AN ABSTRACT OF THE THESIS OF

Nanette Clark Cardon for the degree of Master of Science in Botany presented on May 18, 1981.

Title: Effect of nutrient enrichment on marine benthic diatoms in Yaquina Bay, Oregon

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Abstract approved by: ___

Dr. Harry K. Phinney

Sediment was fertilized with f/2 algal growth medium in situ and in the laboratory daily for one week. Sampling strategy incorporated two intertidal heights and two sites. Experiments were done in August and January. No significant changes in chlorophyll a or diatom community structure were observed after ten days of growth in either the field or the laboratory experiments. Laboratory experiments also showed slightly increased gross primary production ($p < .10$) and increased oxygen uptake ($p < .01$) associated with nutrient enrichment.

Unlike planktonic diatoms, sediment-associated diatoms in Yaquina Bay show no nutrient limitation. Thus other factors probably control diatom growth in these sediments such as light intensity, photoperiod, intertidal height, sediment stability and organic content, and animal consumption.

Effect of Nutrient Enrichment on Marine Benthic Diatoms in Yaquina Bay, Oregon

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EFFECT OF NUTRIENT ENRICHMENT ON MARINE BENTHIC DIATOMS IN YAQUINA BAY, OREGON

I. INTRODUCTION

Several studies have been completed concerning the distribution and ecology of marine benthic diatom assemblages of Yaquina Bay, Oregon. Environmental gradients of exposure time, salinity and day length interact with the species pool of benthic marine diatoms. Patterns of community structure and function are formed by these interactions. Some factors which influence diatom community structure and function are exposure time (McIntire and Overton, 1971), taxonomy and distribution (Riznyk, 1973; Amspoker, 1978), salinity (Martin, 1970), primary productivity (Wulff and McIntire, 1972) and community function and infaunal interactions (Davis and Lee, unpublished; Riznyk and Phinney, 1972).

The effect of nutrient addition to these assemblages remains to be determined. With increasing development of the Yaquina Bay area, the addition of nutrient-containing wastewater from domestic and industrial sources make it opportune to determine the possible role of nutrient addition to diatom growth. Determining the role of nutrient addition in part helps answer the larger

question, i.e. what controls benthic diatom growth? Controlling factors could be nutrients, photoperiod, light intensity, herbivory, or an interaction of these factors. This study addresses itself to the question: Are the marine benthic diatom assemblages of Yaquina Bay nutrient limited?

Previous work suggests response of some marine benthic flora to fertilization (Valiella et al., 1973; Van Raalte et al., 1976a; Van Raalte et al., 1976b; Darley, in press). However this work was done in salt marsh systems of the east coast. Influence of the nutrient uptake of the vascular plants, and differences in flora and associated fauna may make these results inapplicable to Yaquina Bay. Other enrichment experiments on the east coast involved monthly pulses of nutrients over a period of months (Sullivan and Daiber, 1975; Sullivan, 1976). Addition of high concentrations of nutrients presents the possibility of toxic effects on the diatom assemblages. Therefore I proposed smaller, more constant dosages of nutrients over a shorter period of time.

Experiments were proposed using sites having different sediment characteristics, exposure times, and included effects of season to evaluate the possibility that nutrient addition could stimulate diatom growth. Sufficient ranges

of conditions were included in these experiments to increase the probability of detecting any response to nutrient addition.

Toxic effects of nutrients were discussed by Admiraal (1977a) who found 0.04 mM NH_3-N inhibited growth of all benthic diatom species cultured. The highest concentrations of NO_3-N (1.21 mM) and NO_2-N (3.57 mM) inhibited only some species of benthic diatoms. The highest concentrations of phosphate (0.3 mM) inhibited benthic diatom cultures only slightly. My intention was to provide a nutrient environment adequate for diatom growth, if the diatom assemblage was nutrient limited, yet low enough in concentrations to remain non-toxic if the diatom assemblages were not nutrient limited.

Nutrients must be added during periods of intertidal exposure (2-6 hours). Therefore nutrient enrichment is short term only. Examples of nutrient uptake kinetics of diatoms in the literature are dominated by studies of planktonic forms (Wallen and Cartier, 1975; Nelson et al., 1976; Collos and Slawyk, 1979). These kinetics indicate that short term nutrient enrichment would be adequate to remove nutrient limitation.

Previous workers have used chlorophyll a as an indicator of change in benthic community biomass (Steele and

Baird, 1968; Fenchel and Straarup, 1971; Valiella et al., 1973; Estrada et al., 1974; Sullivan, 1975). However there is an inherent lag time between nutrient uptake by nutrient limited cells of an assemblage, and measurable change in pigment concentration. Hypothetically two processes would be occurring. First, nutrients taken up would be processed by existing cells in the community, and after some time the nutrient would enter into synthesis of chlorophyll a. Second, the diatom community structure would be changing in the more nutrient rich environment. Those taxa readily adaptable to nutrient enrichment would become dominant while those taxa adapted to low nutrient concentrations would tend to decrease in relative abundance. Chlorophyll a analysis could provide indication of overall change in community biomass. Community structure analysis identifies specific responses to nutrient addition by changes in relative abundance of taxa.

Each factor influencing algal growth can potentially limit growth. Factors which have been shown to be of vital importance to algal growth are light intensity, photoperiod, type of substrate, grazing, and nutrients. Algal inter- and intraspecific competition arises as a response to the interaction of these factors.

Limitation of light due to seasonal and physical

factors was cited by Admiraal (1979). This occurs due to shorter photoperiod and lower light intensities in winter. Limitation of light was also due to infaunal movement "burying" algal cells beneath the photic zone of the sediment. Pamatmat (1968) and Leach (1970) both found a high correlation of levels of primary productivity with the amount of available solar radiation. More relevant to my experiments, Estrada (et al., 1974) found the amount of algal chlorophyll was affected more by the decreased light levels due to Spartina growth in fertilized plots than by the addition of nutrients themselves. Sullivan (1975, 1976) cites limitation of light resulting from growth of Spartina as a major factor in the east coast salt marshes. Many benthic diatoms have exhibited active migration as a means of more efficient use of the existing light. Fenchell and Straarup (1971) discuss migration of diatoms downward thus preventing photoinhibition. Other research, including Baillie and Welsh (1980) and Pomeroy (1959) have observed upward migration of diatoms toward light, in a persistent diurnal rythym (Round and Eaton, 1966; Round and Palmer, 1966).

Physical factors include temperature, salinity and exposure time. Admiraal (1977a; 1977b) and Pomeroy and Stockner (1976) address physical factors, as do papers

regarding the Yaquina Bay system discussed earlier. Research by Baillie and Welsh (1980) and Roman and Tenore (1978) evaluated tidal resuspension and scouring in terms of chlorophyll *a* and C_{14} primary production. This breakdown of the "biphasic nature of the sediment-water interface" would have a great impact on the community import-export processes.

Substrate type influences both colonization of primary space by epipsammic diatoms and migration of epipelic forms. The available primary space of a sand grain is much less than the mean surface area. Personal observation, and observations of Meadows and Anderson (1968) and Amspoker (1978) show that the epipsammic forms cluster in concave grain surfaces. These areas are less subject to abrasion and may themselves be favorable microhabitats. Grain size and packing would greatly influence sediment stability, which has been positively correlated to standing crop by Moss (1968). Organic content (Jitts, 1959; Barlow *et al.*, 1963) and inorganic chemical composition (Stephanson, 1949) of the sediment itself would influence the nutrient regime of the benthic diatom community (Van Bennekom *et al.*, 1974).

Grazing by herbivores limits growth of algal communities and primary productivity. Cadée and Hegeman (1974) suggested that infaunal interactions may have an influence

on the microphytobenthos and resulting primary productivity of the benthic system. Davis and Lee (unpublished) have demonstrated this effect in Yaquina Bay.

Available nutrients also influence algal growth. The diatom community takes up either inorganic nutrients to be used autotrophically, or organic nutrients to be used heterotrophically. Many benthic diatoms couple migration with heterotrophic ability and adaptive nutrient uptake to make efficient use of the existing nutrient regime (Admiraal, 1979; Pomeroy, 1959; Lewin and Lewin, 1960; Lewin, 1963; Droop, 1973). Toxic concentrations of nutrient elements may limit growth of certain species in the sulphide layer beneath the surface of anaerobic mud. Opinions in the literature are mixed as to the importance of this sulphide factor on community structure (Admiraal and Peletier, 1979; Hopkins, 1964; McIntire and Moore, 1977). The literature regarding nutrient limitation of marine benthic diatoms is dominated by those working on east coast salt marsh systems. Sullivan and Daiber (1975) and Sullivan (1976) found lower diatom species diversity in fertilized plots, and some indicator species became apparent. Valiela (et al., 1973) and Darley (in press) found the benthic diatoms to be nutrient limited. Van Raalte (1976a) also found a greater abundance of dominant species in fertilized plots. It must be stressed that these studies were conducted in a

system dominated by vascular plants. The nutrient uptake of these vascular plants would greatly influence the concentrations of nutrients available to the benthic microalgae.

The uniqueness of each system regarding not only nutrients but all factors affecting growth make generalization between ecosystems difficult. Thus, it is relevant to discern the impact of light, physical factors, sediment type, grazing, and nutrients as they relate to the Yaquina Bay system.

In the context of my study the question then becomes: Among all the factors influencing benthic algal growth, what is the role of nutrients on the marine benthic diatoms of Yaquina Bay?

Yaquina Bay is located on the central Oregon coast at 44° 37' N. latitude. The major channel is formed by Yaquina River. Extensive mudflats and sloughs surround the channel in Yaquina Bay. The bay experiences mixed semi-diurnal tides with a mean tidal amplitude of approximately three meters. During a complete tidal cycle 70% of the estuarine water is exchanged for ocean water (Karentz and McIntire, 1977). In late summer upwelling can occur offshore of this estuary. This nutrient-rich water is readily available to the diatom assemblages of Yaquina Bay due to tidal exchange. During this time, fresh-water runoff and turbulence is

minimal. During the winter months the high discharge of fresh-water by the Yaquina River, in addition to rain, can lower the salinity temporarily to as little as 8^{o}/oo over the flats near Oregon State University Marine Science Center. Additional nutrients are introduced to the system from the discharge of Coast Range runoff by the Yaquina River. More detailed descriptions of the physical and hydrological processes of Yaquina Bay can be found in the works of Burt and Marraige (1957) and Burt and McAlister (1959). The climatic and tidal characteristics are expanded upon in McIntire and Overton (1971), and geomorphology and minerology described in Kulm and Byrne (1966).

II. MATERIALS AND METHODS

Experimental Analysis

Two sites were used during the field experiments. The sediment at Small Boat Dock (SBD) had a mean grain size of 2.42 Φ, and had an organic content of 0.38%. This site is a low energy beach, 2.3 km from the bay entrance (Figure 1). A small fresh-water stream flowed 23 meters from the high intertidal level. The National Aquaculture Laboratory site (NAL) was 3.6 km from the bay entrance. The sediment had a mean grain size of 2.50 Φ and an organic content of 0.96%. Fresh-water influence through ground-water seepage occurred at the high intertidal level.

