light of this, Bhattacharyya's Similarity Index was calculated between samples from the INT site and the VAL site at these particular times. The similarity index between the August INT community and the June VAL community was 0.75, while the similarity value was 0.82 between the September INT and June VAL samples. These values indicate that the community composition at the INT site in late summer is very much like the community found at the VAL site earlier in the growing season.

A total of 186 diatom taxa (species and varieties) were recorded from the three sites. At the TBT site, the Shannon Diversity Indices ranged 3.18 - 4.59. The range of diversity values at the INT site was 3.03 to 4.87. The VAL site range in diversity was 4.34 to 4.70. ANOVA indicated that the Shannon Diversity Index did not differ significantly between the three sites within the South Slough Estuary ($P < 0.05$).

Seasonal and site comparisons. For the ordination analysis, only the 36 most common diatom taxa were used. Common taxa included those with a mean relative abundance >1% or a maximum relative abundance >5%. Correspondence Analysis (CA) was used to

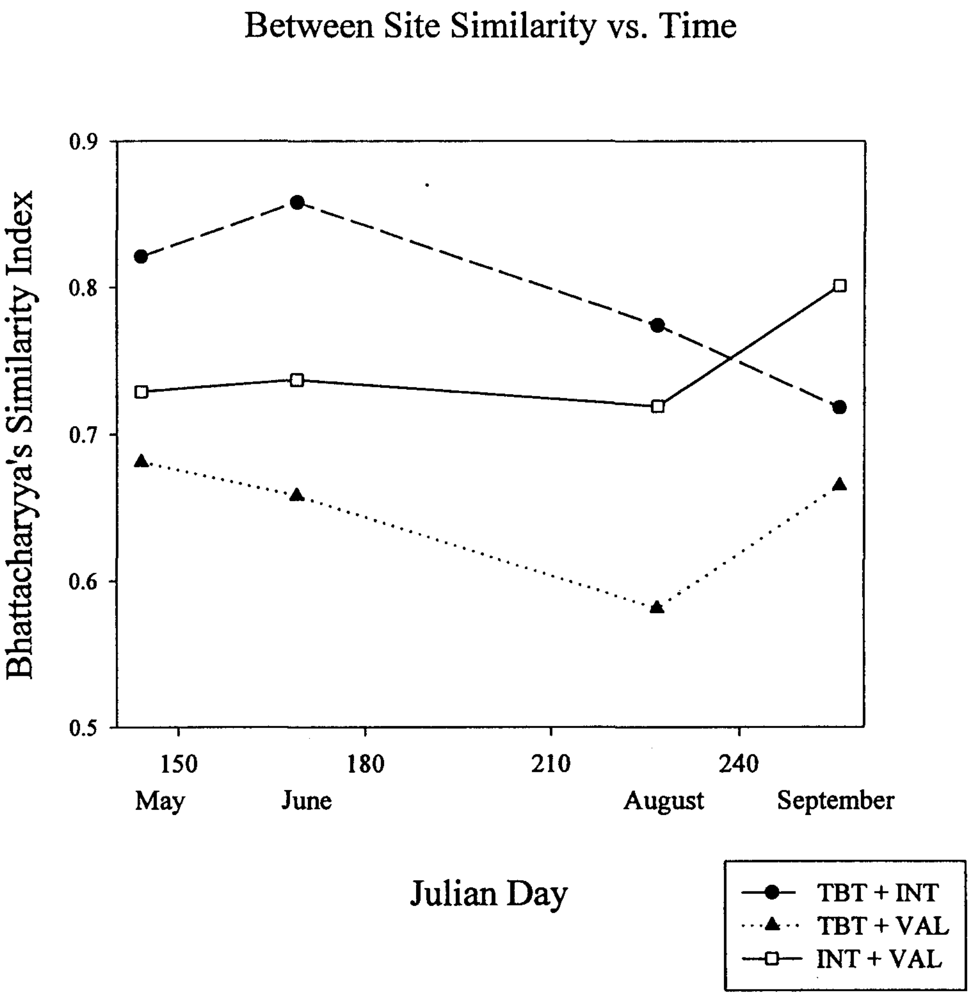


Fig. 6. Bhattacharyya's Similarity Index (1946) calculated between mean relative abundance values at the three sites over the 1996 growing season.

examine trends and gradients in the species data. For the CA, the eigenvalues (a measure of the importance of the ordination axes) were 0.530 and 0.319 for CA axis 1 and CA axis 2, respectively. The cumulative variance explained by the first CA axis was 33.4% while that explained by the first and second axis was 53.4%. Low percentages of variance expressed in the first two axes are common for data sets with many species (Pan and Stevenson 1996, Stevenson et al. 1991, Cumming et al. 1992).

Qualitative evidence for the lack of a treatment effect on the community composition was seen in the ordination plots. In Figure 7, the treatment and control groups were plotted on the same ordination. In all instances, control samples plot out in the same groupings with the treated samples. The same was true for the individual sites. All of the treated and control samples had similar community compositions. This trend further indicated that after 14 days there was no difference in community composition between the treatment and control groups.

In May and June, the TBT and INT community compositions were similar. Communities from both dates and sites clustered on the positive CA axis 1 (Fig. 7). The VAL communities for the same time periods plotted near the origin or slightly negative on CA axis 1, and were slightly negative on CA axis 2 (Fig. 7). This indicated that, in May and June, the community compositions of the VAL site differed from the TBT and INT sites. Figure 8 (along with Table 2) shows that among the common species, the VAL site differed in having greater abundances of *Nitzschia palea*, *N. agnita*, *Navicula perminuta*, and *Synedra fasciculata*. Conversely, the INT and TBT sites had greater abundances of several *Achnanthes* species, a lineate *Navicula* species, and *Ctenophora pulchella*. The difference in community composition shown through ordination was consistent with the similarity comparisons of the three sites. In May and June, the similarity indices between the TBT and the INT sites were 0.82 and 0.85, respectively (Fig. 6). Those between the

Fig. 7. CA ordination diagram of the samples collected at the three sites over the growing season. Open symbols indicate mechanically manipulated samples. Solid symbols indicate untreated samples. Samples from the VAL site are depicted by a (O). Samples from the INT site are indicated by a (∇). Samples from the TBT site are represented by a (◊). The letters indicate the time of sample collection: May (M), June (J), August (A), and September (S).

CA: Ordination Plot of Samples

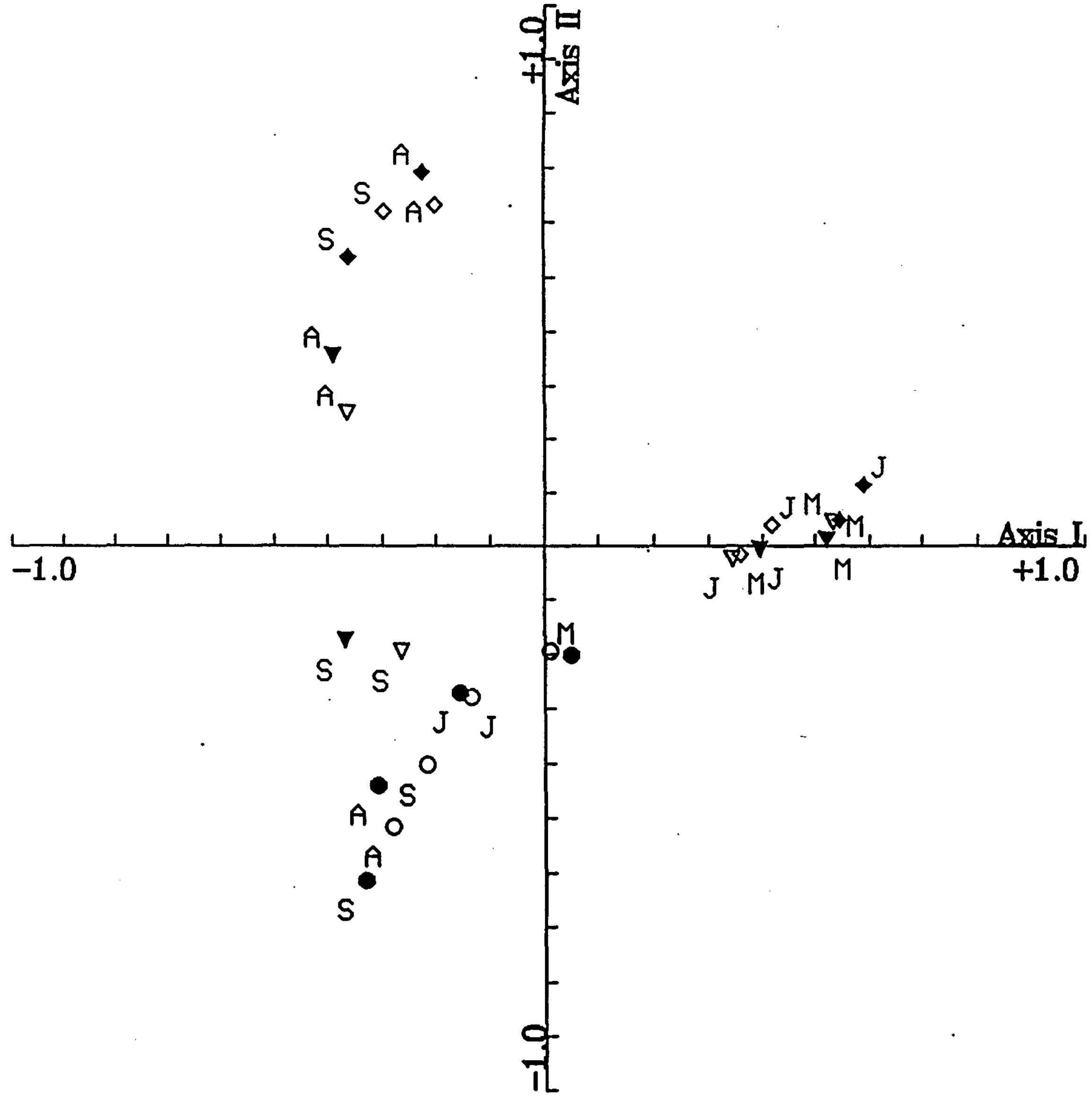


Fig. 8. CA ordination diagram of the species. Table 2 contains the full species names.

