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DIATOM COMMUNITIES IN A LABORATORY MODEL ECO-
SYSTEM

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Abstract approved:

Dr. C. David McIntire

Effects of light intensity, exposure to desiccation, reduced salinity, and thermal elevation on the functional and structural characteristics of marine benthic diatom communities were investigated in a laboratory model ecosystem and a respirometer chamber.

Measurements of biomass (dry weight and ash-free dry weight) and chlorophyll a were made for each of the communities. Population studies were performed to determine community structure. Finally, photosynthetic rates of the communities at selected light intensities were determined in the respirometer for communities developed in experiments designed to test the effects of exposure to desiccation and variations in light intensity.

Biomass accumulated most rapidly on substrates subjected to high light intensities, without exposure to desiccation. Under intertidal conditions, biomass accumulation was progressively greater

with less exposure to desiccation. Organic material (ash-free dry weight) was greater on substrates from summer than winter experiments. Both reduced salinity and thermal elevation interacted with light to stimulate algal production, and mats of Melosira nummuloides developed rapidly and floated to the surface.

Communities acclimated to different light intensities and periods of desiccation responded differently to various light intensities in the respirometer chamber. Substrates receiving little atmospheric exposure developed thicker layers of biomass permitting significantly higher rates of photosynthesis as light intensity increased. Generally, substrates developed at low light intensities attained a maximum photosynthetic rate at the lower light intensities in the respirometer, presumably because of an acclimation phenomenon.

Community structure, as computed by the Shannon-Weaver information function, showed increasing diversity with increasing atmospheric exposure. During the summer experiment this was caused by an increase in the number of species, but in the winter experiment this was caused by a greater evenness of distribution of the species within the community. In the experiments designed to determine the effects of light intensity, diversity decreased with increasing light intensity during the summer, but the opposite pattern was observed in the winter. In both experiments the number of species decreased with progressively higher light intensities; evenness of species

numbers in the summer decreased with increasing light intensity, but increased with increasing light intensity in the winter. Communities developed under conditions of reduced salinity or increased temperature showed decreasing diversity with increasing light intensity. This was due both to fewer species and an unevenness of species distribution.

Results of these experiments demonstrate the potential of the laboratory model ecosystem as a tool for the investigation of simplified communities. It may be used to gain information that can supplement and help understand concurrent field observations.

Structure and Productivity of Marine Benthic Diatom
Communities in a Laboratory Model Ecosystem

by

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STRUCTURE AND PRODUCTIVITY OF MARINE BENTHIC DIATOM COMMUNITIES IN A LABORATORY MODEL ECOSYSTEM

INTRODUCTION

As an increasing emphasis has been placed on the study of entire ecosystems, society has become aware of the dangers resulting from the insidious subversion of nature by man. One prerequisite necessary for understanding environmental problems is a knowledge of the structure and function of plant and animal communities in a spatial area of interest. Another is a comprehension of the developmental and successional processes occurring within the ecosystem.

New approaches to the study of ecosystems and improved methods of data processing have evolved which provide ecologists with additional tools for studying the complexities of nature. One of the most promising new developments in the study of the aquatic environment has been the implementation of laboratory ecosystems, often referred to as microcosms or microecosystems, for the study of simplified communities. Such systems, if properly designed, provide the investigator with some control over the environment while concurrently retaining many of the essential attributes of natural systems. In addition, the development of computer technology has permitted employment of more complex statistical procedures which allow research workers to analyze rapidly vast amounts of data obtained from

multivariable systems.

The purpose of this study was to simulate the estuarine littoral and sublittoral environment in the laboratory and determine the structural and functional attributes of diatom communities developed under these conditions. A laboratory intertidal system was constructed to permit development of benthic communities, primarily of diatoms, under selected regimes of light intensity, degree of desiccation, salinity, and temperature. Once the communities were sufficiently developed they were analyzed functionally by measuring the photosynthetic rates at selected light intensities in a respirometer chamber. In addition, biomass (dry weight and ash-free dry weight) and chlorophyll a were measured for each community and analyzed in relation to the selected developmental conditions. The structural aspects of the communities were assessed through measures of diversity, niche breadth of the component species, and a measure of community difference.