The top centimeter of sediment was used for both grain size analysis and analysis of organic content (Appendix Table 1). Approximately 50 grams of sediment were sieved using nested sieves according to the method of Buchanan and Kain (1971). Sediment properties were calculated using the Inman equations (Inman, 1952). Concentration of organic matter was determined from sediment cores. Samples were dried at 70°C for 48 hours, then weighed, and ashed at 450° C for 24 hours. Ash-free dry weight was calculated and corrected for water of hydration (Appendix Table 1).

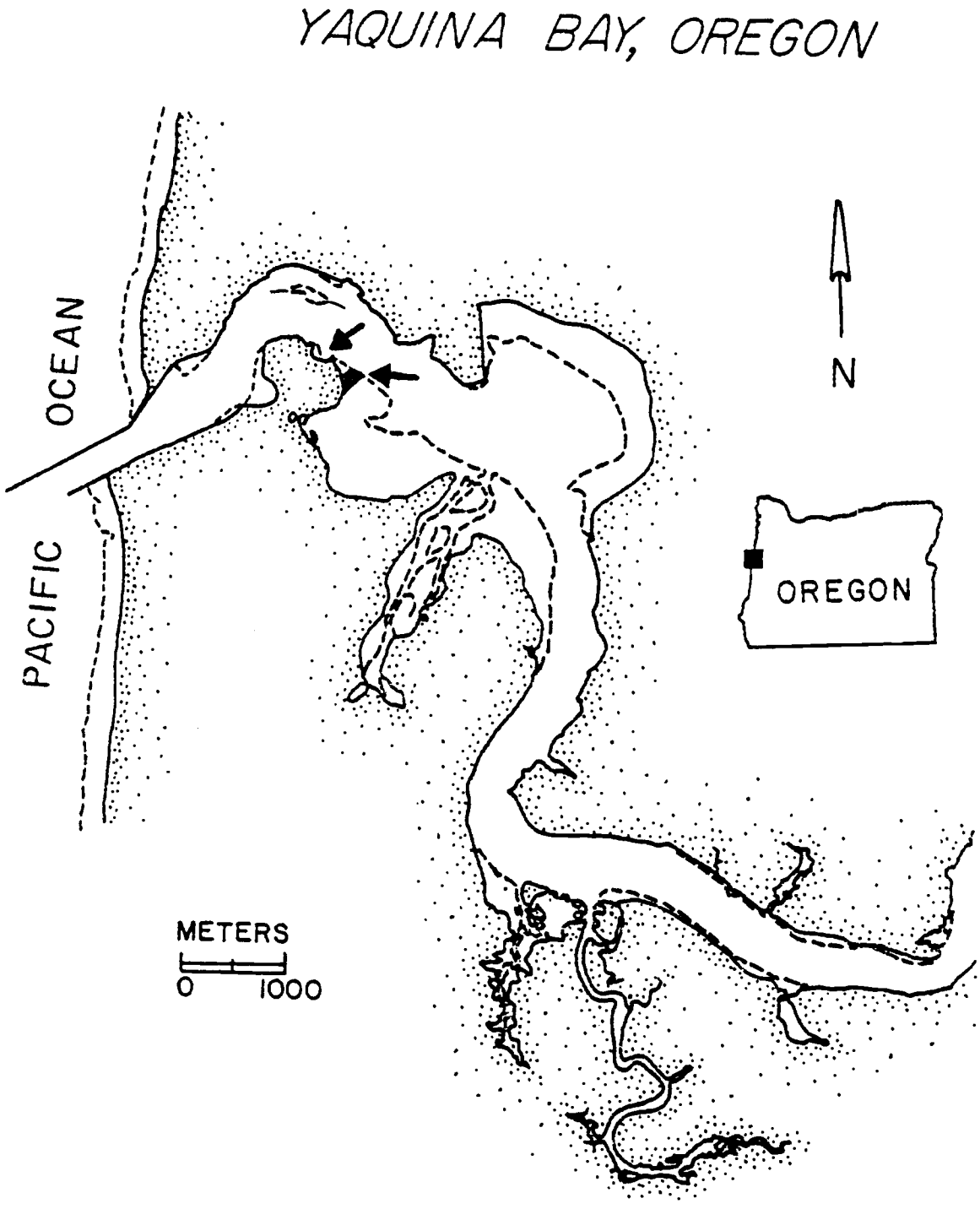

Figure 1. Location of the sampling sites of the field experiment in Yaquina Bay, Oregon. western arrow indicates Small Boat Dock (SBD) eastern arrow indicates National Aquaculture Laboratory (NAL)

Two intertidal levels were studied at both sites. The high intertidal level was 1.9 m above Mean Lower Low Water (MLLW), and the mid intertidal level was 1.2 m above MLLW. The high intertidal levels were exposed approximately twice the number of hours as the mid intertidal levels for the month prior to and including the duration of the field experiments (Table 1). During the experiment in August most of these hours of exposure occurred in the daytime, exposing the sites to relatively high air temperatures. During the field experiment in January, periods of exposure were during the night when the temperature was relatively low. Tidal heights were calculated using the predicted tidal heights of the Oregon State University Marine Science Center 1980-1981 Tide Tables.

Salinities were measured at low tide with a hand refractometer (American Optical Corp.).

Radiation was measured in $uE \cdot m^{-2} \cdot sec^{-1}$ using a Licor. Model 185 light meter.

Temperature was measured with a mercury thermometer. Temperature readings were taken at the time of low tides when the sites were exposed and available for treatment.

Water samples of the incoming tide were taken every other day for nutrient analysis. Samples were taken off the Small Boat Dock at the OSU Marine Science Center and analyzed for concentrations of nitrite plus nitrate,

Table 1. Exposure times of intertidal levels in the field experiments. August exposure times were calculated from 22 July 1980 to 31 August 1980. January exposure times were calculated from 14 December 1980 to 23 January 1981.
Mid = 1.2 m above Mean Lower Low Water (MLLW), datum
High = 1.9 m above MLLW, datum

Site	Total exposure	Light exposure	Dark exposure	% time exposed in light
AUGUST				
Mid	460.5	244.5	216.5	53.0
High	823.0	464.5	358.5	56.4
JANUARY				
Mid	315.5	51.0	264.5	16.2
High	709.0	138.5	570.5	19.5

ammonia, orthophosphate and reactive silicate (Appendix Table 2). Nutrients were analyzed following methods described in Strickland and Parsons (1972).

The field experiments were performed in August and January to compare summer and winter patterns in the diatom assemblages, and to detect any possible change in response to treatment resulting from seasonal differences in the nutrient regime.

The commonly used nutrient solution "f/2" described in Guillard and Ryther (1972) was used as nutrient addition (Table 2). Past studies have indicated that concentrations of nutrients equivalent to those in f/2 are adequate for diatom growth (Goldman and Stanley, 1974; Admiraal, 1977a; Admiraal, 1977b). The f/2 nutrient solution was used as the experimental treatment and filtered seawater as the control.

Two 1.0 m quadrats were located at each intertidal level. The sediment within one quadrat received f/2 nutrient solution, and the sediment within the other quadrat received the filtered seawater control. Initially, replicate areas were chosen randomly within these quadrats. A PVC ring of 7.5 cm diameter was placed on the sediment and within this area two 2.2 cm diameter cores were taken for initial samples before treatment. One of these cores was used for chlorophyll _a_ (CHLR) analysis, and the other for

Table 2. Composition of the nutrient medium, f/2. Guillard and Ryther, 1962.

Compound	Concentration
$NaNO_3$	882.50 uM N
$NaH_2PO_4 \cdot H_2O$	36.25 uM P
$FeCl_2$ + EDTA	11.65 uM Fe
$Na_2SiO_3 \cdot 9H_2O$	107.00 uM Si
Vitamins[1]	
$CuSO_4 \cdot 5H_2O$	0.0390 uM Cu
$ZnSO_4 \cdot 7H_2O$	0.0765 uM Zn
$CoCl_2 \cdot 6H_2O$	0.0425 uM Co
$MnCl_2 \cdot 4H_2O$	0.9150 uM Mn
$Na_2MoO_4 \cdot 2H_2O$	0.0260 uM Mo
Seawater	to one liter

1. Thiamine·HCl, Biotin and B_{12} added in trace amounts: 0.2 mg/liter, 1.0 ug/liter, and 1.0 ug/liter respectively.

analysis of the diatom species composition. A PVC ring of 7.5 cm diameter was placed on the sediment, and 20 ml of f/2 solution (nutrient) or filtered seawater (control) were gently pipetted into the ring once each day for seven days. Six replicate areas were chosen randomly within the quadrats for the final samples. On the tenth day of the field experiments, final samples for CHLR and community analysis were taken using the same sampling method.

CHLR analysis was similar to the method described in Strickland and Parsons (1972). A PVC corer (inner diameter 2.2 cm) was used to take sediment cores. These cores were immediately frozen for later analysis. In the laboratory, the core was thawed, and the upper 1.0 cm was removed and ground in a mortar and pestle with 10 ml 90% acetone (v/v) and a few drops $MgCO_3$. Stray macroalgal filaments were removed, and this slurry was then placed in the cold ($4^{o}C$) and dark for 20-22 hours during which time the pigment was extracted from the chloroplasts. The sample was then decanted, brought up to a uniform 14 ml volume with 90% acetone (v/v) and centrifuged at 4500 rpm for 12 minutes to remove any suspended particles. The supernatant was decanted into a 1 cm light path optical glass cuvette and read with a Perkin and Elmer Model 124D Spectrophotometer at 665 nm. The first reading was the supernatant alone; the second reading was made with the addition of two drops

of 50% HCl (v/v).

The concentration of CHLR ($ug \cdot cm^{-3}$ sediment) was calculated using the Lorenzon equation (Lorenzon, 1967) which corrects for phaeophytin concentrations. Control experiments showed that six replicate cores gave an acceptable coefficient of variation value (25%). CHLR measurements using acetone extraction and correction for phaeophytins are a high estimate of the viable chlorophyll, as this method does not discriminate between viable chlorophyll and chlorophyllides. The method proposed by Whitney and Darley (1979) corrects for this problem but is rather laborious. They estimate that the viable CHLR value from salt marsh mud samples is approximately 80% of the value obtained by acetone extraction.

Analysis of the diatom community structure followed the methods described by Amspoker (1977). Two replicate samples were taken for the preparation of slides for the laboratory experiment. Each sample contained the top 0.5 cm from three 2.2 cm diameter cores. The sediment was boiled 1/2 hour or soaked three days in 50 ml concentrated nitric acid. A small amount of potassium dichromate was added to each sample to enhance breakdown of organic material. Samples were then repeatedly rinsed with distilled water and decanted daily until the wash water was neutral to litmus paper. Permanent mounts were

made using a ratio of 25 ml toluene to 15 g of Cumar® resin. A Zeiss RA research microscope was used at 1250x for identification and counting of diatom species. Relative abundance of each taxon was estimated from a count of 500 cells (McIntire and Overton, 1971). They were counted from 38 slides. The live cell : dead cell ratio was determined by staining the live cells with rose bengal followed by counting all intact frustules at a magnification of 450x in a calibrated counting cell. The following references were used for diatom taxonomy: Amspoker, 1977; Cholnoky, 1968; Cleve, 1894; Hendey, 1964; Hustedt, 1930, 1955; Patrick and Reimer, 1966; Peragallo and Peragallo, 1897; Riznyk, 1969; Van Heurk, 1880.