CA: Ordination Plot of Species

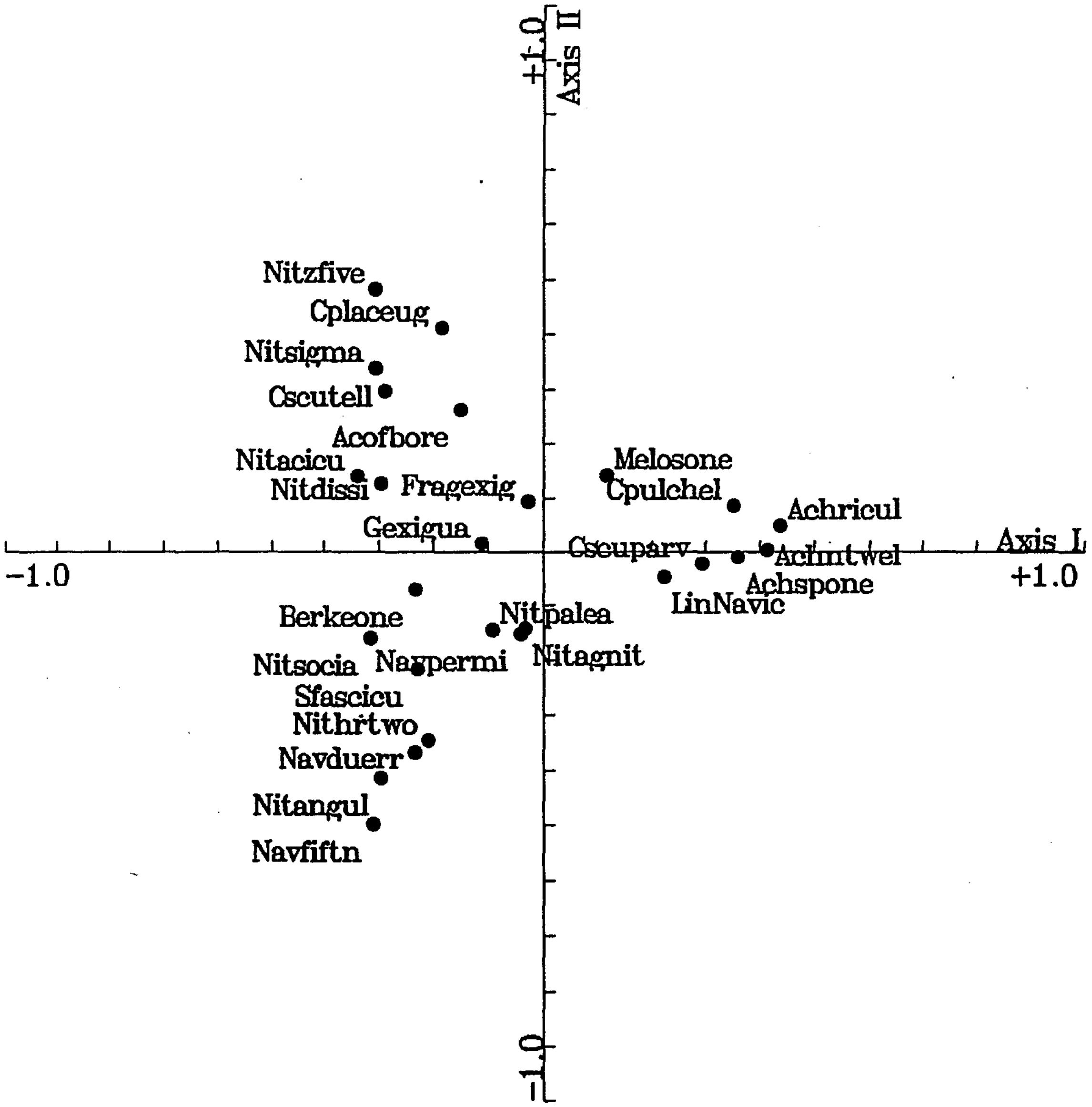


Table 2. *List of species codes in Fig. 8 and their complete species names.*

Code	Species name
Achnseve	Unidentified *Achnanthes* species
Achntwel	Unidentified *Achnanthes* species
Achricul	*Achnanthes ricula* Hohn and Hellerman
Achspone	Unidentified *Achnanthes* species
Acofbore	*Amphora coffaeformis* var. *borealis* (Kützing) Cleve
Amphfour	Unidentified *Amphora* species
Berkeone	*Berkeleya rutilans* (Trentepohl) Grunow
Cplaceug	*Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve
Cpulchel	*Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round
Cscuparv	*Cocconeis scutellum* var. *parva* Grunow ex Cleve
Cscutell	*Cocconeis scutellum* Ehrenberg
Fragexig	*Fragilaria exigua* Grunow
Frellipt	*Fragilaria elliptica* Schumann
Gexigua	*Gomphonemopsis exigua* (Kützing) Medlin
LinNavic	Unidentified *Navicula* species
Melosone	Unidentified *Melosira* species
Navduerr	*Navicula duerrenbergiana* Hustedt
Navfiftn	Unidentified *Navicula* species
Navicone	Unidentified *Navicula* species
Navictwo	Unidentified *Navicula* species
Navpermi	*Navicula perminuta* Grunow
Nitacicu	*Nitzschia acicularis* (Kützing) W. Smith
Nitagnit	*Nitzschia agnita* Hustedt

Table 2. *Continued.*

Code	Species name
Nitangul	*Nitzschia angularis* Smith
Nitdissi	*Nitzschia dissipata* (Kützing) Grunow
Nithrtwo	Unidentified *Nitzschia* species
Nitpalea	*Nitzschia palea* (Kützing) W. Smith
Nitsigma	*Nitzschia sigma* (Kützing) W. Smith
Nitsocia	*Nitzschia socialis* Grunow
Nittwthr	Unidentified *Nitzschia* species
Nitzfive	Unidentified *Nitzschia* species
Nitzsvtn	Unidentified *Nitzschia* species
Nitzthir	Unidentified *Nitzschia* species
Pennasix	Unidentified pennate diatom
Pennseve	Unidentified pennate diatom
Sfascicu	*Synedra fasciculata* (Agardh) Kützing

INT and VAL site were 0.73 in May and 0.74 in June. Finally, the indices for TBT and VAL were 0.68 and 0.66 for May and June.

A different pattern was seen in August and September. At the TBT site, the community compositions were similar with respect to the ordination axes for both months (Fig. 7). At the INT site, the August community was most like that of the TBT site. Both were characterized by high abundances of *Cocconeis placentula* var. *euglypta* and an unidentified *Nitzschia* species. Unlike the TBT site, the August INT assemblage also had high abundances of *Cocconeis scutellum*, *Nitzschia dissipata*, *N. sigma*, and *N. acicularis*. The community composition found at the INT site in September was more like those of the VAL site, particularly that found in June. At this time, the community was largely composed of *Berkeleya rutilans*, *Nitzschia socialis*, and *Synedra fasciculata*. The August and September VAL communities were similar to one another in that *Navicula duerrenbergiana*, *Nitzschia angularis*, and an unidentified *Navicula* species were abundant.

The CA ordination also showed that the species composition at the TBT and INT sites changed more than at the VAL site (Fig. 7). Communities at the TBT site changed approximately one unit along the first CA axis and about one half of a unit on the second CA axis. A similar degree of change was evident at the INT site as well. The VAL site only changed less than one half of a unit on both the CA axes.

When these patterns are compared to trends in the similarity indices, the results are again consistent. Between the TBT and INT site, there was a slight decrease in similarity from May and June (0.82 and 0.85, respectively) to August (0.77) and then again from August to September (0.72). The similarity between the INT and VAL site remained relatively constant from May to August, but then increased in September (Fig. 6). Thus, there was a marked transition in community composition over the course of the growing season. In addition, within both the TBT and INT sites, there was a significant difference ($P < 0.05$) between similarities for sampling times within May - June and August - September and similarities calculated across the May -June and August - September time periods. That is, similarities between May and June communities and between August and September communities were significantly higher than similarities calculated across the early and late summer groupings. At the VAL site, however, similarities within the early and late summer were not significantly different than those between these time periods, despite a large seasonal salinity range.

DISCUSSION

Physical conditions shifted throughout the 1996 growing season at the TBT site. In May, the temperatures were relatively low, but increased in June (Fig. 2). This increase leveled off in July, and a decrease in temperature occurred into September. A similar pattern was evident for salinity (Fig. 3) with an increase in June and continued increases throughout the summer. These trends in the physical conditions were likely the result of changes in the rainfall pattern. During spring on the southern Oregon coast, there is relatively high input of freshwater into the South Slough Estuary, resulting in lower salinities. This influx of freshwater may also have lowered temperature in the estuary. As the summer approached, daylength increased and resulted in warming of the mudflats and estuarine waters. Also at this time, the freshwater inputs decreased. Thus, an increase in temperature and salinity was observed that persisted, in large part, throughout the remaining summer months. The transition between the two predominant physical regimes in the South Slough Estuary most likely played a role in the community structure of the resident biota.

The fact that salinity at lower low tide was significantly different between sites indicates the presence of a strong salinity gradient in the South Slough Estuary. Freshwater inputs had a greater influence at the TBT and INT sites than at the VAL site. Conversely, the VAL site experienced a greater impact from the influx of nearshore coastal waters. Over time, as the freshwater inputs decreased, the salinities at the TBT and INT sites diverged (Fig. 4). This salinity gradient may affect the community structure of epiphytic diatom assemblages.

The lack of a treatment effect on diatom community structure and density has some interesting implications. Only 14 days after removal, a diatom assemblage subjected to a disturbance early in its development was indistinguishable from one which had not been disturbed. This suggests high growth and/or immigration rates of epiphytic diatoms. Possible sources of immigrating diatoms include: (1) cells and sediments suspended in the water column, (2) neighboring epiphytic communities, and (3) benthic populations of diatoms contacted by the eelgrass during periods of exposure. This multiplicity of source populations in the estuary could contribute to high immigration rates. At the same time, high current velocities in freshwater streams are known to reduce initial diatom colonization and accumulation rates whereas low current velocities contribute to higher colonization and accumulation rates (Peterson 1987, Steinman and McIntire 1986, Stevenson 1983). In the estuarine environment, current velocities change direction and magnitude with the reversal of the tides. As a result, an estuarine epiphytic community experiences current regimes which at different times may encourage or inhibit diatom immigration. During periods of low velocities, immigration may be enhanced, and as the velocity increases, reductions in the accumulation rate may be offset by promotion of nutrient uptake (Whitford and Schumacher 1964) and subsequent reproduction. Thus, one can expect rapid colonization of emerging eelgrass shoots, as well as rapid recovery of diatom communities which have been removed as a result of sloughing or grazing.

Additionally, removal of epiphytes may be a useful technique for determining the age of the epiphytic community. New eelgrass blades emerge from a central location on the shoot and move laterally with age. Thus, the position of an individual eelgrass blade within the shoot has been used as an estimate of community age (Sand-Jensen 1975). Unfortunately, such estimates of leaf age do not account for differences in eelgrass growth rate, and they do not provide the precise amount of time the substratum has been available for colonization. Therefore, mechanical detachment of epiphytes might be appropriate for investigating community succession, determining immigration rates, or avoiding the use of artificial substrata.

There is evidence for community differences both between locations and over the course of the growing season. The CA ordination plot (Fig. 7) demonstrates a distinct difference in the clustering of the TBT and INT samples corresponding to time of collection. This pattern indicates that the community composition of the epiphytic diatom assemblage was more similar during May and June than it was later in the growing season. At the TBT site, there were two distinct assemblages. The late spring assemblage was characterized by several *Achnanthes* species, *Ctenophora pulchella*, a lineate *Navicula* species, and *Cocconeis scutellum* var. *parvum*. Individuals of C. scutellum var. parvum were also found to be abundant in May in Yaquina Bay, Oregon (Main and McIntire 1974). The summer assemblage was characterized by *Cocconeis placentula* var. *euglypta*, and *Synedra fasciculata*. At the INT site, there were three different assemblages. The May and June assemblages were similar to the May and June assemblages at the TBT site, suggesting that conditions at the two sites were similar. In August, coincident with an increase in the salinity at the INT site (Fig. 4), the INT assemblage began to diverge from the TBT assemblage. This trend can be seen in both the CA plot as well as the decrease in the similarity index (Fig. 6). *C. scutellum*, *Nitzschia dissipata*, and *N. sigma* became abundant at the INT site. It is reasonable to hypothesize that the shift in the physical conditions affected the diatom community composition. The divergence in community composition continued into September, by which time the INT community became more like that at the VAL site in June. A comparison of the salinities from the INT site in August and September and the VAL site in May and June (Fig. 4) shows that lower low tide salinities were not significantly different. Thus, species such as *S. fasciculata* and *N. socialis* could have expanded their distributions up the estuary as higher salinities were found further in the estuary. In fact, *S. fasciculata* was found by McIntire (1978) to have a strong association with saline waters. This association, coupled with the high similarity values between the August and September INT samples and the June VAL samples, supports the idea of an upstream expansion in the distribution of halophilic diatoms.