LITERATURE REVIEW

Benthic, marginal areas of the sea, estuaries, and salt marshes are among the most productive areas of the world. The standing crop of macroalgae in these areas often is as much as 100 times that of phytoplankton per unit area, and the annual production frequently is 10 times larger, or about $1000-2000 \text{ g C/m}^2 \text{ yr}$ (Mann, 1969). The contribution of the benthic microalgae, especially that of the diatoms, to total primary production has never been adequately assessed.

Benthic diatoms not only provide food for primary consumer organisms (Castenholz, 1961), but have recently been implicated in the production of dissolved organic matter (Chapman and Rae, 1969). Williams (1962) cites evidence for their importance in the consolidation of the sediment surface.

Community studies of benthic algae have been concerned with the distribution and zonation of macrophytes, and with the measurement and determination of the relative importance of the ecological factors in various habitats. In general, sublittoral macrophytes have less tolerance for desiccation and wide variations in light intensity, temperature and salinity than species that inhabit the higher littoral zone (Biebl, 1962; Hartog, 1968). To what extent this generalization also applies to benthic marine diatoms is not yet established, although a few papers have contributed some information.

The ecology of marine littoral diatoms in three areas on the south coast of England was investigated by Aleem (1950a), and he recognized 11 distinct diatom associations that exhibited an intertidal distribution similar to that displayed by macroalgae. He also noted that diatoms in areas exposed to long periods of desiccation had weakly silicified frustules and frequently exhibited an abnormal morphology. In another study Aleem (1949) discussed the distribution of littoral diatoms on rocky substrates, calcareous substrates and mud-flats. Members of the Naviculaceae were better represented on mud-flats, while the Fragilariaceae and Achnanthaceae were more frequent on solid substrates. Further studies were performed on the diatom communities inhabiting the mud-flats of Whitstable (Aleem, 1950b) and of Salstone, near Plymouth (Hustedt and Aleem, 1951).

Hendey (1964) described characteristic littoral and supralittoral diatom communities of British coastal waters and diagrammed the seasonal distribution of nearly 100 species. He noted that salinity, period of submergence, oxygen availability, and pH were influential in providing conditions that determined the broad floristic features in the littoral zone.

Castenholz (1963) evaluated the effects of exposure to direct insolation and desiccation on the distribution of littoral diatoms, in the absence of grazers and macrophytes, on vertical cement surfaces near Coos Bay, Oregon. He found that some species tolerated almost

no direct insolation exposure or intertidal emergence, while others withstood 2.5 to 4.0 hours or more in a single exposure. Furthermore, he found that diatoms quickly colonized areas devoid of grazers and larger algal forms. Castenholz (1967) also studied the seasonal ecology and made some estimates of the productivity of benthic diatoms on the west coast of Norway near Espeyrend.

Edsbackge (1965) compared the vertical distribution of attached diatoms on the Swedish west coast at Fiskerbäckskil with that of the Kieler Förde in the Baltic described by Simonsen (1962) and at Swange, England described by Aleem (1950a). He found few differences between the Baltic and Swedish areas, but the greatest similarity was between the Swedish sublittoral region and the lower littoral zone of England. Edsbackge (1966) elaborated further on these observations and discussed other aspects of the ecology of benthic diatom populations on the west coast of Sweden.

In general, aquatic microorganisms are considered to be opportunistic species. These are species that may become extremely abundant when conditions are favorable and are quick to respond to minor climatic perturbations and other density-independent factors. Therefore, diatom taxa possess all the necessary properties to qualify as bioindicators of environmental change. Patrick (1964) suggested that we examine the properties of entire diatom communities rather than try to unravel the niche requirements of all the constituent

species, which would be a hopeless undertaking. Such properties include the total number and kinds of species in the communities and the manner in which the individuals are proportioned among these species.