In the laboratory experiment, samples of sediment in 7.5 cm corers were stoppered to eliminate nutrient seepage. In the laboratory, the cores were incubated in a seawater bath at 24°C for ten days. The salinity was 33°/oo, and the light intensity was 180 $uE \cdot m^{-2} \cdot sec^{-1}$ with a 12 hour light : 12 hour dark photoperiod. The cores were drained and exposed for two hours each day. During this exposure time, the f/2 nutrient solution or filtered seawater (control) was added. Two hours represented the minimum exposure time of sediment in the field experiments. Calculation of rates of nutrient uptake by benthic and planktonic diatoms show that two hours is an adequate time to

satisfy nutrient deficiencies (Wallon and Cartier, 1975; Nelson et al., 1976; Colles and Slawyk, 1979; Sullivan, 1980).

Metabolic measurements during the laboratory experiments were made in stirred light and dark chambers, using changes in oxygen concentration (Strickland and Parsons, 1972). Nutrient addition, CHLR analysis and diatom assemblage analysis were performed as described above.

Data Analysis

The analysis of the chlorophyll data comparing the initial field samples involved small-sample t-tests on the differences of values representing each site, intertidal level, or season. Differences in CHLR were also tested by analysis of variance. CHLR analysis comparing the control and nutrient samples of the field experiment and the laboratory experiment was done using small-sample t-tests on the differences between initial and final sample values. Differences in CHLR were also tested by analysis of variance.

The Information measure H" (Shannon and Weaver, 1949), was used as an expression of community structure. H" represents the relative uncertainty in predicting the species to which a randomly picked individual will belong. A diatom assemblage with greater diversity would exhibit greater H" values.

$$H'' = - \sum_{i=1}^{s} \left(\frac{n_i}{N} \right) \log_2 \left(\frac{n_i}{N} \right),$$

where n_i is the number of individuals in the i-th species, N is the number of individuals in the sample, and s is the total number of species or varieties in the sample. H" is

a biased estimate of H", but with sample sizes of 500 the bias is small (McIntire and Overton, 1971).

Simpson's Diversity Index (SDI) was also used.

$$SDI = 1 - \sum_{i-1}^{s} \left(\frac{n_i}{N} \right)^2$$

where n_i, N and s are defined as in the above equation (Simpson, 1949). It ranges from zero to one. SDI represents the probability that two taxa drawn at random (with replacement) belong to different species.

The niche breadth of each taxon was measured by

$$B_i = \exp \left[- \sum_{r=1}^{Q} \left(\frac{n_{ir}}{N_i} \right) \log_e \left(\frac{n_{ir}}{N_i} \right) \right]$$

where n_{ir} is the number of individuals in the i-th taxon found in the r-th sample, N_i is the total number of individuals in the i-th taxon found in all the samples, and Q is the total number of samples. The range of B_i is from one to Q (Levins, 1968). B_i indicates how evenly a particular taxon is distributed over all the samples.

SIMI was used as an objective measure of similarity between diatom assemblages.

$$SIMI(1,2) = \sum_{i=1}^{s} p_{1i}p_{2i} \Big/ \left(\sum_{i=1}^{s} p_{1i}^2 \sum_{i=1}^{s} p_{2i}^2 \right)^{1/2}$$

where SIMI is the degree of similarity between assemblages one and two, p_{1i} and p_{2i} are the proportion of individuals of the i-th taxon in assemblage one and two respectively, and s is the total number of taxa in the sample (Stander, 1970). If the two communities being compared have no taxa in common, SIMI is zero. If both species composition and relative abundance are equal in the two communities, SIMI has a maximum value of one.

III. RESULTS

The results of the study of the concentrations of CHLR will be reviewed first, followed by results of the study of diatom community structure. Initial samples from the field experiment were analyzed separately first to more clearly distinguish existing environmental patterns from experimental effects.

Chlorophyll a Analysis

Grouping initial samples from both August and January field experiments showed that there was a significant difference ($p < .001$, Table 3) in CHLR values between intertidal levels. The high intertidal samples had greater CHLR values than the mid intertidal samples at both sites, during both seasons (Figure 2).

Comparing sites using initial samples from the August and January field experiments showed that in January, NAL CHLR values were greater than SBD CHLR values ($p < .001$, Table 3). There were no site differences in CHLR values in August. There was a significant seasonal difference in CHLR ($p < .001$, Table 3) due to the influence of the January NAL high intertidal samples.

Table 3. Analysis of variance in the concentration of chlorophyll *a* in the initial field samples. df = (1,40) $\bar{n}$ = 48

FACTOR	F VALUE	p
LEVEL	292.6832	$p < .001$
SITE	175.3975	$p < .001$
SEASON	26.2040	$p < .001$
SEASON • SITE	121.6408	$p < .001$
SITE • LEVEL	10.2689	$p < .005$
SEASON • SITE • LEVEL	71.6390	$p < .001$

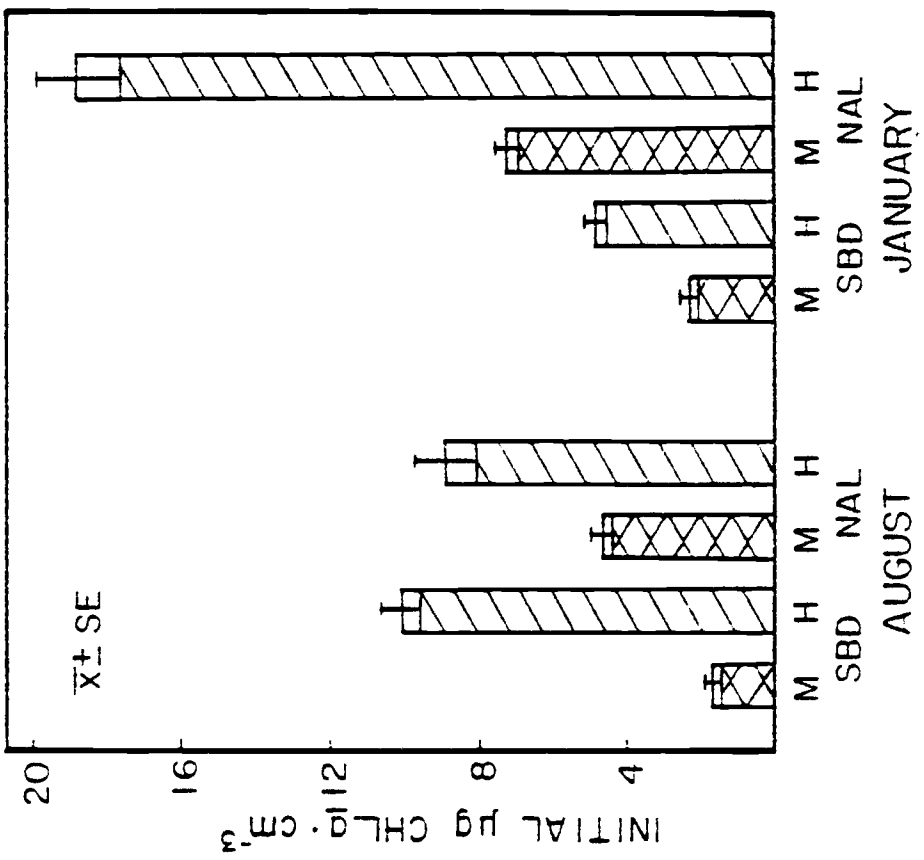

Figure 2. Data from initial samples.
M = mid intertidal level
H = high intertidal level

CHLR data from the field experiment showed no significant effect of the nutrients added. Nutrient response was tested for the following sample sets: August mid intertidal samples, August high intertidal samples, January mid intertidal samples, January high intertidal samples (Figures 3 to 6). Analysis of variance also showed nutrients to be a non-significant factor in all the field experimental data (Table 4).

CHLR showed no response to nutrient enrichment in the laboratory experiment. There was no significant difference between nutrient and control samples for CHLR (Figure 7, Table 5). Gross primary production showed a slightly significant nutrient effect ($p < .10$, Table 5). Oxygen uptake did show a response to nutrient addition. Nutrient addition to sediment produced a significantly greater oxygen uptake rate than in the control sediment ($p < .01$, Table 5). Raw data for the laboratory experiment is listed in Appendix Table 4.

Analysis of Diatom Community Structure

A total of 19,000 cells were counted from 38 samples. These include 16 initial field samples, 16 field experimental samples and 6 laboratory experimental samples. Percent live cells of total cells counted ranged from 56.0% to 73.7%

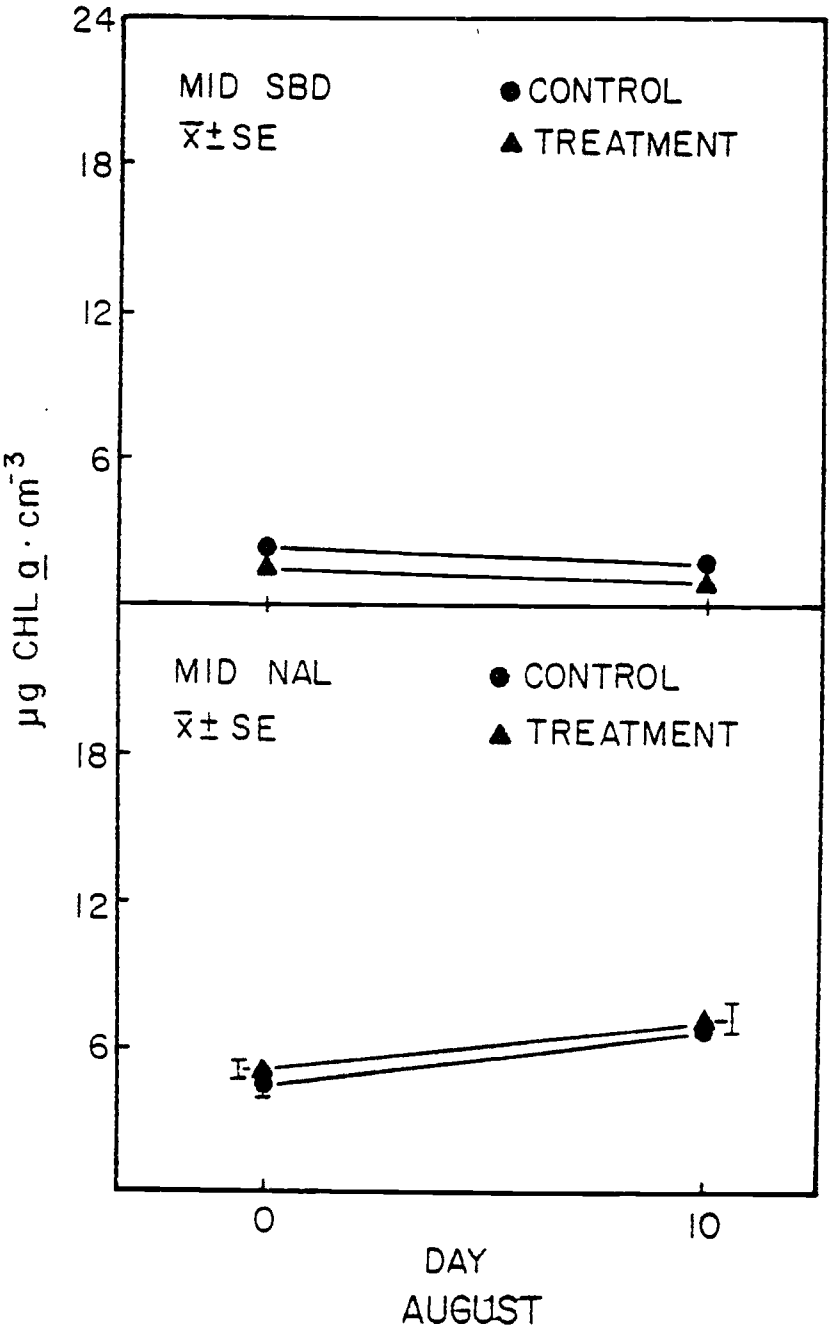

Figure 3. Chlorophyll a data from the samples of the field experiment.
Control (filtered seawater)
Treatment (nutrient solution, f/2)