The change in species composition at the VAL site over the growing season was more subtle than that found at the other two sites. Although community composition changed with time, the magnitude of change was smaller than was seen at the TBT and INT sites. As the most seaward of the three sites, the VAL site experienced the least influence from the freshwater input. Thus, the effect of a reduction in freshwater input and the resultant changes in physical conditions may have been of lesser significance. It is possible, however, that other factors were retarding succession. Steinman et al. (1989) found that grazing delayed succession in lotic algal assemblages and altered its trajectory, much like has been described for terrestrial ecosystems (Brown 1985). Conceivably, higher grazing rates at the VAL site could have regulated the rate of succession.

Changes in community composition coincident with changes in the temperature and salinity of the water column suggests that the diatoms may have responded to physical conditions in particular. Physical conditions can directly or indirectly affect the distribution of organisms (Connell 1961, Doty 1946). Seasonal variations in rainfall and insolation are likely capable of initiating shifts in species distributions. The observation that species associated with the most seaward site became more abundant at the INT site as freshwater inputs declined supports this hypothesis. In addition, studies of diatom distributions in Yaquina Bay, Oregon (McIntire and Overton 1971, McIntire 1978) described similar discontinuites in distributions that occurred both along the horizontal salinity gradient and with seasonal changes. Although, no cause and effect relationship is presented here, the most obvious potential structuring component in this system may be salinity. As the defining variable in the estuarine system, salinity might be the foremost factor to investigate in searching for a cause and effect relationship.

Previous studies have characterized diatoms based on their associations with salinity. Edsbagge (1966) classified diatoms into salinity intervals described by Simonsen (1962). Although many of the species from the South Slough Estuary were not included in the classification, three taxa of the genus *Cocconeis* were classified. Both *Cocconeis placentula* var. *euglypta* and C. scutellum var. parva were classified as typical species in salinities from 0 PSU to approximately 20 PSU. *Cocconeis scutellum* was classified as typical of salinities ranging from approximately 3 PSU to 35 PSU. These ranges are quite broad, yet they are consistent with the distributions found in the South Slough Estuary. *Cocconeis scutellum* var. *parva* was abundant during May and June at the INT and TBT sites when salinities were low, while *C. placentula* var. *euglypta* and *C. scutellum* were most abundant at these sites in August and September after salinities increased. Also, *Ctenophora pulchella* was considered an oligosaline taxon by Gell and Gasse (1990). This taxon was most abundant at the TBT and INT sites during the low salinity sampling dates in May and June. Conversely, *Synedra fasciculata* was associated with high salinity in September at the INT site and was abundant in June and August at the VAL site. This species was also strongly associated with high salinity in Yaquina Bay, Oregon (McIntire 1978). In addition, Gell and Gasse (1990) categorized *Navicula duerrenbergiana* as a mesosaline taxon. This taxon was most abundant at the VAL site in the high salinity sampling periods in August and September. Although the specific salinity tolerances of many of the taxa could not be corroborated in the literature, the available information is consistent with the distribution of the diatom taxa in the South Slough Estuary.

In the South Slough Estuary, the epiphytic diatom community found on *Zostera marina* L. changed both temporally and spatially. In the early portion of the growing season, the community compositions at the TBT and INT sites were similar, while the community at the VAL site was distinct. As time progressed, the species compositions at the three sites shifted. In particular, the communities found at the INT and VAL sites became more alike. These changes in community composition occurred as the relative influence of freshwater input into the estuary decreased, suggesting a possible role of salinity in structuring the epiphytic community. In addition, the mechanical removal of epiphytic diatoms early in community development had no effect on the community structure two weeks later. Thus, diatom communities exhibit rapid recovery from mechanical disturbance.

BRIDGE

The preceding chapter focused on both the temporal and spatial patterns of change within the epiphytic diatom community. The community dynamics at three sites within the estuary were characterized as the growing season progressed. The TBT and INT sites were similar in their community compositions in the early portions of the growing season, but as summer advanced, the diatom assemblage at the INT site became more like that at the VAL site. Physical parameters were tracked at the same time, showing a decrease in the relative importance of freshwater inputs with the onset of summer. The changes in community composition coincided with the changes in the physical conditions within the estuary. This finding suggested that the transition in physical variables influenced the distribution of diatom species. In addition, an experiment was conducted to investigate whether the mature diatom assemblages that developed on mechanically altered eelgrass blades were similar in structure and quantity to assemblages that grew on control blades. It was found that the communities that developed on treated and control eelgrass blades were indistinguishable in both diatom density and composition.

The following chapter is a more detailed analysis of the community dynamics that occurred at the TBT site. Detailed salinity and temperature measurements were taken at the TBT site during the 1996 growing season. These physical variables were compared to the changes in the composition of the epiphytic diatom community over the course of the summer in 1996. An attempt was made to associate temporal changes in the physical variables with temporal change in the pattern of species at this site. Also, a finer sampling regime provided a closer look at the development of the epiphytic assemblage on a shorter temporal scale. The influence of community age on both the species composition and overall abundance of diatoms was investigated. The effect of mechanical removal of diatoms at an early stage in community development was considered further.

CHAPTER III

TEMPORAL PATTERNS IN THE DEVELOPMENT OF DIATOM COMMUNITIES ASSOCIATED WITH CHANGING PHYSICAL CONDITIONS IN THE SOUTH SLOUGH ESTUARY

INTRODUCTION

One of the defining characteristics of an estuary is the occurrence of a salinity gradient. This salinity gradient changes with the daily tidal cycling, the lunar cycling, and the changing of the seasons. As a result, any particular location in an estuary can experience large variations in salinity. Fluctuations of salinity, and other covarying physical and chemical variables can structure the distributions of biotic communities (Connell 1961, Doty 1964).

Diatoms have often been the focus of studies that attempt to describe changes in community structure over time. Main and McIntire (1974) examined the seasonal distribution of epiphytic diatoms on a variety of host macrophytes in Yaquina Bay, Oregon. They found that *Cocconeis scutellum* var. *parva*, *Navicula diserta*, and *Nitzschia frustulum* var. *perpusilla* were abundant at most of the sampling sites throughout the year. Other species, however, were abundant only seasonally. Correlations with salinity and desiccation were found for September 1970 and May 1971 assemblages, but correlations were weak for samples collected in January of 1971. In a similar study of the distribution of benthic estuarine diatoms, McIntire (1978) found positive correlations between the abundance of *Fragilaria striatula* var. *californica*, *Synedra fasciculata*, and *Navicula diserta* and high salinity, while negative correlations were found between high salinity and abundances of *Achnanthes minutissima*, *A. deflexa*, *A. lanceolata*, *Navicula viridula* var. *avenacea*, *N. gregaria*, and *N. mutica*.

Similar studies have been conducted on epiphytic diatom communities throughout the world. Jacobs and Noten (1980) described the epiphyton on *Zostera marina* L. at Roscoff, France, and the epiphyton of various macrophytes were characterized by Medlin (1983) along the Gulf Coast of Texas. The diatom flora of *Thalassia testudinum* was also investigated by Reyes-Vasquez (1970). Sullivan (1979) characterized the epiphyton on three seagrass species in Mississippi Sound. In addition, freshwater periphyton communities have also been analyzed (Hoagland et. al. 1982, Lobo et. al. 1995, Rodriguez 1992, 1994).

Many studies have used artificial settlement devices to sample diatom communities. Glass slides or plastic panels were commonly used (Hoagland et. al. 1982, Hudon and Bourget 1981, Kawamura and Hirano 1992, Lobo et. al. 1995, McIntire and Overton 1971). A study by Cattaneo and Amireault (1992) analyzed the success of artificial substrata in freshwater streams to support development of periphytic communities that duplicate those on natural substrata. For these taxonomic comparisons, only 57% agreement between diatom communities on natural plants and artificial ones was described for colonization times of less than 15 days. In the case of *Zostera marina* L., a given portion of an eelgrass blade may begin to slough on time scales of this short magnitude. Thus, studies of epiphytic diatom communities using artificial substratum may be susceptible to misrepresentation of community structure. This lack of precision could be due to the absence of usable exudates from the host (Penhale and Thayer 1980), different hydrodynamics surrounding the substratum (Stevenson 1983), the absence of secondary inhibitory compounds, or changes in the leaf that occur with aging. However, a common problem associated with natural substrata is the inability to discern the precise age of the epiphytic community. It is important to know the age of the community of interest in order to assess the rates of accumulation and allow for comparisons with other epiphytic communities. Without standardization of the onset of colonization, questions of community age will inherently confound the interpretation of experimental results.

To minimize the possible concerns associated with the use of artificial and natural substrata, this study used an *in situ* technique in an effort to take a close look at the development of the epiphytic diatom community on *Z. marina*. The study investigated the trajectory of diatom community development at a location within the South Slough Estuary (Coos Bay, Oregon, USA). Potential differences between control and manipulated blades were evaluated to determine the effects of the *in situ* manipulation on community structure. The primary goal of the study was to determine whether the development of the diatom community would vary over the course of the growing season, given the differences in physical parameters and the introduction of new substratum.

MATERIALS AND METHODS

Study site. The field site for the study was located in the South Slough National Estuarine Research Reserve (NERR) in Charleston, Oregon, near the point at which Talbot Creek enters the Sengstacken Arm of the estuary (Fig. 9) and is referred to below as the Talbot Creek (TBT) site. Due to its landward location, the site experiences some of the lowest salinities in the estuary during the summer growing period. The mean salinity for lower low tides at this site from April to June 1996 was 0.5 ppt (SD = 0.80). From July to September, the lower low tide mean salinity was 8.8 ppt (SD = 1.93).

The tidal elevation of the site was surveyed in relation to an established benchmark located in the Ferrie Ranch portion of the South Slough NERR (Fig. 9). The TBT site was located at 0.595 m above North American Vertical Datum (NAVD). The lag period of the tide reaching the TBT site, in reference to an established NOAA tide recording station in