Methods for the quantitative characterization of the structure and diversity of benthic diatom communities have been developed by Ruth Patrick and her associates at the Academy of Natural Sciences of Philadelphia (Patrick, 1961, 1963, 1964, 1967a, 1967b, 1968; Patrick et al., 1954; Patrick and Strawbridge, 1963). This group demonstrated that while the species composition may vary greatly with the location, the number of species comprising a diatom community and the proportionate sizes of the populations of the species were relatively constant with time under stable environmental conditions.

Pomeroy (1959) measured algal production on salt marshes in Georgia using a bell jar pressed down into the sediments. He estimated that the annual gross algal production was 200 g C/m^2 . Working in the same area, Williams (1962) studied the diatom populations inhabiting the open mud-flats and vegetated areas and monitored their numbers as a function of environmental factors. He also observed a photosynthetic maximum for benthic diatoms at an intensity of 50% full sunlight. Pamatmat (1968) also used a bell jar to measure photosynthesis of benthic algae on an intertidal sand-flat in False Bay, San Juan Island, Washington. The annual gross primary production was

between 210-233 liters O_2/m^2 , depending on the period of intertidal exposure.

The biogeographic distribution of marine benthic diatoms is very poorly understood. Many papers have appeared describing the diatom flora of northern Europe, and to a lesser degree that of Africa and North America. In addition, much of the knowledge of the diatom distribution comes from ecological studies.

Bracher (1929), Carter (1932, 1933a, b) Ghazzauri (1933), Ross and Abdin (1946), Aleem (1949, 1950a, b), Hustedt and Aleem (1951), Hendey (1951, 1964), Smyth (1955), Round (1960), Hopkins (1963, 1964a, b), and Meadows and Anderson (1968) have all contributed significantly to the knowledge of the benthic diatom flora of Great Britain. Among significant contributions to the diatom flora of the Scandinavian countries are the works of Gemeinhardt (1935), Simonsen (1959, 1960, 1962), Edsbagge (1965, 1966, 1969a, b), and Castenholz (1967). Hustedt (1939) and Brockman (1950) have described the diatoms of the North Sea coast of Germany.

Among the more important works describing the African flora are Mills (1932), Hendey (1957), Giffen (1963, 1967), and Chohnoky (1963, 1968). An early and important study from the western hemisphere was that of Hagelstein (1939) in the Carribbean. On the North American continent, studies have been reported from Massachusetts (Drum and Webber, 1966), North Carolina (Hustedt, 1955), Georgia

(Williams, 1962), Texas (Wood, 1963), Oregon (Castenholz, 1963; Riznyk, 1969; Martin, 1970), and Washington (Phifer, 1929).

Benthic diatoms comprise a significant portion of the benthic microflora along the Oregon coast. Riznyk (1969) and Martin (1970) studied the physiological ecology of diatoms in the Yaquina River estuary, and Castenholz (1961, 1963) studied the ecology of littoral diatom communities on the southern Oregon coast.

APPARATUS AND METHODS

Model Intertidal Ecosystem

The laboratory "intertidal" system was located at the Oregon State University Marine Science Center, Newport, Oregon. The system consisted of a fibreglassed, plywood trough, 3 m long, 76 cm wide and 80 cm deep (Figure 1). The bottom of the trough was graduated in a "stair-step" manner to provide a water depth of about 64 m at one end and a small uncovered area at the opposite end when it was full of water. A 12 rpm electric motor (Dynatron 5K934) pivoted a board back and forth at the deep end of the system to provide water circulation. When the trough was greater than half full of water, the movement of the board generated waves that had a period greater than one second and a height of about one or two centimeters.