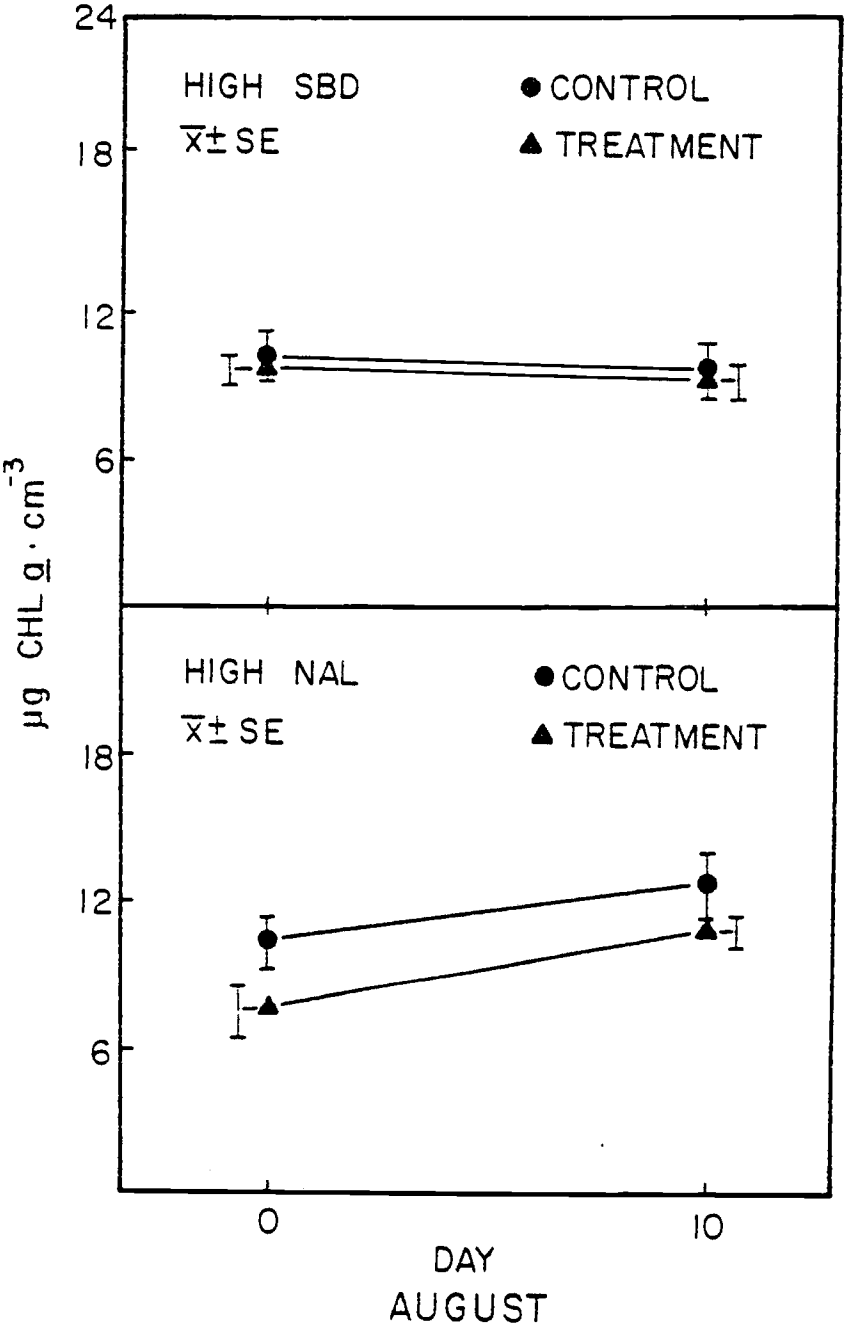

Figure 4. Chlorophyll a data from the samples of the field experiment.
Control (filtered seawater)
Treatment (nutrient solution, f/2)

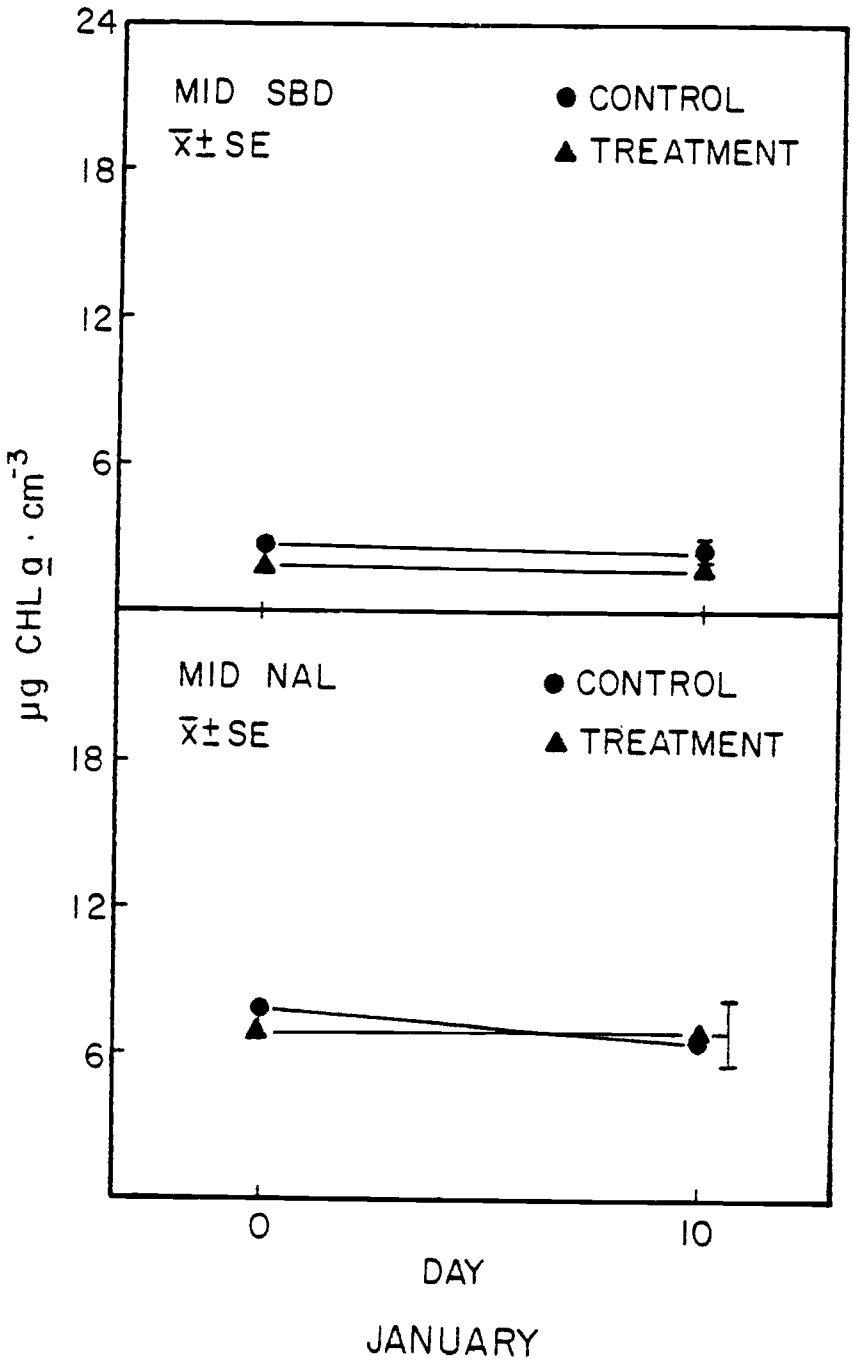

Figure 5. Chlorophyll a data from the samples of the field experiment.
Control (filtered seawater)
Treatment (nutrient solution, f/2)