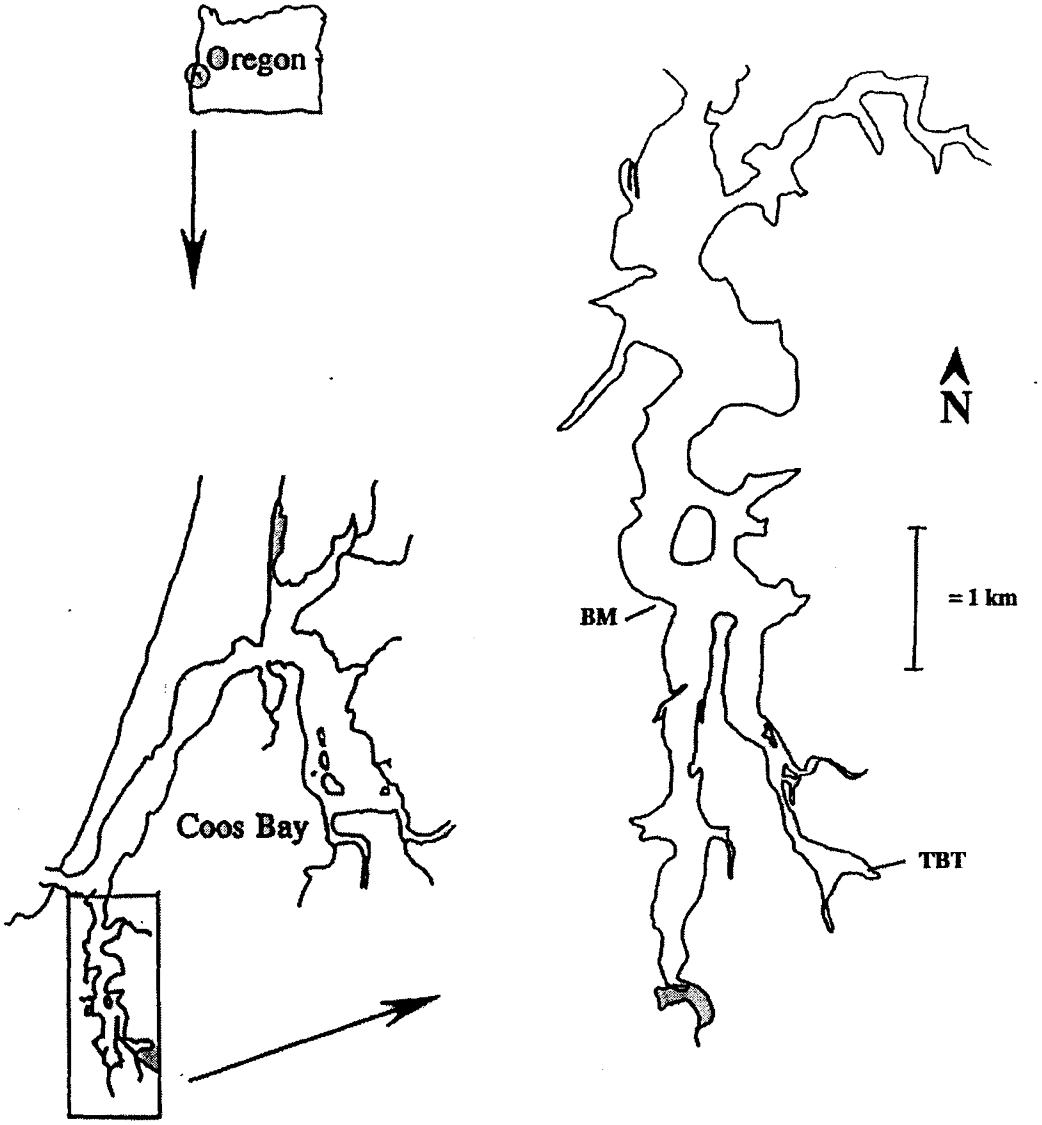


Fig. 9. Location of the South Slough Estuary and the TBT site. A) Map of Oregon showing the location of the greater Coos Bay area. B) Map of the Coos Bay area highlighting the South Slough. C) Detailed map of the South Slough showing the TBT site and the benchmark (BM) at Ferrie Ranch. Scale bar represents one kilometer. (Adapted from Miner 1993).

Charleston, OR, was calculated using a cross-correlation to be +1 hour in May and June, and +2 hours in August and September.

Diatom analysis. The epiphytic diatom community was sampled throughout the 1996 growing season. Four distinct, two-week sampling periods were chosen from May to September. Each sampling effort was preceded by the mechanical removal of the epiphytic diatom community from twelve randomly selected eelgrass blades. Mechanical removal of epiphytic diatoms from eelgrass blades has been shown by Borum (1987) to be greater than 90% effective. This technique was modified for implementation in the field by construction of a device that contained two glass slides between which an eelgrass blade was drawn. Each eelgrass blade was then marked by creating a pattern of small holes with a 22 gauge syringe needle at the base of the leaf. To identify each plant, a cable tie was used to secure a strip of colored flagging tape to the stem.

Three blades were collected 4, 7, 11, and 14 days after the initial removal of epiphytic diatoms. At the same time, three unaltered eelgrass blades were collected from comparable positions on the eelgrass shoot (Sand-Jensen 1975). New blades emerge from a central location in the eelgrass shoot and move laterally as they age. In this study, the position of the eelgrass blade within the shoot was used to estimate the age of the control blades. A 10 cm square segment starting 5 cm from the distal end of each blade was collected at low tide. Thus, portions of six eelgrass blades (three each from the treatment and control) were collected on each sampling date.

In the laboratory, the individual blades and resident diatoms were rinsed and cleaned with potassium permanganate and concentrated hydrochloric acid (Hasle and Fryxell, 1970). One milliliter subsamples of the cleaned diatoms from each portion of eelgrass blade were mounted onto separate slides with Cumar (a high refractive mounting medium). Diatom preparations were observed and enumerated at 1250X on a Zeiss Universal microscope. Transects across the diameter of the cover slip were counted for each slide, until at least 500 diatom valves were counted for each sample. The area of the transects and volume of the subsample were used to calculate diatom abundances x cm^{-2} of eelgrass blade. Taxonomic identification followed keys by Krammer and Lange-Bertalot (1986, 1988, 1991a, b) Patrick and Reimer (1966, 1975) and Cleve-Euler (1951).

Chemical and physical measurement. Chemical and physical properties of the water in the tidal channel were recorded at the site by a YSI 6000 automated data logger. The YSI 6000 measured pH, turbidity, conductivity, salinity, temperature, depth, and dissolved oxygen at 30 minute intervals. In addition to the data collected by the YSI 6000, salinity and temperature measurements were taken on sampling days and four days prior to sampling. These were collected with a refractometer and thermometer at lower low tide.

Data analysis. Bhattacharyya's Similarity Index was used to measure relative changes in community composition between dates and treatments. This index

$$Sij = \sum (PikPjk)^{1/2}$$

utilizes the proportional abundances of species. P*ik* and P*jk* refer to the proportion of species $\underline{k}$ for replicates $\underline{i}$ and $\underline{j}$, respectively (Bhattacharyya 1946).

For measurements of the community diversity, the Shannon Index

$$H = -\sum (Pi^{*}\ln Pi)$$

was used. Here P*i* represents the proportion of the *i*th species (Shannon 1948).

Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA) were performed on species relative abundances using the computer program CANOCO v.3.1 (ter Braak 1990). CA was used to distinguish the primary patterns in the distribution of species and samples. The axes derived through CA are "theoretical variables" that can best explain the variation within the diatom species data. The patterns that were elucidated by CA were related to environmental variables using CCA (ter Braak 1986). This procedure allows the determination of the portion of the pattern described by CA that can be attributed to the environmental variables (ter Braak 1987). Only species with mean relative abundances of > 1% or maximum relative abundance > 5% were included in the CA and CCA. Environmental variables were excluded if severe multicollinearity was indicated by a variance inflation factor of greater than 10 (Pan personal communication). An unrestricted Monte Carlo permutation test (999 permutations) was performed to test the significance of the first ordination axis (ter Braak 1990). Environmental gradients associated with the ordination axes were determined by the canonical coefficients and intracorrelation coefficients (ter Braak 1986).

RESULTS

Physical variables. The physical conditions recorded at the TBT site showed a transition from a regime in which freshwater inputs were relatively high, to one in which inputs were low. During 1996, May was characterized by low temperatures and salinities, whereas in August and September higher values were observed (Figs. 10 and 11). The salinity maxima and minima increased over the course of the 1996 growing season. The initial salinity maximum was 21.2 ppt in May, rising to 31.1 ppt by September. Similarly, the salinity minimum increased from 0.1 ppt at the inception of the study to 4.9 ppt by its conclusion in September. The increase in salinity was also seen in the lower low tide measurements taken on the sampling dates (Fig. 12). Thus, a marked change in the physical conditions at the TBT site occurred across the 1996 growing season with the most rapid changes in June and July.

Treatment effects. When treated samples were compared with untreated controls taken from equivalent positions in the shoot, similarity indices between treated and control samples were high. Values ranged from 0.978 to 0.851, with a mean similarity value between the treatment and control of 0.944 (SD = 0.04). Thus, the treatment did not affect the community composition of the subsequent epiphytic community.

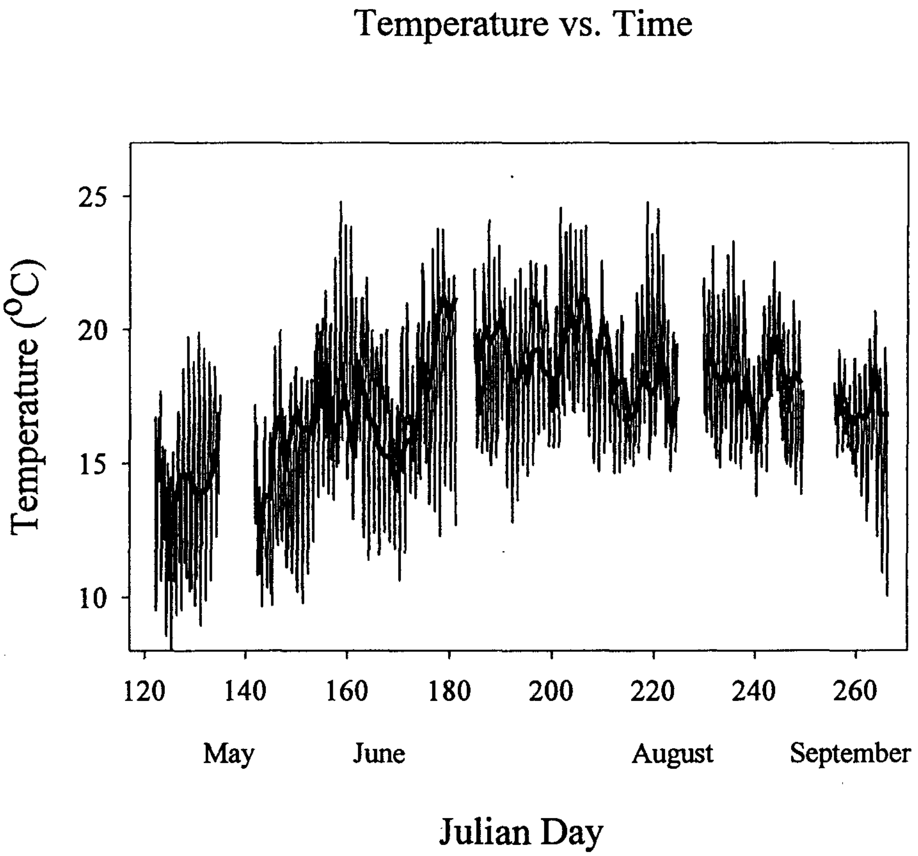


Fig. 10. Temperature (°C) recorded at the TBT site between 2 May and 23 September, 1996. The bold line represents the semidiurnal moving average.

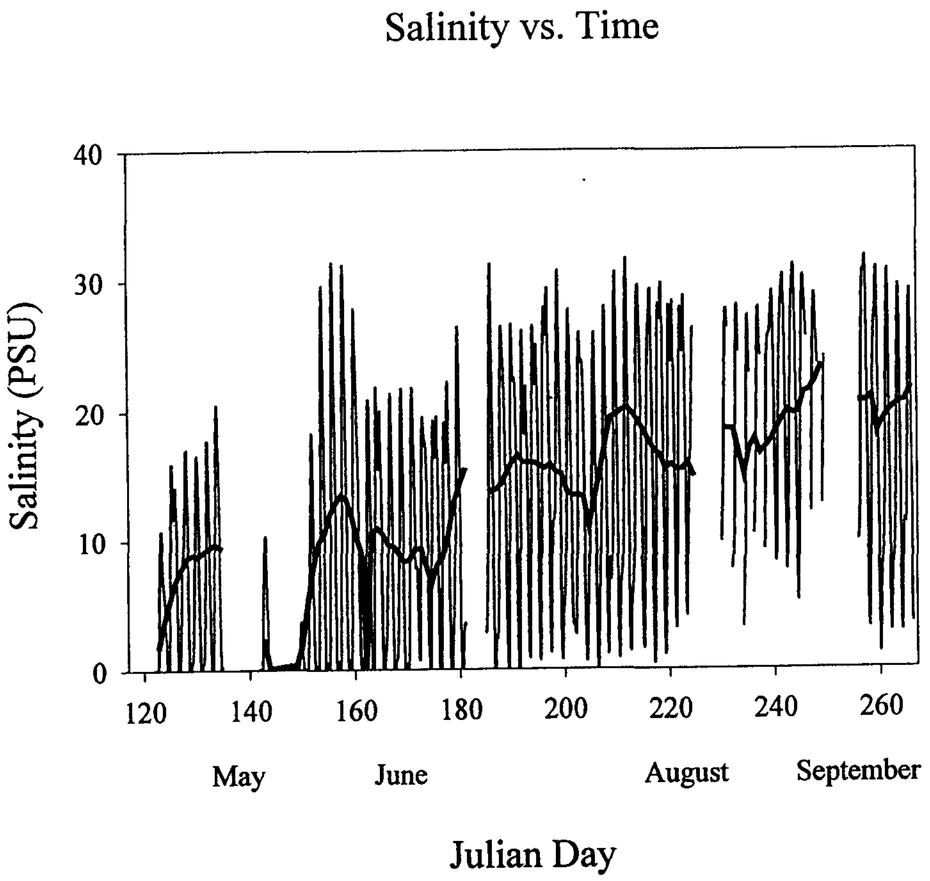


Fig. 11. Salinity (PSU) recorded at the TBT site between 2 May and 23 September, 1996. The bold line represents the semidiurnal moving average.