Seawater for the system was tapped from the polyvinyl chloride (PVC) pipe lines of the Marine Science Center. Water for the laboratory was obtained from lower Yaquina Bay. Some of the physical and chemical characteristics of Yaquina Bay and estuary have been described by Burt and Marriage (1957), Burt and McAlister (1959), Frolander (1964), and Kjeldsen (1966). Yaquina Bay has been classified as a partly-mixed system in the winter and spring and well-mixed during the summer and fall. The chemical and physical properties in

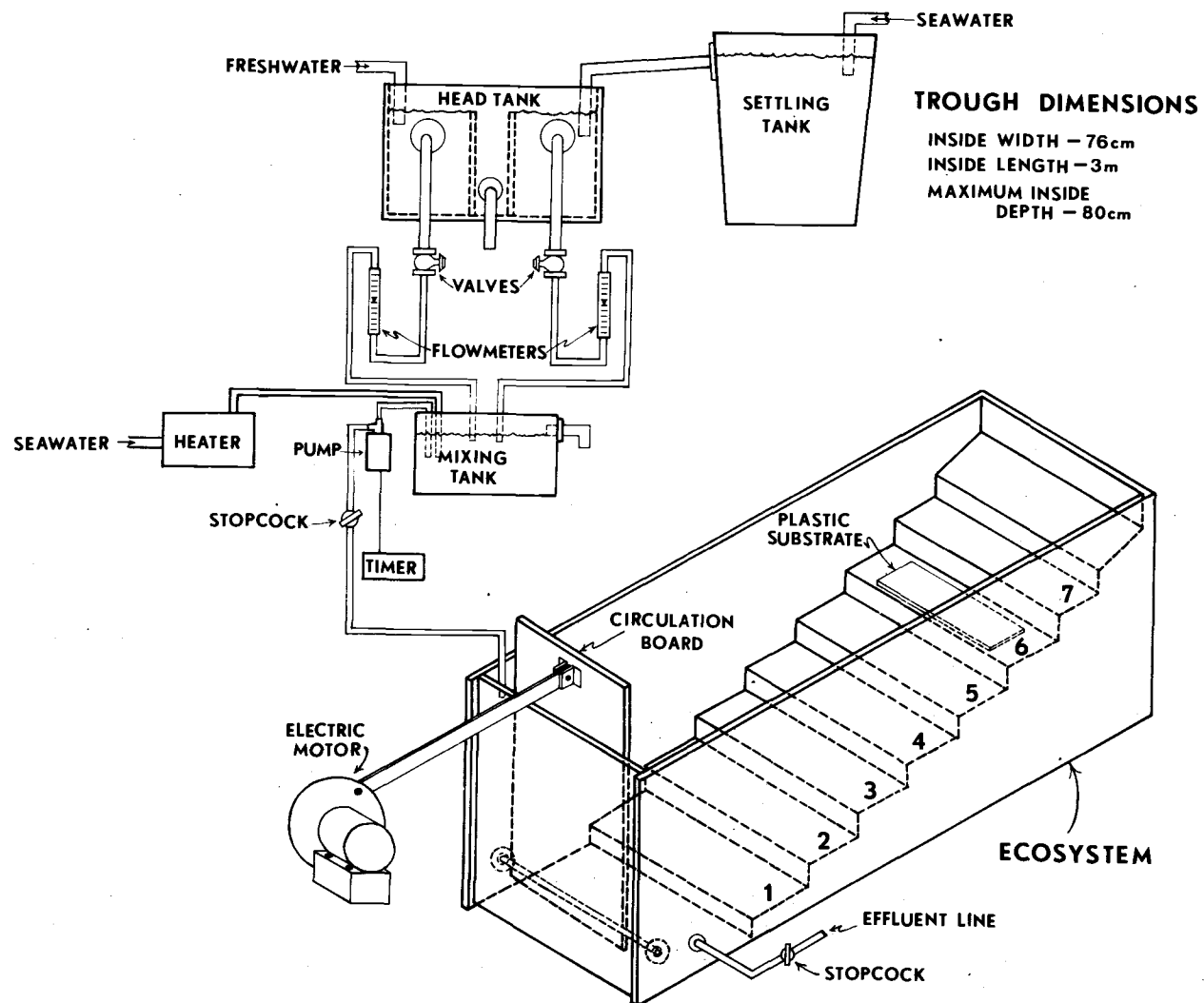


Figure 1. Diagram of the laboratory trough and associated water supply system.