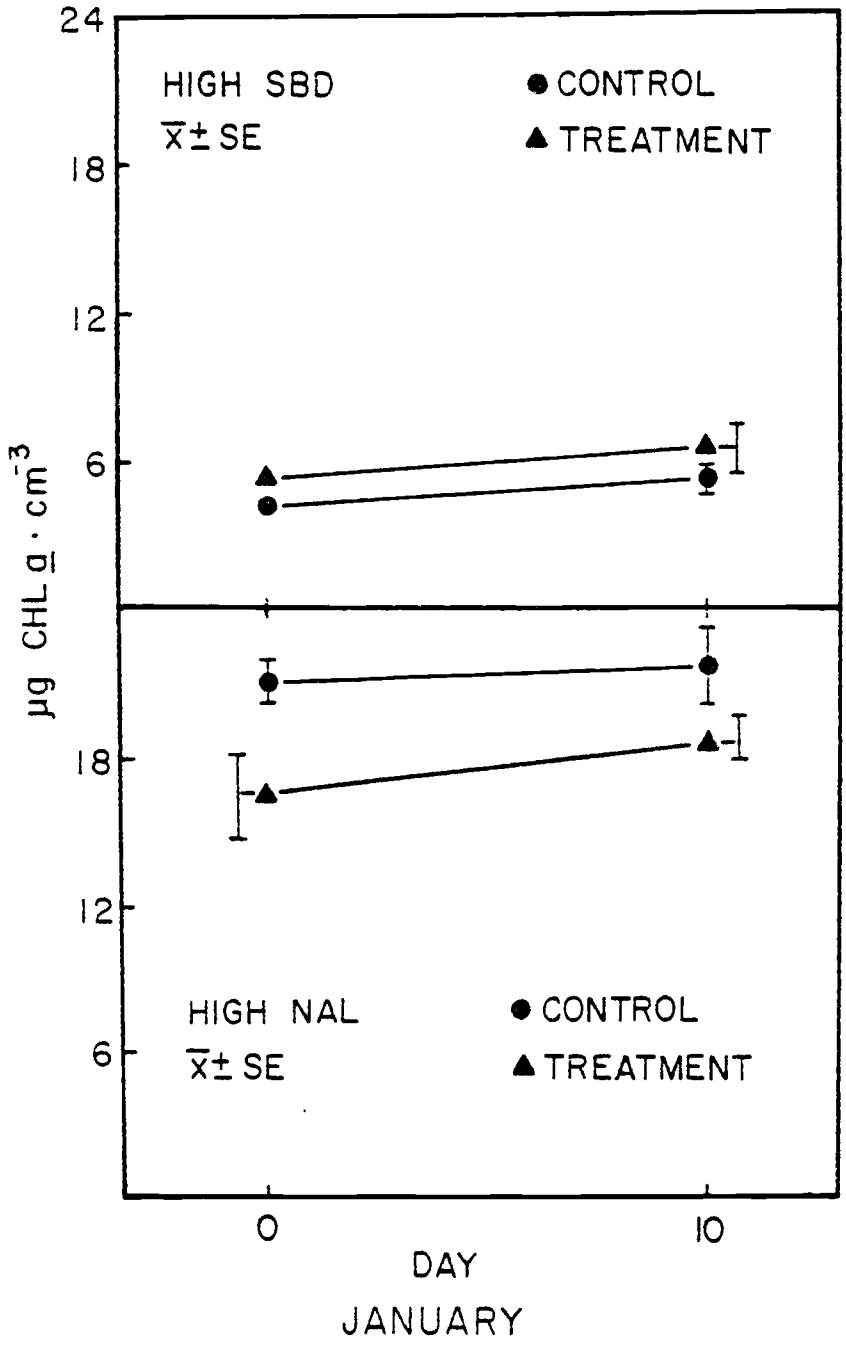

Figure 6. Chlorophyll a data from the samples of the field experiment.
Control (filtered seawater)
Treatment (nutrient solution, f/2)

Table 4. Analysis of variance in the concentrations of chlorophyll *a* in the field experiment.
df = (1,40) n = 48

AUGUST MID INTERTIDAL

FACTOR	F VALUE	p
SITE	210.9370	$p < .001$
TIME	13.6990	$p < .001$
TIME • SITE	17.7824	$p < .001$

AUGUST HIGH INTERTIDAL

FACTOR	F VALUE	p
TIME • SITE	7.1173	$p < .025$

JANUARY MID INTERTIDAL

FACTOR	F VALUE	p
SITE	364.6159	$p < .001$

JANUARY HIGH INTERTIDAL

FACTOR	F VALUE	p
SITE	377.5655	$p < .001$
TREATMENT • SITE	11.8588	$p < .005$

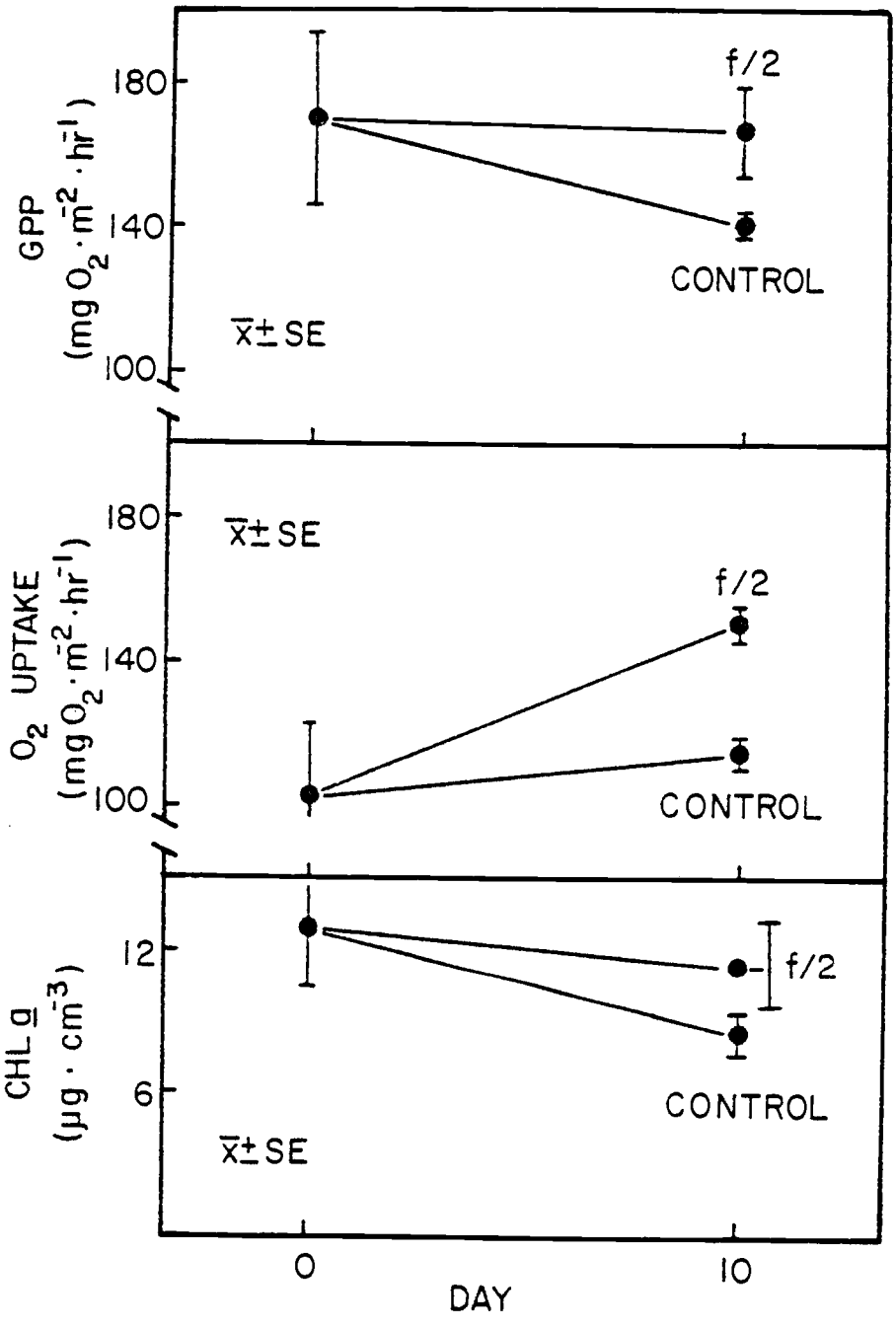

Figure 7. Laboratory experiment data.
CHL a = chlorophyll a
O_2 UPTAKE = oxygen uptake
GPP = gross primary production

(Table 6).

From the field experiment initial and final samples there were 208 taxa. 65 taxa (31.9%) were represented by only one individual. There were 142 taxa, or 69.6% were represented by less than ten individuals. Of these 208 taxa, 68 were not possible to identify to species using available literature. Many of these however, were described by Amspoker (1977) in his work on the sediment-associated diatoms of Yaquina Bay. Taxa and abundances are listed in Appendix Tables 5 and 6.

Analysis of the initial samples will be described first, followed by results of the field experiment, and the laboratory experiment.

Seven taxa each accounted for 3% or more of the individuals counted from the initial field samples. The dominant taxa were Achnanthes hauckiana, representing 30.0% of all individuals counted, and Cocconeis placentula representing 17.3%. These were followed by Navicula gregaria (12.0%), Nitzschia fundi (5.9%), Opephora pacifica (4.6%), Achnanthes lemmermanni (4.5%), and Amphora tennerimma (3.0%).

There was a significantly greater abundance of Cocconeis placentula in the mid intertidal samples ($t = 2.49$, $p < .05$). High intertidal samples had a significantly higher proportion of Nitzschia fundi ($t = 2.47$, $p < .05$).

Table 5. Significance levels of the laboratory experiment t-tests.
$Ho = u_c - u_{f/2} = 0$
$Ha = u_c - u_{f/2} \neq 0$

FACTOR	t	df	p
OXYGEN UPTAKE	-4.71	4	$p < .01$
GROSS PRIMARY PRODUCTION	-2.18	4	$p < .10$
CHLOROPHYLL *a*	-1.45	4	not significant

Table 6. Percentage of live cells in total cells counted. df = 2

SITE	$\bar{x} \pm s$	coefficient of variation
SBD MID	73.7 ± 2.5	3.4%
SBD HIGH	68.7 ± 13.0	18.9%
NAL MID	56.0 ± 3.6	6.4%
NAL HIGH	71.7 ± 8.3	11.6%

Fragilaria striatula v. californica and Nitzschia frustulum v. perpusilla showed greatest niche breadth with respect to intertidal level. The pooled diatom assemblages as a whole had a SIMI value = .705 (Table 7). This may be broken down further by site and season. At SBD, August mid intertidal samples had an average SIMI of .763 while this was .869 in January. At NAL the SIMI was lower, averaging .152 in August and .469 in January (Table 7).

Achnanthes lemmermanni ($t = 3.15$, $p < .01$), Navicula gregaria ($t = 5.25$, $p < .001$), and Nitzschia fundi ($t = 2.39$, $p < .05$) showed a significantly greater abundance at SBD. Cocconeis placentula had a significantly greater proportion of individuals at NAL ($t = 2.86$, $p < .02$). Nitzschia frustulum v. perpusilla had the greatest niche breadth with respect to site. SIMI value for SBD assemblages compared with NAL assemblages was .692. The assemblages may also be compared on the basis of season and intertidal levels. Comparing mid intertidal assemblages between SBD and NAL gave an average SIMI of .189, and .442 for August and January respectively. High intertidal comparisons gave an average of SIMI of .604 and .801 for August and January respectively (Table 7).

One taxon showed a discrepancy in seasonal abundance. A significantly greater proportion of Opephora pacifica occurred in August ($t = 2.54$, $p < .05$). Navicula cincta

and Synedra tenera v. tenera showed high niche breadth values with data pooled as to season. These two taxa however, were represented by a total of only six and four individuals respectively. The SIMI value comparing August assemblages with January assemblages was .926 (Table 8).

Community structure determined in the initial field samples showed high values for Simpson's Diversity Index (SDI), ranging from 0.520 to 0.878. The lower values of this range occurred at NAL. Information measure H" ranged from 1.98 to 3.96 with the lower values again occurring at NAL. Number of species observed per sample of 500 cells ranged from 23 to 57 (Table 9).

In the field experiment there was no response of the diatom community structure to nutrient enrichment. Small-sample t-tests were done comparing relative abundances of individual taxa from control and f/2 samples. None of the taxa at either SBD or NAL showed significant effect of nutrients. SIMI values comparing assemblages from control and f/2 samples of the field experiment were very high. SBD values ranged from .878 to .993, NAL SIMI values ranged from .971 to .994. Overall value when comparing all control assemblages with all f/2 assemblages was .978 and .995 for SBD and NAL respectively. No effect of enrichment on assemblage similarity was evident.

The assemblages from the laboratory experiment com-

Table 7. SIMI values of initial field sample comparing intertidal levels at each site, and comparing sites at each intertidal level. SIMI value listed is an average of four values.

	AUGUST	JANUARY
SBD MID : SBD HIGH	.763	.869
NAL MID : NAL HIGH	.152	.469
pooled MID : HIGH SIMI = .705		
SBD MID : NAL MID	.189	.442
SBD HIGH : NAL HIGH	.604	.804
pooled SBD : NAL SIMI = .692		

Table 8. SIMI values of initial field samples comparing August and January samples at each intertidal level at each site. SIMI value listed is an average of four values.