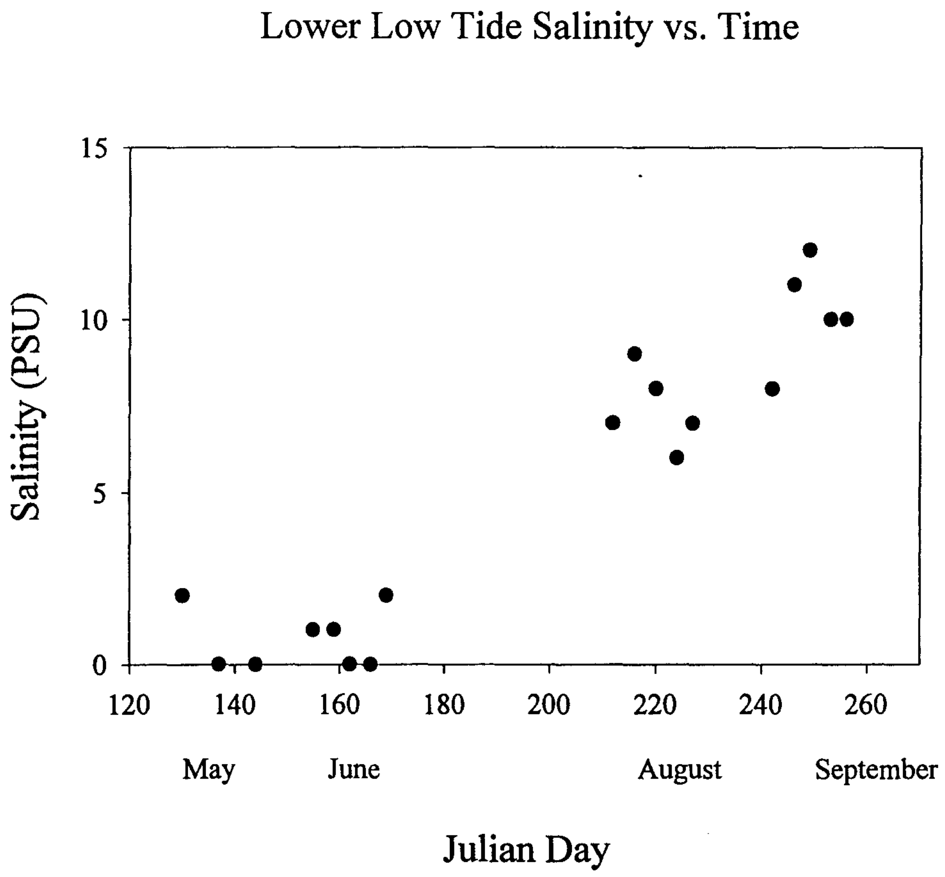


Fig. 12. Lower low tide salinity recorded on the sampling dates at the TBT site.

In addition, the density between the treatment and control was not significantly different (Table 3). There was, however, an effect of community age, as the abundance of diatoms collected after 4 days was significantly lower than for samples collected after 7, 11, and 14 days on both treated and control blades (Table 3; $P < 0.05$; Fig. 13). The month in which the samples were collected had no effect on the diatom density. There was no significant difference in diatom density between any of the sampling periods (Table 3).

The removal treatment did have an effect on the Shannon diversity index. Diversity values ranged from 4.57 to 3.18 for the untreated samples, while the range for the treated samples was 4.63 to 3.86. The mean diversity indices were 3.98 (SD = 0.429) and 4.32 (SD = 0.222) for the untreated and treated samples, respectively. Diversity indices were significantly lower for control samples (Table 4). On the other hand, neither the age of the community nor the sampling period during which the sample was collected had an effect on the Shannon Diversity Index.

Community indices. A total of 186 diatom taxa were recorded in the samples throughout the growing season. Shannon diversity index values ranged from 3.18 to 4.63 and did not vary significantly across the four sampling periods. In addition, the results of an ANOVA indicated that the time allowed for colonization (i.e. 4, 7, 11, or 14 days) had no effect on the diversity of the community.

Similarity indices comparing samples of the same colonization time across the growing season were moderate. The mean similarity values were 0.617 (SD = 0.191), 0.639 (SD = 0.168), 0.626 (SD = 0.161), and 0.650 (SD = 0.170) for 4, 7, 11, and 14 days since removal. However, a T-test showed that the similarity index of samples that span the transition in physical variables was significantly lower than similarity indices within early or late summer comparisons ($P < 0.05$). The mean similarity for comparisons of samples within either the early or late summer was 0.838 (SD = 0.037), while mean similarity between those time periods was 0.536 (SD = 0.061).

Table 3. *Results of two-way ANOVA on overall diatom density.*

Two-way ANOVA	Factor	df	P-value
	Treatment	1	0.401
	Age	3	0.000
	Treatment*Age	3	0.825
	Treatment	1	0.238
	Sampling period	3	0.150
	Treatment*Sampling period	3	0.451

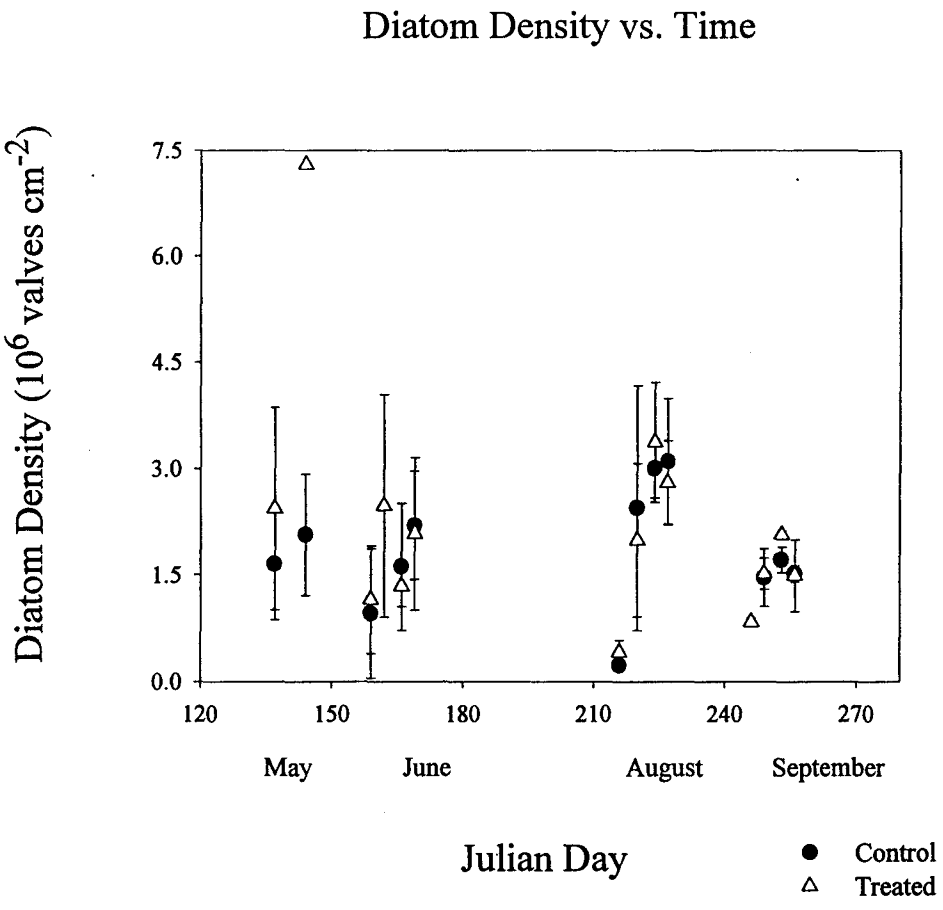


Fig. 13. Diatom density (10^6 valves x cm^{-2}) measured for treated and control samples 4, 7, 11, and 14 days after the initial treatment at the TBT site.

Table 4. *Results of two-way ANOVA on Shannon Diversity Indices (1948).*

Two-way ANOVA	Factor	df	P-value
	Treatment	1	0.038
	Age	3	0.832
	Treatment*Age	3	0.713
	Treatment	1	0.003
	Sampling period	3	0.285
	Treatment*Sampling period	3	0.115

In comparisons within sampling periods, the similarity values were high. The mean similarity of samples within a sampling period was 0.931 (SD = 0.021; range 0.964 to 0.885).

Ordination analyses. A total of 26 of the most common diatom taxa were included in the ordination analyses. The eigenvalues (a measure of the importance of the ordination axes) for the first and second CA axes were 0.604 and 0.217, respectively. These axes explained 72.8% of the cumulative variance in the species data.

Figure 14 (see Table 5 for species names) is the CA biplot of the samples and species. The samples fell out in three distinct groupings. The May (M) and June (J) samples cluster on the positive CA axis 1, indicating that the community composition during those time periods were indistinguishable from each other. The May and June samples were characterized by abundances of *Achnanthes ricula*, *A. delicatula*, *Ctenophora pulchella*, and a lineate *Navicula* species. The samples taken in August (A) fell out in their own distinct cluster. These samples had abundances of a *Nitzschia* species, *Cocconeis placentula* var. *euglypta*, and *Gomphonemopsis exigua*. The samples collected in September (S) were associated with yet another set of diatoms; *Synedra fasciculata*, *Nitzschia dissipata*, and *N. acicularis*.

For the CCA, the eigenvalues for the first two axes dropped slightly. The eigenvalue for the first CCA axis was 0.57, while that for the second was 0.065. The cumulative percent variance in the diatom data that was explained by the two axes was 50.5% and 56.3%, respectively. The species-environment correlation for the first axis was high (0.975), but the correlation for the second axis was only (0.597). Only the first CCA axis proved to be significant using an unrestricted Monte Carlo permutation test ($P < 0.05$).

Mean salinity had the greatest association with the first ordination axis (Figs. 15 and 16) The relative importance of the environmental axes can be inferred from the length of the vector. Long environmental axes are more strongly correlated with the ordination axes than

Fig. 14. CA sample - species biplot. Species are represented by solid symbols. Untreated samples are represented by (∇). Mechanically manipulated samples are depicted by (O). The time of collection is indicated by the first letter of the month in which the sample was taken followed by the age of the community in days. Samples were collected in May (M), June (J), August (A), and September (S). (e.g. M4 was collected in May, 4 days following mechanical removal). Table 5 contains the full names for the coded species. Some species names were hidden in the diagram.