the lower estuary are primarily influenced by the amount of freshwater runoff. During the summer, upwelling of water from near the bottom off the Oregon coast combined with an insignificant fluvial influence account for high salinities (33-34‰) and temperatures of about 13-15 C in the Bay. In the winter and early spring, freshwater runoff often lowers the salinity to between 5-10‰ in the lower bay near the Marine Science Center, while the temperature remains between 10-13 C.

A plastic garbage container served as a settling tank to remove terrigenous material from the influent seawater. Freshwater and seawater entered separate compartments of a wooden head tank and subsequently flowed downward through flowmeters into a mixing tank. Salinity of the water supply in the mixing tank was regulated by manipulating PVC ball valves. Salinity of the water supply was monitored with a continuous salinity recorder (Thayer and Redmond, 1969).

At a flow rate of 6 l/min, seawater could be heated from a temperature of about 10 C to 33 C with a booster water heater (Abco 309B). The inside of the heater was lined with stainless steel, and the 9000 w element was fabricated from Inconel. The water lines directly associated with the heater unit were PVC pipe, while all other plumbing connections for the system consisted of black plastic pipe. A continuous recording of the water temperature in the trough was made with a Marshalltown 1000 thermograph.

Water flowing into the settling, head, and mixing tanks was always in excess of the volume needed for the system, and overflow outlets were placed in these tanks to insure a constant head. Water was pumped from the mixing tank into the trough by a centrifugal pump (Gormann-Rupp Industries, Model 11888), and a glass stopcock controlled the rate of influent flow. The effluent flow likewise was controlled by a glass stopcock. The flow rate through these valves varied between 5 and 6 l/min.

Illumination for the system was provided by six 244-cm cool white, power groove, fluorescent lamps (General Electric Corp.) supplemented with 16, 60 w incandescent lamps mounted on a fixture that could be raised or lowered over the trough. Intensities on the lower substrates were also adjusted by placing one or more layers of nylon screen over the top of the trough. Intensities up to about 17,000 lux were obtained on the upper steps when the light fixture was at its lowest level. Measurement of illumination intensity was made with a Weston Sunlight Illumination Meter (Model 756) in the air, or under water with a hermetically sealed, selenium barrier photocell (International Rectifier DP-3), which had been calibrated with the Weston meter. The lights were controlled by timers (Paragon, Model 4001) to provide a photoperiod appropriate for the season.

A smooth, clear acrylic plastic plate, 26.5 x 51.3 x 0.5 cm, was placed on each step to provide a substrate for the colonization and

growth of diatoms. Such substrates were convenient sampling units that could be transferred from the system to a respirometer chamber for studies of community metabolism. The communities that colonized the substrates were seeded naturally by organisms entering the system through the water supply. During the experiments reported in this work, the communities consisted almost entirely of diatoms and associated heterotrophic microorganisms.

Respirometer Chamber

The respirometer chamber (Figure 2) was a modification of the P-R chamber designed by McIntire et al. (1964). The chamber was constructed entirely of clear acrylic plastic and measured 31.6 x 55.7 x 10.8 cm. The main compartment was separated from a small chamber at each end by a perforated baffle. This arrangement helped provide a laminar flow over the enclosed substrate. The top portion of the chamber was lined with a rubber automobile door gasket and was held to the bottom plate by a series of C-clamps. Two centrifugal pumps provided continuous circulation within the chamber, and the exchange rate of the influent water was regulated by a stopcock located between the influent sample bottle and the mixing tank (Figure 3). The general water supply arrangement for the respirometer was similar to that described for the model ecosystem, with the exception that a 1500 w immersion heater was inserted in the mixing box.