SAMPLE	SIMI
SBD MID AUGUST : SBD MID JANUARY	.907
SBD HIGH AUGUST : SBD HIGH JANUARY	.827
NAL MID AUGUST : NAL MID JANUARY	.916
NAL HIGH AUGUST : NAL HIGH JANUARY	.905
pooled AUGUST : JANUARY SIMI = .926	

Table 9. Diversity indices of the initial field samples.

C = Control M = Mid intertidal
f/2 = Nutrient H = High intertidal
A = August
J = January

SITE	SAMPLE	H"	SDI	No. species observed
SBD	C MA	3.465	.8194	49
	f/2MA	3.958	.878	57
	C HA	3.058	.821	28
	f/2HA	3.174	.843	25
	C MJ	3.275	.782	41
	f/2MJ	3.365	.777	42
	C HJ	2.995	.729	36
	f/2HJ	3.503	.850	42
NAL	C MA	2.102	.520	26
	f/2MA	1.979	.520	23
	C HA	3.142	.808	29
	f/2HA	2.838	.741	15
	C MJ	3.358	.806	42
	f/2MJ	3.326	.791	40
	C HJ	2.252	.592	25
	f/2HJ	2.621	.663	29

prised comparable number of species observed, H" and SDI values to those in samples from the field experiment. Relative abundances were tested comparing control and f/2 assemblages of the laboratory experiment using small-sample t-tests. There was no significant difference in relative abundance for any taxa.

SIMI values for all assemblages in the laboratory experiment ranged from .944 to .986 (Table 10). With the abundance values of the replicate samples pooled the SIMI values were even higher; .980 to .985 (Table 11).

Coefficient of variation using replicates of the laboratory experiment was calculated for abundances of dominate taxa. The range of the coefficient of variation was 1.8% to 39.0%, with an average of 16.3%. Taxa and abundances are listed in Appendix Tables 7 and 8.

Table 10. Laboratory experiment SIMI values.
(1) initial rep. 1
(2) initial rep. 2
(3) control final rep. 1
(4) control final rep. 2
(5) f/2 final rep. 1
(6) f/2 final rep. 2

	(1)	(2)	(3)	(4)	(5)	(6)
(1)	1.000					
(2)	.985	1.000				
(3)	.965	.954	1.000			
(4)	.981	.983	.975	1.000		
(5)	.971	.957	.986	.982	1.000	
(6)	.970	.965	.944	.968	.958	1.000

Table 11. Laboratory experiment SIMI values with replicate samples pooled.
(1) initial
(2) control final
(3) f/2 final

	(1)	(2)	(3)
(1)	1.000		
(2)	.980	1.000	
(3)	.980	.985	1.000

IV. DISCUSSION

Chlorophyll a

Initial field samples showed significant influence of intertidal level at both sites during both August and January ($p < .001$). Some possible reasons for the greater CHLR values of the high intertidal samples could be: 1) higher temperatures of the sediment resulting in increased metabolic rates, 2) higher light intensity resulting in increased photosynthetic activity, 3) possible decrease in grazing pressure, and 4) greater sediment stability. The mid intertidal quadrat at SBD experienced sediment erosion in January. This was due to increased wave action and rainfall at the end of the sampling period.

In general, comparing sites, NAL had greater CHLR values than SBD ($p < .001$). This is probably a response to differing sediment type. Both sites had comparable grain size and distribution, but the organic content of the NAL sediment was greater ($t = 3.68$, $p < .005$, Appendix Table 1). This increases effective size of silt particles (Jitts, 1959) and enhances auto- and heterotrophic growth (Admiraal, 1979).

The field experiment showed no significant effect of added nutrients for either intertidal level, at either

site, for either season. Thus within the experimental range of exposure time, sediment character and season there was no response of benthic diatoms to nutrient enrichment.

Two relevant questions are apparent. First, was the nutrient enrichment solution flowing past the surface sediment and out of the monitoring system. If this was occurring, the added nutrients were not remaining in contact with the flora being sampled. Second, possibly the nutrients were being taken up by the algal cells, but the cells were being resuspended during the subsequent tidal flood and exported out of the monitored system. Thus a laboratory experiment was designed to eliminate the factors of nutrient seepage and tidal resuspension.

CHLR data from the laboratory experiment showed no significant effect of nutrient addition with the possibility of either nutrient seepage and tidal resuspension eliminated. Gross primary production showed a decrease of borderline significance in the control samples ($p < .01$). Oxygen uptake showed a significant increase in the f/2 samples ($p < .01$). This may be due to an increase in denitrifying bacteria stimulated by added nitrate. It may also be due in part to increased chemical oxygen demand of the sediment due to addition of nutrients.

Diatom Community Structure

Analysis of the initial field samples showed high diversity of the sediment-associated diatom assemblages. The H" and SDI values were found to be slightly lower than in other studies of benthic diatom assemblages. Amspoker (1977) found a comparable SDI range (.794-.915), yet his Information measure (H") average was .407. The average H" of my initial samples was 3.02. The H" values of this study was also found to be slightly lower than those obtained by Sullivan (1975). The greater diversity of the assemblages in these studies could result from the wider range of habitat included in their sampling strategy. A high diversity seems typical of sediment-associated assemblages (Amspoker, 1977; Van Raalte et al., 1976a; Sullivan, 1976). The marine benthic diatoms have adapted both physiological and behavioral means to maintain a more stable environment within the highly variable intertidal environment. The sediment itself offers very diverse and patchy microhabitats which can supply many ecological niches for the benthic flora.

Contamination also is a factor in analyzing the taxonomy of the benthic flora. Planktonic forms can enter the estuary with the flood tide and together with the resident

planktonic forms can settle out of the water column onto the sediment. Settling of resuspended epiphytic, epilithic and imported benthic forms also occurs. When analyzing community structure it is assumed the contamination contributes few species of low abundance and therefore does not influence the parameters as a whole. The assumption of negligible influence of contamination upon community structure analysis is considered more desirable than the ambiguity of live-cell identification. It has been found that in the live state, especially if the cell is upon an organic substrate, striation of the frustule is very difficult to count (Hendey, 1964; Round, 1971; Mare, 1942; Smyth, 1955). Analysis of community structure using cleared frustules includes both living and dead cells, imported as well as cells which grew in situ. With these constraints in mind, counting cleared frustules is used more as a workable compromise to defining community structure patterns than as a definitive end in itself.

The dominant species by far in all samples was Achnanthes hauckiana. The morphology of this diatom was variable, which may be connected with its broad ecological niche. It has been described as having a wide salinity range, and is indifferent to intertidal level (Patrick and Reimer, 1966; Tropper, 1975).

Calculation of SIMI for taxa pooled by intertidal

height showed dissimilar assemblages between mid and high intertidal levels indicating a response of the diatom community to length of exposure. Though a few taxa showed marked abundance at specific levels, differences in community structure were not as dramatic as the differences in CHLR values. Looking at the sites separately shows that SBD assemblages from mid and high intertidal levels were quite similar. This verifies personal observation of the homogeneity of the substrate at this site. There appears to be discrete mid and high intertidal level assemblages at NAL. This may be due directly to the exposure gradient, or perhaps due to indirect factors. For example, at NAL it was observed that the sediment at the high intertidal level was much more stable than at other sites and levels, being more firmly packed into a crust. More animal (tanaid) activity also was observed at the mid intertidal level (Davis and Lee, unpublished).

Evaluating the effect of site showed analogous patterns. A few taxa were more abundant at specific sites. Comparing each intertidal level separately between sites it appears that the greatest dissimilarity is between the mid intertidal assemblages. SBD and NAL high intertidal level assemblages are more similar.

In general, the mid intertidal level diatom assemblages at the NAL site appear to be more discrete than

any of the other assemblages. It is in this area that tanaid density is greatest, hence grazing pressure is greatest (Davis and Lee, unpublished).

August and January assemblages at both sites and intertidal levels were very similar. The summer experienced relatively stable, moderate temperatures. There was intermittant rainfall and groundwater seepage onto sites minimizing stress from desiccation. The winter was also mild. It was sunny with no period of freezing prior to the sampling period. There was an overall decrease in photoperiod, but not necessarily in light intensity between seasons. It must be assumed that the seasonal differences between benthic diatom assemblages vary from year to year.

In both the field and laboratory enrichment experiments, there was no effect of nutrients shown by any individual taxa or the benthic community as a whole. From both these experiments it can be concluded confidently that there was no response in structure of the diatom community to nutrient enrichment of the sediment.

Diatom Nutrient Regime

Why would the marine benthic diatoms of Yaquina Bay not be nutrient limited? The water column overlying the

benthos undergoes seasonal fluctuations in nutrient concentrations. Specht (1974) discussed a "boundary point" within Yaquina Estuary. Seaward from this point the water has a greater concentration of phosphorous. It was more likely to be nitrogen-limiting to phytoplankton growth except during summer upwelling. From this boundary point, upriver toward the runoff from tributaries, the water was richer in nitrate, nitrite, and silica and had greater potential for supporting phosphate-limiting phytoplankton growth (Karentz and McIntire, 1977; Specht, 1974). This interface between two nutrient regimes moves seasonally within Yaquina Estuary. Increased rain and runoff from tributaries in winter shifts the interface towards the sea. In summer more of the estuary is influenced by incoming seawater of the flood tide. The interface itself is not distinct. Delineation of the boundary of the nutrient regimes would be influenced by flushing hydrography of the tides (Ketchum, 1951) and change in nutrient concentration of the water column due to nutrient uptake by marine plants (Pamatmat, 1968; Engst, personal communication).

Cadée and Hegeman (1974) stated that interstitial water of the sediment was richer in nutrients than the overlying water column. Phosphate can also be released from sediments by wind-created turbulence at the sediment-

water interface (Stephansen, 1949). Phosphate would not be limiting to the microphytobenthos due to the ability of sediments to absorb phosphate (Jitts, 1959) and the regeneration of phosphate from dead organic matter (Smyth, 1955). Bacterial populations release phosphate, nitrate, ammonia (ZoBell, 1946) and vitamins (Frey, 1977). Diagenisis of organic matter may also be a source of trace metals (Frey, 1977).

Inorganic nutrients can be used photosynthetically by the diatom assemblage. Organic nutrients can also be used heterotrophically. The nutritional versatility coupled with the capacity for migration of many benthic diatom species would insure sufficient concentrations for growth in this system.

One must distinguish however between lack of nutrient limitation within a system, and the effects of long-term high concentrations of nutrient waste on that system from domestic and industrial sources.

The chemical content of the input itself must be discerned. Nitrite, nitrate, ammonia and phosphate may not affect the microphytobenthos immediately or directly. But they could very well change the community structure of the benthos (macroalgae, bacteria, infauna), perhaps by increasing organic content of the sediment, or decreasing light levels on the sediment surface, and/or changing

sulphide, oxygen and ammonia concentrations in the sediment (Admiraal and Peletier, 1979). Addition of detergents affect the permeability of cell membranes and are toxic to some algae (Borowitzka, 1972). Free chlorine and chloramine were shown to be algicidal at concentrations of 1.0 mg/liter and 0.1 mg/liter respectively (Specht, 1974).