CA: Sample - Species Biplot

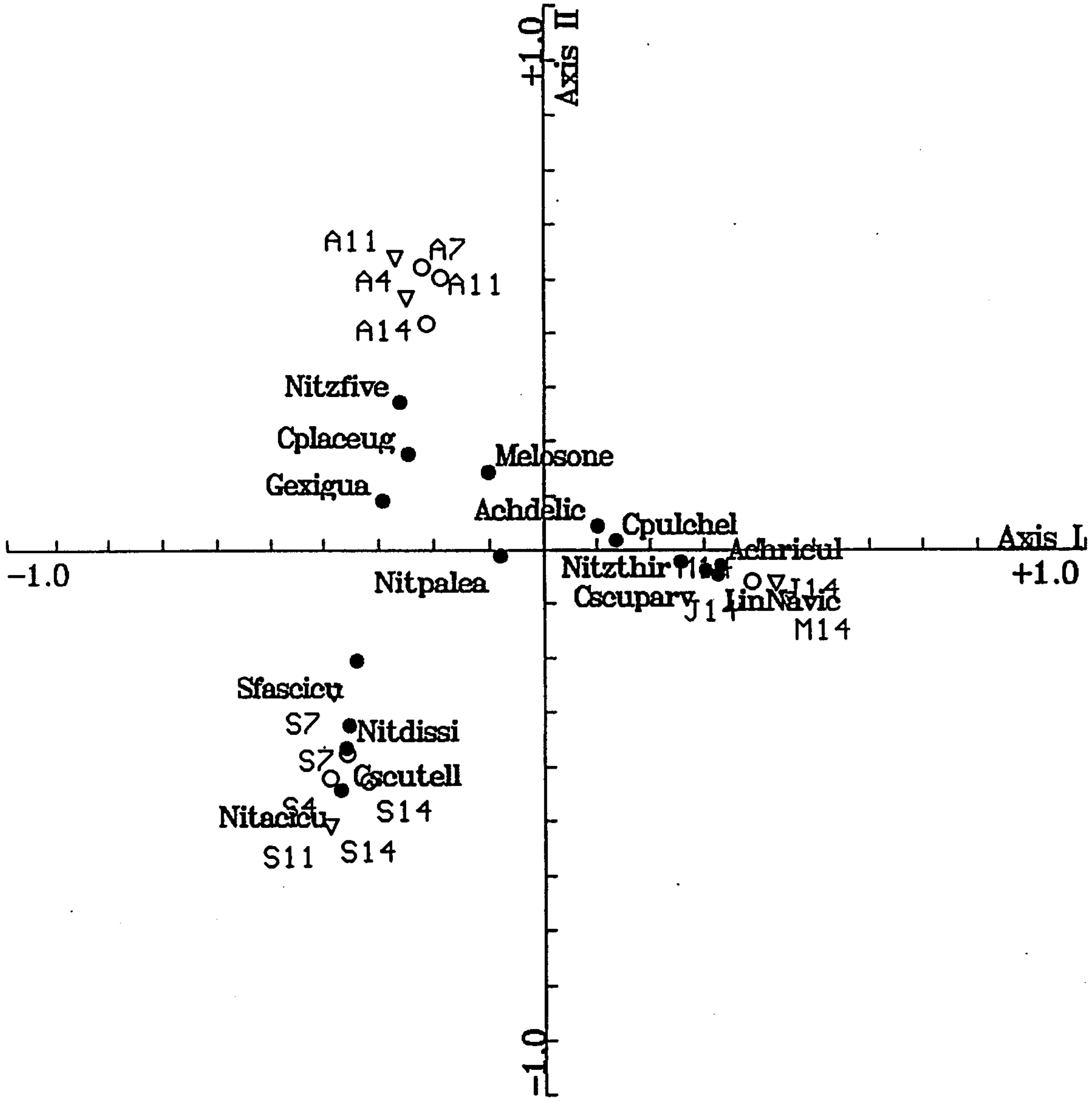


Table 5. *List of species codes in Figs. 14 and 16 and their complete species names.*

Code	Species name
Achdelic	*Achnanthes delicatula* (Kützing) Grunow
Achlemme	*Achnanthes lemmermannii* Hustedt
Achnseve	Unidentified *Achnanthes* species
Achricul	*Achnanthes ricula* Hohn and Hellerman
Achspone	Unidentified *Achnanthes* species
Acofbore	*Amphora coffaeformis* var. *borealis* (Kützing) Cleve
Cplaceug	*Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve
Cpulchel	*Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round
Cscuparv	*Cocconeis scutellum* var. *parva* Grunow ex Cleve
Cscutell	*Cocconeis scutellum* Ehrenberg
Fragexig	*Fragilaria exigua* Grunow
Frellipt	*Fragilaria elliptica* Schumann
Gexigua	*Gomphonemopsis exigua* (Kützing) Medlin
LinNavic	Unidentified *Navicula* species
Melosone	Unidentified *Melosira* species
Navicone	Unidentified *Navicula* species
Navpermi	*Navicula perminuta* Grunow
Nitacicu	*Nitzschia acicularis* (Kützing) W. Smith
Nitdissi	*Nitzschia dissipata* (Kützing) Grunow
Nitpalea	*Nitzschia palea* (Kützing) W. Smith
Nittwthr	Unidentified *Nitzschia* species
Nitzfive	Unidentified *Nitzschia* species
Nitzthir	Unidentified *Nitzschia* species
Pennseve	Unidentified pennate diatom
Sfascicu	*Synedra fasciculata* (Agardh) Kützing

Fig. 15. CCA sample - environment biplot. Untreated samples are represented by (∇). Mechanically manipulated samples are depicted by (O). The time of collection is indicated by the first letter of the month in which the sample was taken followed by the age of the community in days. Samples were collected in May (M), June (J), August (A), and September (S). (e.g. M4 was collected in May, 4 days following mechanical removal).

CCA: Sample - Environment Biplot

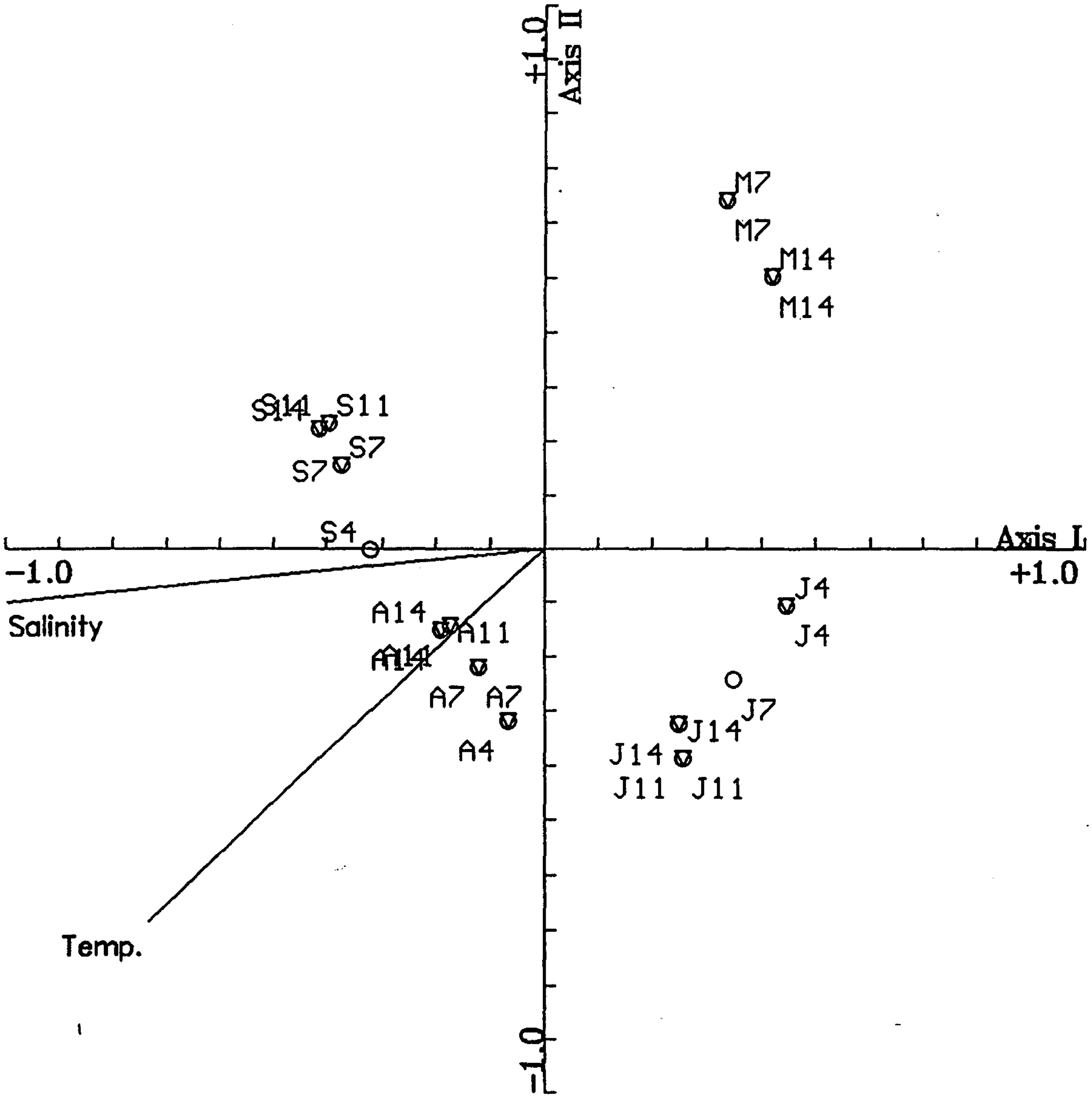
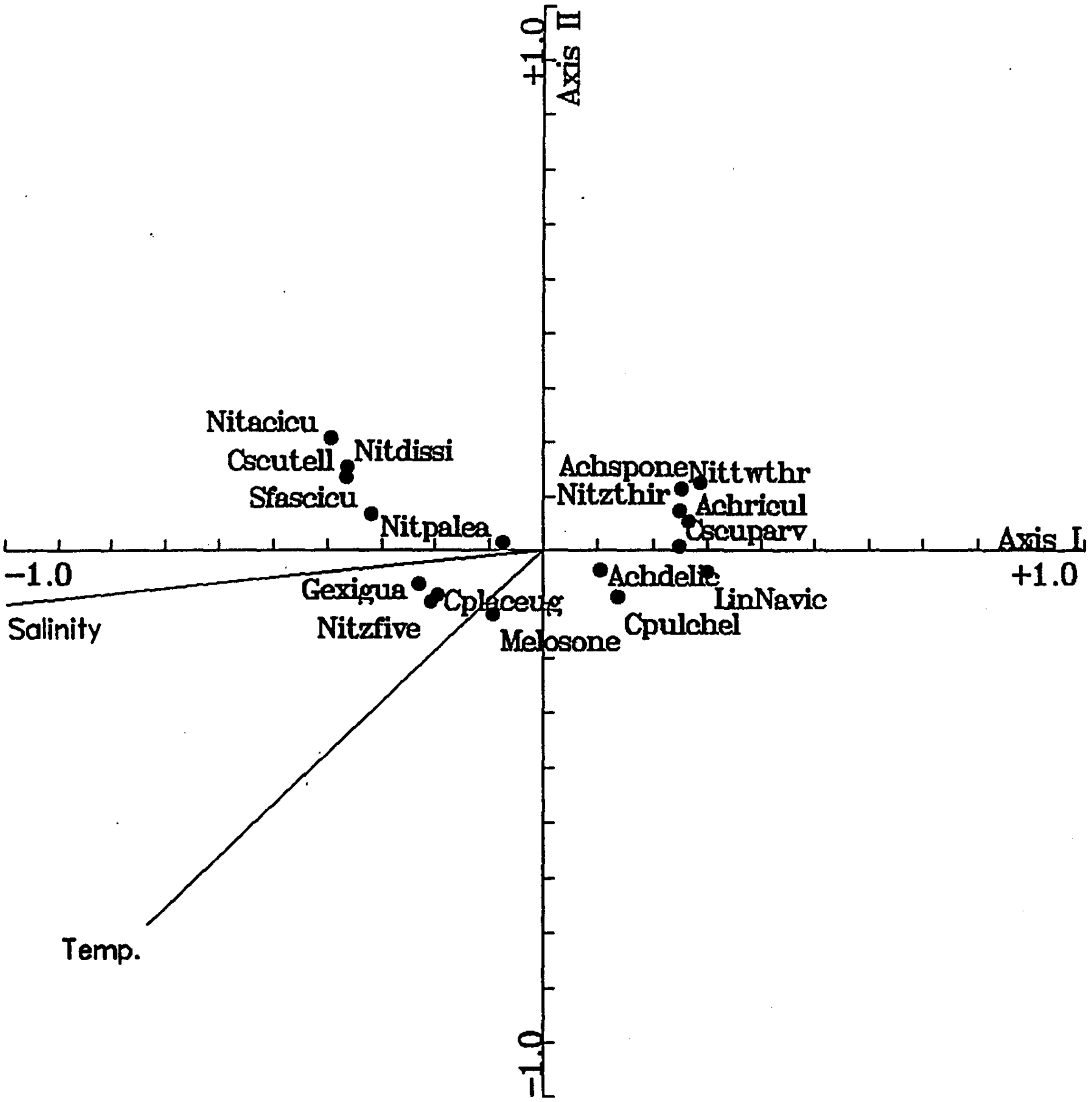


Fig. 16. CCA species - environment biplot. Table 5 contains the full names for the coded species.

CCA: Species - Environment Biplot



are short ones (ter Braak 1987). In addition, the more acute the angle between the environmental axis and the CCA axis, the greater the association between the two.

Additional means of interpreting the association of the environmental data with the CCA axes were provided through the canonical coefficients and intraset correlations (Table 6). From the relative magnitudes of these two measures, the importance of the environmental variables for determining the community structure can be inferred (ter Braak 1986). The canonical coefficients represent the contribution of the environmental variables to the CCA axes (ter Braak 1987). The intraset correlations are the correlations of the environmental variables with the ordination axes (ter Braak 1987). The high values in the intraset correlations for mean salinity (Table 6) indicated that the first CCA axis was largely comprised of a salinity gradient. The low eigenvalue for the second CCA axis indicated that the species variation on the second axis was small. However, this axis had a surprisingly high correlation with temperature (Table 6).

In Figure 15, the sample and environmental data is plotted against the CCA axes. The biplot depicts a clear salinity gradient increasing from right to left. The May (M) and June (J) samples were associated with low salinities, while those of August (A) and September (S) were associated with higher salinities. A similar trend was true in the case of the temperature axis. Extending the axis through the origin, the temperature increase that occurred through May and June becomes evident from the spread of the M and J samples. However, the August and September (A and S) samples were associated with similar temperatures, indicating that temperatures were somewhat constant during that time.

Figure 16 shows the ordination biplot of the species and environmental variables. The physical variables are plotted in exactly the same manner as for Figure 15. The species on the positive CCA axis 1, were associated with lower salinity. In particular, the *Achnanthes* species, a lineate *Navicula* species, *Ctenophora pulchella*, *Cocconeis scutellum* var. *parva*, and two unidentified *Nitzschia* species were abundant in early summer when salinities were

Table 6. *The canonical coefficients and intraset correlations for the environmental variables.*

	Canonical coefficients		Intraset correlations	
Variables	Axis 1	Axis 2	Axis 1	Axis 2
Mean Salinity	-0.113	0.120	-0.995	-0.60
Mean Temperature	0.17	-0.164	-0.730	-0.633

lower. As salinity and temperatures increased, a *Melosira* species, a *Nitzschia* species, *N. palea*, and *Gomphonemopsis exigua* increased in abundance. By September, the community was dominated by *Cocconeis scutellum, Nitzschia dissipata, N. acicularis*, and *Synedra fasciculata*. This pattern is much the same as that described by the "theoretical variable" in CA. In addition, in the CA (Fig. 14), the control samples and the treated samples plotted out in the same location. This fact further suggests that the initial *in situ* manipulation had no effect on the structure of subsequent diatom communities.

DISCUSSION

The results of the treatment effect tests have several implications. The fact that there was no significant effect of treatment on diatom density may mean that growth and immigration rates were similar between the treatment and control groups. Evidently, the initial loss of cells during the removal treatment did not have a substantial impact on the rate of accumulation of the diatom cells. This finding suggests that the rate of recovery from a mechanical disturbance, such as sloughing or grazing, is rapid. In addition, samples that were only four days old had significantly lower densities than those collected after 7, 11, and 14 days. This pattern is consistent with the recovery of lotic stream algae reported by Peterson and Stevenson (1992). In their study, cell densities in slow current regimes returned to control levels 6-9 days following a simulated spate. Thus, dense algal assemblages can develop over a relatively short time period. At the same time, the fact that there was no difference in cell density between 7, 11, and 14 day old communities may indicate that cell accumulation tapered as time progressed, the death and removal rates increased with time, or simply that maximum cell densities are reached after approximately 7 days.

The similarity indices between the treatment and control groups were high and suggest that the species composition was unaffected by the physical removal of diatoms. Steinman et al. (1991) found a similar result for freshwater lotic algae subjected to light elimination. Taxonomic similarity values were very high only two days following the termination of the light elimination period. The similarity in community composition between the treatment and control groups at the TBT site was also seen in the ordination analysis. In the CA, the control and treated samples plotted out in similar locations. Thus, after the mechanical removal both the total number of diatoms and the community structure in treated samples were effectively the same as in the control samples. With the mechanical removal treatment, however, the precise community age was known. This method to determine the community age with natural substratum may be useful for experiments that investigate epiphytic community growth rates or succession.

The physical data collected at the TBT site indicated that a change in the physical conditions occurred as the growing season progressed. This change was a reflection of two important seasonal changes. First, most of the annual rainfall in the Coos Bay area falls between October and May. As the 1996 growing season commenced, substantial freshwater input into the estuary persisted for many weeks. The salinity remained relatively low throughout the month of May, but it started to increase in June. The increase continued throughout June and July and leveled off by the beginning of August.

Second, the temperature measured at the TBT site was low at the end of spring. At this time, the day length and angle of inclination of the sun was increasing as the summer equinox approached. These changes in insolation, coupled with morning lower low tides, allowed for heating of both the mudflats and estuarine waters. The result was an increase in water temperatures through early July. By the middle of July, temperatures stabilized and remained at higher levels into September. These changes in solar heat input and freshwater runoff set the stage for changes in the epiphytic diatom community.

The community structure of the epiphytic diatom assemblage changed with changes in the physical conditions. Although the diversity of the communities remained constant over the four sampling periods, there were changes in the species composition. Comparisons between the early summer and late summer similarity indices showed that the community changed significantly over the 1996 growing season. These changes were concurrent with the change in physical conditions. The importance of seasonal changes in the community was highlighted by the lack of change within both the early and late portions of the growing season and within an individual sampling period. If biotic, interspecific interactions were responsible for the changes in the community composition, it would have been reflected in greater dissimilarity between samples at different stages of community development collected under like physical conditions.

Previous studies have characterized diatoms based on their associations with salinity. Edsbagge (1966) classified diatoms into salinity intervals described by Simonsen (1962). Although many of the species from the TBT site were not included in the classification, three of the *Cocconeis* taxa were classified. Both *Cocconeis placentula* var. *euglypta* and *C. scutellum* var. *parva* were classified as typical species in salinities from 0 PSU (0 ppt) to approximately 20 PSU (20 ppt). *Cocconeis scutellum* was classified as typical of salinities ranging from approximately 3 PSU (3 ppt) to 35 PSU (35 ppt). These ranges are quite broad but are consistent with the distributions found at the TBT site. *Cocconeis scutellum* var. *parva* was abundant during May and June when salinities were low, while *C. placentula* var. *euglypta* was most abundant in August after salinities increased. *Cocconeis scutellum* did not become abundant until September, when the salinity was at its highest point. Also, *Ctenophora pulchella* was considered an oligosaline taxon by Gell and Gasse (1990). This taxon was most abundant at the TBT site during the low salinity sampling dates in May and June. Conversely, *Synedra fasciculata* was associated with high salinity at the TBT site and in Yaquina Bay, Oregon (McIntire 1978). Although the specific salinity tolerances of many of the taxa are not known, the available information is consistent with the distribution of the taxa found at the TBT site.

The Correspondence Analysis further supported the finding that the physical conditions were responsible for the changes in the community composition. Considering the first CA axis (Fig. 14), samples collected in May and June plotted together on the positive CA axis 1. The August and September samples, although separated distinctly on CA axis 2, were plotted in close association on the negative portion of CA axis 1. Thus, the first "theoretical variable" can be used to distinguish between samples taken across the entire growing season, but not between samples within the early or late portions of the growing season or on the basis of community age.

The strongest evidence for physical conditions eliciting the changes in community composition at the TBT site came from the CCA. The high eigenvalues and multiple correlations (species-environment correlations) indicated that the relationship between the species distributions and the measured environmental variables was strong. The dispersion of the samples along the first axis in Figure 15 was largely a result of differences in salinity when the samples were taken. To a lesser extent, temperature, as well as covariates (pH, water depth, insolation, and dissolved oxygen) which could not be included in the analysis, contributed to the pattern described in the ordination plots. The relative rankings of the samples and species with respect to the ordination and environmental axes were inferred from their position on the individual axes.

Other studies have investigated the role of salinity in structuring diatom communities. McIntire and Overton (1971) found that differences in diatom assemblages in Yaquina Bay, Oregon were closely related to the horizontal salinity gradient. A later study of Yaquina Bay (McIntire 1978) indicated that changes in the diatom communities on an artificial substratum occurred along the salinity gradient approximately where the mean salinity decreased below 5 PSU (5 ppt). The distribution of sediment-associated diatoms in Yaquina Bay was also discontinuous at this location in the horizontal salinity gradient (Amspoker and McIntire 1978). The TBT site was located in a similar position in the salinity gradient of the South Slough Estuary in the early portion of the 1996 growing season, but with time, the conditions became more saline. Thus, it appears that the diatom community changed in response to the shift in the salinity gradient.

The salinity gradient described in this study is analogous to physical gradients in other terrestrial and aquatic ecosystems. Doty (1946) correlated the vertical distributions of intertidal algae and discontinuities in exposure resulting from the variations in the tides. The discontinuities resulted in two- or three-fold increases in the exposure time which set the distinct vertical limits of the algal distributions. Similarly, Whittaker (1956) described the distributions of tree populations in the Great Smoky Mountains in Tennessee. The tree populations could, in large part, be arranged according to elevation, aspect of the slope, and moisture. In the South Slough Estuary, the salinity gradient plays a role in determining diatom distributions that is similar to the role of exposure and moisture gradients for intertidal algae and tree populations.

Although salinity and temperature were implicated here as important structuring variables, no cause and effect relationship was established. The results of the analyses do, however, suggest that the variance in the species distributions could, in large part, be explained by the variation in salinity and temperature. The evidence of the potential role of these factors in structuring diatom assemblages at the TBT site indicates that they may also have influenced the community dynamics observed at the INT and VAL sites that were described in the previous chapter.

Determining the precise impact of salinity and temperature on the epiphytic diatom community would require extensive laboratory tests. Mesocosm experiments designed to analyze the diatom community structure under varying salinity and temperature regimes might provide useful insight into the dynamics of epiphytic communities. Similar mesocosm experiments have investigated the role of nutrients (Neckles et al. 1993, Coleman and Burkholder 1994), current velocity (Steinman and McIntire 1986, Peterson and Stevenson 1989), grazing (Steinman et al. 1989), and irradiance (Steinman et al. 1989) in diatom community development. Such experiments, although valuable, cannot account for complex interactions of biological and physical variables in their entirety. To determine the relative roles of individual parameters in influencing community dynamics, the tight integration of field and mesocosm experiments may be the most effective approach.