Although the microphytobenthos was found not to be nutrient limited, the impact of nutrient-containing domestic and industrial wastes should be considered in terms of 1) the nature of the waste, 2) the concentrations of the substances involved, and 3) the hydrology of the affected system. These industrial and domestic wastes could have long-term effects which may ultimately alter community structure and function of the microphytobenthos.

Therefore we can conclude that short-term nutrient additions are not likely to alter the microphytobenthos in Yaquina Bay, but that further experimentation similar to Sullivan (1976) would be most valuable in assessing the impact of chronic nutrient addition. Other factors such as light availability, water-current scouring and grazing are suggested to be the primary controlling factors for assemblages of sediment-associated microalgae.

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APPENDICES

Appendix Table 1. Grain size analysis. Md is phi median diameter, M Φ is the phi mean diameter, $\sigma\ \Phi$ is Inman's sorting coefficient, and $\alpha\Phi$ is Inman's skewness coefficient.

SAMPLE	Md	M	$\sigma\ \Phi$	$\alpha\Phi$	% organic content
SBD M A	2.36	2.36	0.35	-0.01	0.41
SBD M J	2.37	2.56	0.34	-0.03	
SBD H A	2.37	2.36	0.34	-0.03	0.36
SBD H J	2.40	2.42	0.36	0.06	
NAL M A	2.63	2.64	0.34	0.03	1.14
NAL M J	2.56	2.56	0.33	0.00	
NAL H A	2.38	2.37	0.44	-0.03	0.78
NAL H J	2.42	2.44	0.36	0.06	

Appendix Table 2. Analysis of nutrients for the August experimental period. (uM)

Sample	NO_2 + NO_3 ±0.185	ammonia ±0.555	ortho-phosphate ±0.105	reactive silicate ±0.132
Day 1 22 Aug1980	4.8	1.7	0.7	22.4
Day 1 22 Aug1980	4.6	1.7	0.7	23.7
Day 3 24 Aug1980	6.5	1.1	0.8	23.7
Day 3 24 Aug1980	6.5	1.1	0.8	23.7
Day 5 26 Aug1980	6.8	1.1	0.8	23.7
Day 5 26 Aug1980	6.8	1.1	0.8	23.7
Day 7 28 Aug1980	6.7	1.7	0.8	23.7
Day 9 30 Aug1980	6.7	1.7	0.8	22.4
Day 9 30 Aug1980	6.7	1.7	0.8	22.4

Appendix Table 3. Temperatures and salinities during field experimental periods. Temperature °C, Salinity °/oo.

Site	Day 1 22Aug 80	Day 2 23Aug 80	Day 3 24Aug 80	Day 4 25Aug 80	Day 5 26Aug 80	Day 6 27Aug 80	Day 7 28Aug 80
SBD MID							
air temp.	11	10	12	10	10	14	9
sediment temp.	11	10	12	11	10	13	10
interst-tial sal.	25	32	33	32	34	33	26
SBD HIGH							
air temp.	11	10	12	10	10	14	10
sediment temp.	11	10	13	12	11	14	10
intersti-tial sal.	-	-	-	-	-	-	-
NAL MID							
air temp.	11	10	13	10	10	15	11
sediment temp.	10	10	12	12	10	14	12
intersti-tial sal.	33	32	34	32	32	32	33
NAL HIGH							
air temp.	11	10	15	10	10	16	12
sediment temp.	11	11	14	13	12	16	14
intersti-tial sal.	22	30	27	27	32	25	27

Appendix Table 4. Raw data for the laboratory experiment.

	CHLOROPHYLL *a* ug $CHL \cdot cm^{-3}$
TIME	$\bar{x} \pm s$
CONTROL	8.47 ± 1.44
FINAL	11.32 ± 3.08
	GROSS PRIMARY PRODUCTION $mgO_2 \cdot m^{-2} \cdot h^{-1}$
TIME	$\bar{x} \pm s$
CONTROL	139.32 ± 5.25
FINAL	166.65 ± 21.11
	OXYGEN UPTAKE $mgO_2 \cdot m^{-2} \cdot h^{-1}$
TIME	$\bar{x} \pm s$
CONTROL	115.09 ± 9.46
FINAL	151.43 ± 9.46

Appendix Table 5. Benthic diatom taxa from the field experiment. Numberical representation used in Appendix Table 6.

1. Achnanthes brevipes Ag.
2. A. clevei Grun.
3. A. cocconeioides Riznyk
4. A. conspicua A. Meyer
5. A. curvirostrum Brun.
6. A. deflexa Reim.
7. A. delicatula (Kütz) Grun.
8. A. hauckiana Grun.
9. A. lanceolata (Brèb.) Grun.
10. A. lanceolata v. dubia Grun.
11. A. latestriata Riznyk
12. A. lemmermanni Hust.
13. A. oregonensis Riznyk
14. A. wellsiae Reim.
16. Achnanthes b
18. Amphiprora alata Kütz.
19. A. paludosa W. Sm.
20. Amphora coffaeformis Ag.
21. A. exigua Greg.
22. A. helenensis Giff.
23. A. lineolata Ehr.
24. A. ostrearia Brèb.
25. A. ovalis Kütz
26. A. polita Krasske
27. A. sabyii Salah
28. A. staurophora (Castr.)Cl.
29. A. sublaevis Hust.
30. A. tenerrima Al. and Hust.
31. A. turgida Greg.
32. Amphora 16
33. 19
34. a
35. b
36. C
37. c
38. d
39. e
40. f
41. g
42. G
43. h
44. i
45. j
46. k
47. K
48. l
49. m

52. o
53. Anorthoneis eccentrica (Donk.)Grun.
54. Berkeleya rutilans (Trent.) Grun.
55. Biddulphia aurita (Lyngb.) Brèb. and God.
56. Camplyosira cymbelliformis (A.Sch.) Grun. ex V.H.
57. Cocconeis amydrofilum Riznyk
58. C. costata Greg.
59. C. diminuta Pant.
60. C. pediculus Ehr.
61. C. placentula (Ehr.)Cl.
62. C. scutellum Ehr.
63. C. scutellum v. parva (Grun.)Cl.
64. C. thumensis A. Mayer
65. Cocconeis b
66. c
67. d
68. e
69. f
70. g
71. i
72. 5
73. 9
74. 11
75. Coscinodiscus lineatus Ehr.
76. C. sublineatus (Grun.) Rattray
77. Cyclotella stelligera Cl. and Grun.
78. Cylindrotheca closterium (Ehr.) Reimann and Lewin
79. Dimerogramma minor (Greg.) Ralts
80. Diploneis bombus Ehr.
81. D. didyma (Ehr.)Cl.
82. D. elliptica (Kütz) Cl.
83. D. incurvata v. dubia Hust.
84. D. interrupta v. heeri (Pant.) Hust.
85. D. littoralis (Donk.) Cl.
86. D. smithii (Breb.) Cl.
88. Eunotia tenella (Grun.) Hust.
89. Fragilaria striatula v. californica Grun. ex V.H.
90. Gyrosigma fasciola (Ehr.) Griff. and Henfr.
91. G. wansbecki (Donk.) Cl.
92. Gyrosigma a
93. b
94. Hannaea a
95. Hantzchia marina (Donk.) Grun.
96. Hantzchia virgata (Roper) Grun.
97. Licmophora juergensii v. dubia Grun.
98. Licmophora a
99. b

100. c
101. Mastogloia pumila (Grun.) Cl.
102. Melosira dubia Kütz
103. M. moniliformis (Mull.) Ag.
104. M. nummuloides (Dillw.) Ag.
105. M. sulcata (Ehr.) Kutz.
108. Navicula cancellata Greg.
109. N. cancellata v. apiculata Greg.
110. N. capitata v. luneburgensis (Grun.) Patr.
111. N. cincta (Ehr.) Ralfs
112. N. complanatoides Hust.
113. N. complanatula Hust.
114. N. cryptocephala Kütz.
115. N. digito-radiata (Greg.)
116. N. diserta Hust.
118. N. diversistriata Hust.
119. N. eta Cl.
120. N. finmarchica (Cl. and Grun.) Cl.
121. N. granulata Bail.
122. N. gregaria Donk.
123. N. heufleri v. leptocephala (Brèb.ex Grun.) Patr.
124. N. inflexa (Greg.) Ralfs
125. N. majuscula Hust.
126. N. miniscula v. miniscula (Grun.) Patr.
127. N. mutica Kütz
128. N. my Cl.
129. N. normaloides Chol.
130. N. palpebralis Brèb.
131. N. phyllepta Kütz
132. N. portanova Riznyk
133. N. protracta v. protracta Grun.
134. N. pseudony Hust.
135. N. pygmaea Kütz
136. N. salinarum Grun.
137. N. salinicola Hust.
138. N. seminulum Grun.
139. N. seminulum v. radiosa Hust.
140. N. tenelloides Hust.
141. N. tripunctata v. schizemenoides (V.H.) Patr.
142. Navicula lyrate 1
143. 2
144. 3
145. Navicula a
146. b
147. c
148. g
152. 2
154. 49B
155. 54H
156. 77M
157. 7900

159. Nitzschia acuminata (W. Sm.) Grun.
160. N. angularis W. Sm.
161. N. apiculata (Greg.) Grun.
162. N. clausii Hantz.
163. N. closterium (Ehr.) W. Sm.
164. N. dissipata v. media Hantz.
165. N. fonticola Grun.
166. N. fontifuga Chol.
167. N. frustulum Kutz.
168. N. frustulum v. perminuta Grun.
169. N. frustulum v. perpusilla (Babh.) Grun.
170. N. fundi Chol.
172. N. lanceolata W. Sm.
174. N. palea (Kutz.) W. Sm.
175. N. sigma (Kutz.) W. Sm.
176. N. sigmaeformis Hust.
177. N. socialis Greg.
178. N. subhybrida Hust.
179. N. subtilis (Kutz.) Grun.
180. N. thermaloides Hust.
181. Nitzschia a
182. b
222. c
183. d
184. e
185. 2
186. 9
187. 52H
188. Q
189. 63S
190. 65U
191. Opephora pacifica (Grun.) Petit
192. O. schultzii (Brock.) Simon.
193. Plagiogramma brockmanni Hust.
194. P. staurophorum (Greg.) Heiberg
195. P. vanheurkii Grun.
196. Pleurosigma angulatum v. aestuarii (Breb.) V.H.
199. Rhaphoneis amphiceros Ehr.
200. R. minutissima Hust.
201. R. psammicola Riznyk
202. Rhaphoneis l
203. a
204. b
206. d
207. E
208. Skeletonema costatum (Grev.) Cl.
209. Stauroneis anceps Ehr.

210. Stauroneis a
211. Surirella ovata Kutz.
212. Synedra fasciculata (Ag.) Kutz.
213. S. fasciculata v. truncata (Grev.) Patr.
214. S. robusta Ralfs
215. S. tenera v. tenera (W. Sm.) Patr.
216. Thalassionema nitzschioides Grun.
217. Thalassiosira decipens (Grun.) Jorg.
218. Thalassiosira 3A
219. B
220. D
221. Triceratium alternans Bail.
222. Nitzschia c

Appendix Table 6. Diatom taxa abundances from initial field samples. Taxa are limited in numerical order as designated in Appendix Table 5. 500 cells were counted per sample. Number of samples pooled under each heading is in parentheses.

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
1.	1		1		1	1	
2.	12	6	6	11	1		12
6.	72	66	6	3	69	56	16
7.	1	1		1		1	
8.	2396	875	1521	1278	1118	900	1496
11.	1	1		1		1	
12.	361	150	211	276	86	153	208
13.	5	5		2	3		5
16.	4		4		4		4
18.	1	1			1		1
19.	8	4	4	7	1	1	7
20.	1	1		1		1	
21.	5	5		4	1	1	4
22.	11	8	3	4	7		11
23.	5		5	4	1	5	
26.	1	1		1			1
27.	143	110	33	11	132	32	111
28.	4	1	3	1	3	1	3
29.	2	2		2		2	

Taxa i.d.	Total No. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
30.	219	119	100	100	119	131	88
31.	26	17	9	7	19	7	19
32.	65	55	10	28	37	18	47
34.	17	17		16	1	16	1
35.	2	2		2		2	
36.	9	4	5	7	2	6	3
37.	2	2		2		2	
38.	16	6	10	7	9	10	6
40.	24	13	11	24		24	
41.	18	18		12	6	2	16
42.	2	2			2	1	1
43.	1	1		1		1	
44.	5	3	2	5		2	3
45.	4	3	1		4		4
46.	7	7			7	5	2
47.	6	6			6	5	1
48.	3	3		1	2	2	1
49.	5		5		5	5	
53.	2		2		2		2
54.	2	2		2		2	
55.	2	2		2		2	

Taxa i.d. no.	Total cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
56.	2	1	1	2		2	
58.	1	1			1	1	
59.	21	21		8	13	21	
60.	1	1		1		1	
61.	1387	1198	189	140	1247	777	610
62.	1		1	1			1
63.	63	38	26	9	55	3	61
64.	1	1		1		1	
65.	7	7		5	2	2	5
66.	4	4		4			4
67.	16	9	7	16		3	13
68.	1	1		1		1	
69.	1	1			1	1	
71.	1	1			1	1	
72.	1	1		1		1	
73.	2	2		2		2	
74.	1	1		1		1	
75.	7	7		7		7	
76.	1	1		1		1	
80.	7	2	5	5	2	1	6
82.	2		2	1			2

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
83.	2		2	1		1	
84.	1	1		1		1	
85.	1	1		1		1	
86.	1	1		1		1	
88.	3	3			3	1	2
89.	34	17	17	31	3	32	2
90.	3	3		1	2	1	2
91.	1		1		1	1	
92.	29	1	28	1	28	28	1
93.	1		1		1	1	
95.	1	1		1			1
96.	1	1		1			1
97.	1		1		1	1	
98.	2		2	2			2
99.	1	1		1		1	
100.	1	1		1		1	
101.	1		1	1		1	
102.	8	3	5	3	5	1	7
103.	5	1	4	5		2	3
105.	8	6	2	3	5	3	5
109.	1	1		1			1

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
111.	6	4	2	4	2	3	3
112.	28	3	25	28		28	
113.	160	1	159	92	68	129	31
114.	1	1		1		1	
115.	1		1	1		1	
116.	26	16	10	22	4	5	21
118.	48	44	4	12	36	31	17
120.	2		2	2			2
122.	957	467	490	735	222	503	454
123.	23	14	9	7	16	15	8
124.	4	3	1		4		4
125.	1	1		1		1	
126.	1	1		1		1	
127.	1	1			1		1
129.	1		1	1			1
130.	17	17		17		2	15
135.	1	1		1		1	
136.	2		2	2			2
137.	335	80	255	84	251	72	263
138.	14	12	2	2	12	1	13
139.	2		2	1			2
140.	9	7	2		9		9

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
141.	3		3	1			3
142.	195	74	121	103	92	126	69
143.	2		2	2			2
144.	11	1	10	6	5	2	9
145.	4	3	1	3	1	3	1
146.	13	7	6	12	1	4	9
147.	2	1	1	2		2	
152.	5	1	4	5		4	1
154.	2	2		1	1	1	1
155.	7	2	5	7		1	6
156.	1	1			1		1
159.	1	1		1			1
160.	1	1		1		1	
161.	4		4		4	3	1
163.	7	7		6	1	7	
164.	5	5		4	1		5
165.	21	12	9	17	4	6	15
166.	48	23	25	43	5	28	20
167.	1	1			1		1
169.	20	10	10	8	12	7	13
170.	475	50	425	424	51	304	171

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
172.	1		1	1		1	
175.	10		10	1	9	10	
176.	3	2	1	2	1	1	2
177.	1	1		1		1	
178.	1	1		1		1	
179.	1		1	1			1
180.	13	9	4	7	6	1	12
181.	1	1		1		1	
182.	6		6		6	6	
183.	4		4	1	3	3	1
184.	3		3	3			3
185.	4		4		4	4	
188.	1	1		1		1	
189.	4	3	1	4		3	1
190.	L	1			1		1
191.	375	155	220	152	223	272	103
193.	1	1		1			1
194.	1	1			1		1
195.	5	3	2	4	1	2	3
196.	6		6	2	4	5	1
200.	1	1		1			1

Taxa i.d. no.	Total no. cells observed (16)	Intertidal Level		Station		Date	
		M (8)	H (8)	SBD (8)	NAL (8)	1980 22Aug (8)	1981 14Jan (8)
201.	14	12	2	5	9	2	12
202.	2	2		2		2	
203.	2	1	1	1	1	1	1
204.	1		1	1			1
206.	4	3	1		4		4
207.	1	1			1		1
208.	1	1		1		1	
212.	9	9		9		9	
213.	36	15	21	23	13	26	10
215.	4	2	2	4		2	2
216.	3	1	2	1	2		3
217.	4	2	2	3	1	3	1
218.	6	4	2	1	5	1	5
219.	15	10	5	8	7		15
220.	6	4	2	4	2	1	5
222.	4		4		4	1	3

Appendix Table 7. Benthic diatom taxa from the laboratory experiment. Numerical representation used in Appendix 8.

1. Achnanthes deflexa Reim.
2. A. haukiana Grun.
3. A. lemmermanni Hust.
4. Achnanthes a
5. E
6. Amphora proteus Greg.
7. A. sabyii Salah
8. A. tenerrima Al. and Hust.
9. A. turgida Greg.
10. Amphora 16
11. d
12. g
13. h
14. n
15. N
16. Cocconeis costata Greg.
17. C. diminuta Pant.
18. C. placentula v. euglypta (Ehr.) Cl.
19. C. scutellum v. parva (Grun.) Cl.
20. Cocconeis b
21. d
22. Diploneis bombus Ehr.
23. Diploneis a
24. Gyrosigma a
25. Licmophora b
26. Melosira dubia Kütz
27. M. moniliformis (Mull.) Ag.
28. M. sulcata (Ehr.) Kütz
29. Navicula abunda Hust.
30. N. agnita Hust.
31. N. complanatula Hust.
32. N. diserta Hust.
33. N. dissipata v. media (Kutz.) Grun.
34. N. diversistriata Hust.
35. N. gregaria Donk.
36. N. heufleri v. leptocephala (Brèb. ex Grun.) Patr.
37. N. salinicola Hust.
38. N. seminulum Grun.
39. Navicula lyrate 1
40. 6
41. b
42. e
43. f

44. Neidium opaceliniatum Riznyk
45. Nitzschia closterium (Ehr.) W. Sm.
46. N. dissipata v. media Hantz.
47. N. fonticola Grun.
48. N. fontifuga Chol.
49. N. frustulum v. perpusilla (Rabh.) Grun.
50. N. fundi Chol.
51. N. holsatica Hust.
52. N. litteralis Grun.
53. N. sigma (Kütz.) W. Sm.
54. N. sigmaeformis Hust.
55. N. subhybrida Hust.
56. N. subtilis (Kütz.) Grun.
57. N. thermaloides Hust.
58. Nitzschia 52H
59. Opephora pacifica (Grun.) Petit
60. Plagiogramma vanheurkii Grun.
61. Pleurosigma delicatulum W. Sm.
62. Pleurosigma 4A
63. Rhaphoneis psammicola Riznyk
64. Rhaphoneis b
65. c
66. Surirella ovata Kütz.
67. Synedra fasciculata v. truncata (Grev.) Patr.
68. Thalassiosira decipiens (Grun.) Jorg.
69. Thalassiosira 3A
70. D

Appendix Table 8. Diatom taxa abundances from the laboratory experiment. Taxa are listed in numerical order as designated in Appendix Table 7. 500 cells were counted per sample.

Taxa i.d. no.	Total no. cells observed	Initial rep. 1	Initial rep. 2	Control rep. 1	Control rep. 2	f/2 rep. 1	f/2 rep. 2
1.	2		2				
2.	670	126	11	142	111	137	143
3.	28	1	2	3	6	6	10
4.	65	7	10	17	14	11	6
5.	30				2	12	16
6.	14			1	6	5	2
7.	132	34	28	21	17	12	20
8.	235	40	39	39	45	42	30
9.	28	5	6	4	4	3	6
10.	50		7	7	12	13	11
11.	17	6	3	4	3	1	
12.	1			1			
13.	1	1					
14.	5		3		2		
15.	5	5					
16.	1						1
17.	2	2					
18.	769	139	144	100	117	105	164
19.	10	1		1	2	3	3
20.	2	1		1			
21.	1		1				
22.	1	1					
23.	2					2	
24.	28	2	3	10	3	6	4
25.	9	3	4	1		1	
26.	6				3	2	1
27.	1			1			
28.	23	4	2	1	9	6	1
29.	1						1
30.	5				3	2	1
31.	6			6			
32.	18				4	3	11
33.	2					2	
34.	18	2	7	1	3	2	2
35.	277	45	62	52	46	46	26
36.	6	2		2		1	1

Taxa i.d. no.	Total no. cells observed	Initial rep. 1	Initial rep. 2	Control rep. 1	Control rep. 2	f/2 rep. 1	f/2 rep. 2
37.	46	5	5	14	9	5	8
38.	2		2				
39.	4	1					
40.	2			2	1		
41.	2		1			1	
42.	1	1	2				
43.	1						
44.	2	1				1	
45.	8		1				
46.	2		2		5		1
47.	8	2			2		
48.	4		6				
49.	31	3			1	3	
50.	59	8	3	2	12	5	6
51.	4		12	13	14	7	5
52.	3			4			
53.	2			3			
54.	2			1		1	
55.	1					2	
56.	1			1			
57.	1		1				
58.	1	1		1			
59.	156	42	22	24	23	32	13
60.	3				2	1	
61.	8	1	7				
62.	3					2	1
63.	22	2	1	1	6	11	1
64.	3	2			1		
65.	7			1	2	2	2
66.	1	1					
67.	24		1	11	7	2	3
68.	7		1	3	2	1	
69.	11	3	4	3		1	
70.	2				1		1