The recovery of epiphytic diatom communities, following mechanical removal of diatom cells, was rapid. This finding suggests relatively high accumulation rates on *Zostera marina* blades. The similarity between communities from mechanically scraped and control blades indicates that this technique may be an effective alternative to the use of artificial substrata for epiphytic diatom community analyses. In addition, the South Slough Estuary undergoes a physical transition from a system of high freshwater input to one in which coastal oceanic waters dominate. Through the course of this transition, temporal salinity and temperature gradients arise throughout the Sengstacken Arm over the growing season. Along with these temporal gradients, there is a corresponding shift in the epiphytic diatom community structure. Both the salinity and temperature appear to be strong structuring influences on the diatom assemblages. Species common in the early growing season are associated with low salinity and temperature while those common later in the season are associated with higher values for these parameters.

CHAPTER IV

CONCLUSION

The experiments outlined in the previous chapters characterized the epiphytic diatom community development within the South Slough Estuary. The goal of the experiments was to investigate three primary questions. 1) Does mechanical removal of an early stage diatom assemblage affect the overall density of the diatom community or alter the trajectory of its development? 2) How does the epiphytic diatom community on *Zostera marina* change throughout the growing season? 3) How does this community vary spatially within the estuary?

In the first set of experiments, no differences were apparent in the community structure of mechanically altered and unaltered diatom assemblages. Moreover, statistical analyses showed both a spatial and temporal component to community structure. In May and June of 1996, a distinction was made between the communities found at the most seaward site and those found at the intermediate and landward sites. As the 1996 growing season progressed, however, the community at the intermediate site became more similar to the seaward site. The communities at all three sites underwent changes throughout the course of the growing season. These compositional changes were concurrent with changes in the physical conditions within the estuary.

The second set of experiments focused closely on the community dynamics at the most landward site. As was found in the first experiments, the mechanical manipulation had no effect on diatom density or community structure. Thus, it appears that the mechanical removal procedure may be an effective means of establishing a community of known age without the use of artificial substrata. In addition, ordination analysis was used to compare the temporal patterns in species abundances with the variation in salinity and temperature. The analysis showed a strong association between these variables and the shifts in species abundances. This finding suggests that changes in salinity and temperature may elicit changes in the community compositions.

APPENDIX A

SUMMARY OF SPECIES ABUNDANCES AT THE TBT SITE

Table 7. *Summary of the mean relative abundance of common species (only those species included in the ordination analyses in Chapter II) in 14 day old treatment samples collected at the TBT site during the 1996 growing season. Estimations of the relative abundance are indicated with p = predominant (> 20%), f = frequent (5 - 20%), c = common (1 - 5%), r = rare (<1%), and - = absent (0%).*

Species code	Taxon	Month			
		May	June	August	September
Achnseve	Unidentified *Achnanthes* species	c	c	c	c
Achntwel	Unidentified *Achnanthes* species	c	-	-	-
Achricul	*Achnanthes ricula* Hohn and Hellerman	f	f	c	c
Achspone	Unidentified *Achnanthes* species	c	f	r	r
Acofbore	*Amphora coffaeformis* var. *borealis* (Kützing) Cleve	-	r	c	c
Amphfour	Unidentified *Amphora* species	-	r	c	r
Berkeone	*Berkeleya rutilans* (Trentepohl) Grunow	-	-	c	c
Cplaceug	*Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve	r	c	p	p
Cpulchel	*Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round	r	c	c	r
Cscuparv	*Cocconeis scutellum* var. *parva* Grunow ex Cleve	f	f	c	c
Cscutell	*Cocconeis scutellum* Ehrenberg	-	-	r	f
Fragexig	*Fragilaria exigua* Grunow	c	c	c	c

Table 7. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Frellipt	*Fragilaria elliptica* Schumann	f	f	c	c
Gexigua	*Gomphonemopsis exigua* (Kützing) Medlin	-	-	c	c
LinNavic	Unidentified *Navicula* species	f	p	c	c
Melosone	Unidentified *Melosira* species	-	c	c	r
Navduerr	*Navicula duerrenbergiana* Hustedt	-	r	r	r
Navfiftn	Unidentified *Navicula* species	-	-	-	-
Navicone	Unidentified *Navicula* species	r	c	c	r
Navictwo	Unidentified *Navicula* species	-	-	r	r
Navpermi	*Navicula perminuta* Grunow	c	c	c	c
Nitacicu	*Nitzschia acicularis* (Kützing) W. Smith	-	-	r	f
Nitagnit	*Nitzschia agnita* Hustedt	r	c	c	r
Nitangul	*Nitzschia angularis* Smith	-	-	-	-
Nitdissi	*Nitzschia dissipata* (Kützing) Grunow	-	r	c	c

Table 7. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Nithrtwo	Unidentified *Nitzschia* species	r	r	r	r
Nitpalea	*Nitzschia palea* (Kützing) W. Smith	c	c	c	r
Nitsigma	*Nitzschia sigma* (Kützing) W. Smith	-	-	c	r
Nitsocia	*Nitzschia socialis* Grunow	-	-	r	r
Nittwthr	Unidentified *Nitzschia* species	c	c	r	c
Nitzfive	Unidentified *Nitzschia* species	-	-	f	c
Nitzsvtn	Unidentified *Nitzschia* species	r	r	c	r
Nitzthir	Unidentified *Nitzschia* species	f	c	r	c
Pennasix	Unidentified pennate diatom	r	r	-	-
Pennseve	Unidentified pennate diatom	c	r	c	c
Sfascicu	*Synedra fasciculata* (Agardh) Kützing	-	r	c	c

APPENDIX B

SUMMARY OF SPECIES ABUNDANCES AT THE INT SITE

Table 8. *Summary of the mean relative abundance of common species (only those species included in the ordination analyses in Chapter II) in 14 day old treatment samples collected at the INT site during the 1996 growing season. Estimations of the relative abundance are indicated with p = predominant (> 20%), f = frequent (5 - 20%), c = common (1 - 5%), r = rare (<1%), and - = absent (0%).*

Species code	Taxon	Month			
		May	June	August	September
Achnseve	Unidentified *Achnanthes* species	r	r	r	r
Achntwel	Unidentified *Achnanthes* species	f	-	-	r
Achricul	*Achnanthes ricula* Hohn and Hellerman	p	f	c	r
Achspone	Unidentified *Achnanthes* species	f	f	r	r
Acofbore	*Amphora coffaeformis* var. *borealis* (Kützing) Cleve	r	c	r	r
Amphfour	Unidentified *Amphora* species	r	c	r	r
Berkeone	*Berkeleya rutilans* (Trentepohl) Grunow	-	r	c	f
Cplaceug	*Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve	c	c	f	c
Cpulchel	*Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round	c	c	r	r
Cscuparv	*Cocconeis scutellum* var. *parva* Grunow ex Cleve	f	f	r	r
Cscutell	*Cocconeis scutellum* Ehrenberg	-	-	r	c
Fragexig	*Fragilaria exigua* Grunow	r	r	c	c

Table 8. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Frellipt	*Fragilaria elliptica* Schumann	r	c	c	c
Gexigua	*Gomphonemopsis exigua*(Kützing) Medlin	c	r	c	c
LinNavic	Unidentified *Navicula* species	f	f	c	f
Melosone	Unidentified *Melosira* species	-	c	r	r
Navduerr	*Navicula duerrenbergiana* Hustedt	-	r	r	c
Navfiftn	Unidentified *Navicula* species	-	-	r	-
Navicone	Unidentified *Navicula* species	r	c	r	c
Navictwo	Unidentified *Navicula* species	r	r	c	c
Navpermi	*Navicula perminuta* Grunow	f	f	c	f
Nitacicu	*Nitzschia acicularis* (Kützing) W. Smith	-	-	f	f
Nitagnit	*Nitzschia agnita* Hustedt	r	c	r	c
Nitangul	*Nitzschia angularis* Smith	-	-	r	c
Nitdissi	*Nitzschia dissipata* (Kützing) Grunow	r	r	p	c

Table 8. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Nithrtwo	Unidentified *Nitzschia* species	r	c	r	r
Nitpalea	*Nitzschia palea* (Kützing) W. Smith	r	c	c	f
Nitsigma	*Nitzschia sigma* (Kützing) W. Smith	-	r	c	r
Nitsocia	*Nitzschia socialis* Grunow	-	-	r	f
Nittwthr	Unidentified *Nitzschia* species	c	c	r	c
Nitzfive	Unidentified *Nitzschia* species	-	-	f	r
Nitzsvtn	Unidentified *Nitzschia* species	r	r	c	r
Nitzthir	Unidentified *Nitzschia* species	c	c	r	c
Pennasix	Unidentified pennate diatom	r	r	r	r
Pennseve	Unidentified pennate diatom	r	c	c	r
Sfascicu	*Synedra fasciculata* (Agardh) Kützing	r	c	f	f

APPENDIX C

SUMMARY OF SPECIES ABUNDANCES AT THE VAL SITE

Table 9. *Summary of the mean relative abundance of common species (only those species included in the ordination analyses in Chapter II) in 14 day old treatment samples collected at the VAL site during the 1996 growing season. Estimations of the relative abundance are indicated with p = predominant (> 20%), f = frequent (5 - 20%), c = common (1 - 5%), r = rare (<1%), and - = absent (0%).*

Species code	Taxon	Month			
		May	June	August	September
Achnseve	Unidentified *Achnanthes* species	r	r	r	r
Achntwel	Unidentified *Achnanthes* species	r	-	-	-
Achricul	*Achnanthes ricula* Hohn and Hellerman	c	c	r	r
Achspone	Unidentified *Achnanthes* species	c	c	-	r
Acofbore	*Amphora coffaeformis* var. *borealis* (Kützing) Cleve	r	r	r	r
Amphfour	Unidentified *Amphora* species	r	r	r	r
Berkeone	*Berkeleya rutilans* (Trentepohl) Grunow	r	f	c	c
Cplaceug	*Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve	c	r	c	c
Cpulchel	*Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round	-	r	-	-
Cscuparv	*Cocconeis scutellum* var. *parva* Grunow ex Cleve	f	c	c	c
Cscutell	*Cocconeis scutellum* Ehrenberg	c	r	r	c
Fragexig	*Fragilaria exigua* Grunow	c	r	r	c

Table 9. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Frellipt	*Fragilaria elliptica* Schumann	c	c	c	c
Gexigua	*Gomphonemopsis exigua*(Kützing) Medlin	f	r	c	r
LinNavic	Unidentified *Navicula* species	f	f	c	c
Melosone	Unidentified *Melosira* species	r	r	r	r
Navduerr	*Navicula duerrenbergiana* Hustedt	c	f	f	f
Navfiftn	Unidentified *Navicula* species	-	-	c	r
Navicone	Unidentified *Navicula* species	r	c	c	c
Navictwo	Unidentified *Navicula* species	r	r	c	r
Navpermi	*Navicula perminuta* Grunow	f	f	f	f
Nitacicu	*Nitzschia acicularis* (Kützing) W. Smith	-	-	c	r
Nitagnit	*Nitzschia agnita* Hustedt	r	c	r	c
Nitangul	*Nitzschia angularis* Smith	r	r	r	c
Nitdissi	*Nitzschia dissipata* (Kützing) Grunow	c	f	c	r

Table 9. *Continued.*

Species code	Taxon	Month			
		May	June	August	September
Nithrtwo	Unidentified *Nitzschia* species	r	r	f	c
Nitpalea	*Nitzschia palea* (Kützing) W. Smith	r	c	c	c
Nitsigma	*Nitzschia sigma* (Kützing) W. Smith	-	r	-	r
Nitsocia	*Nitzschia socialis* Grunow	-	r	r	r
Nittwthr	Unidentified *Nitzschia* species	c	c	r	c
Nitzfive	Unidentified *Nitzschia* species	-	-	-	-
Nitzsvtn	Unidentified *Nitzschia* species	r	r	c	r
Nitzthir	Unidentified *Nitzschia* species	f	f	c	c
Pennasix	Unidentified pennate diatom	r	r	r	c
Pennseve	Unidentified pennate diatom	r	r	r	r
Sfascicu	*Synedra fasciculata* (Agardh) Kützing	f	f	p	p

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