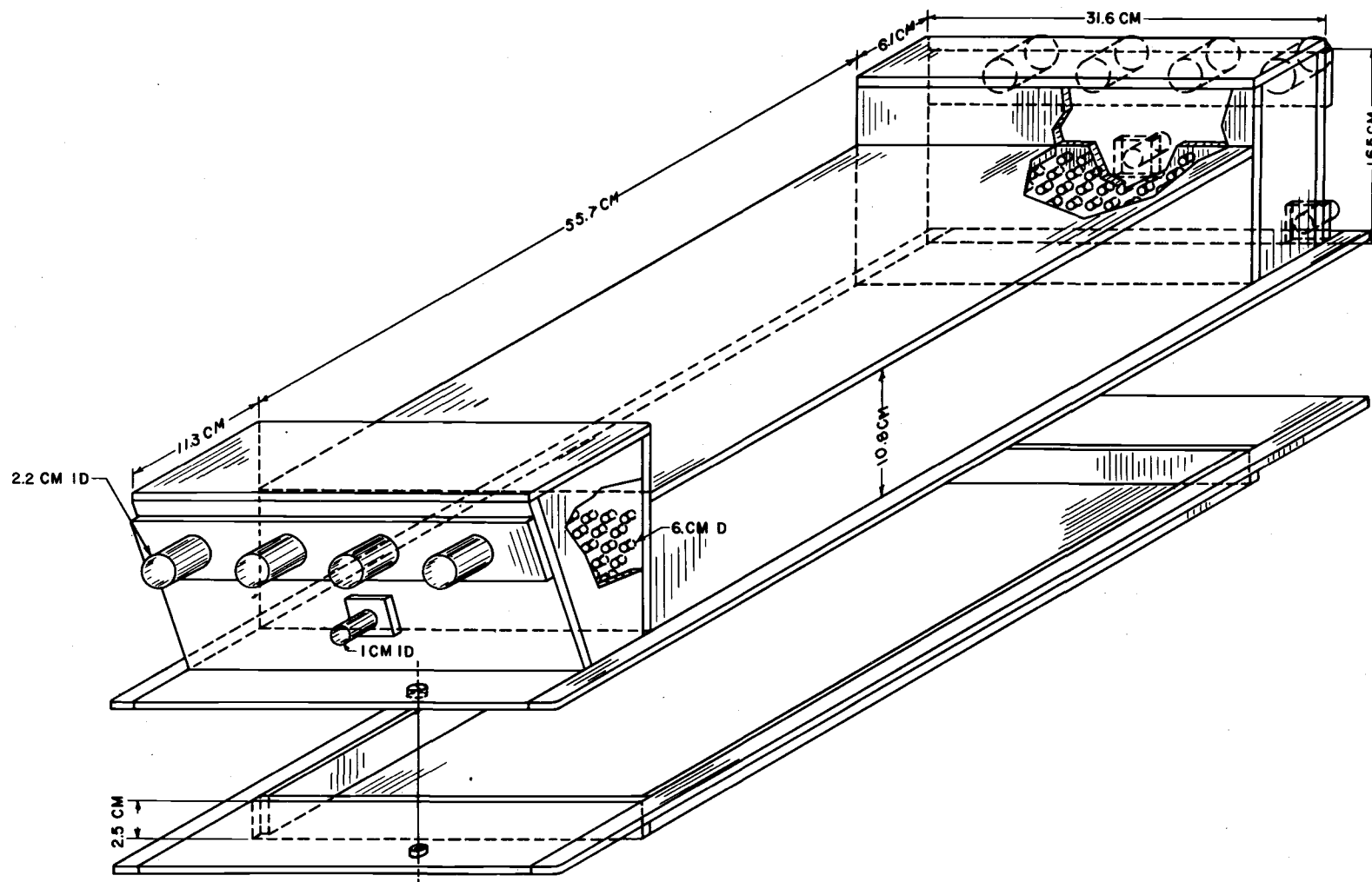


Figure 2. Diagram of the acrylic plastic respirometer chamber.

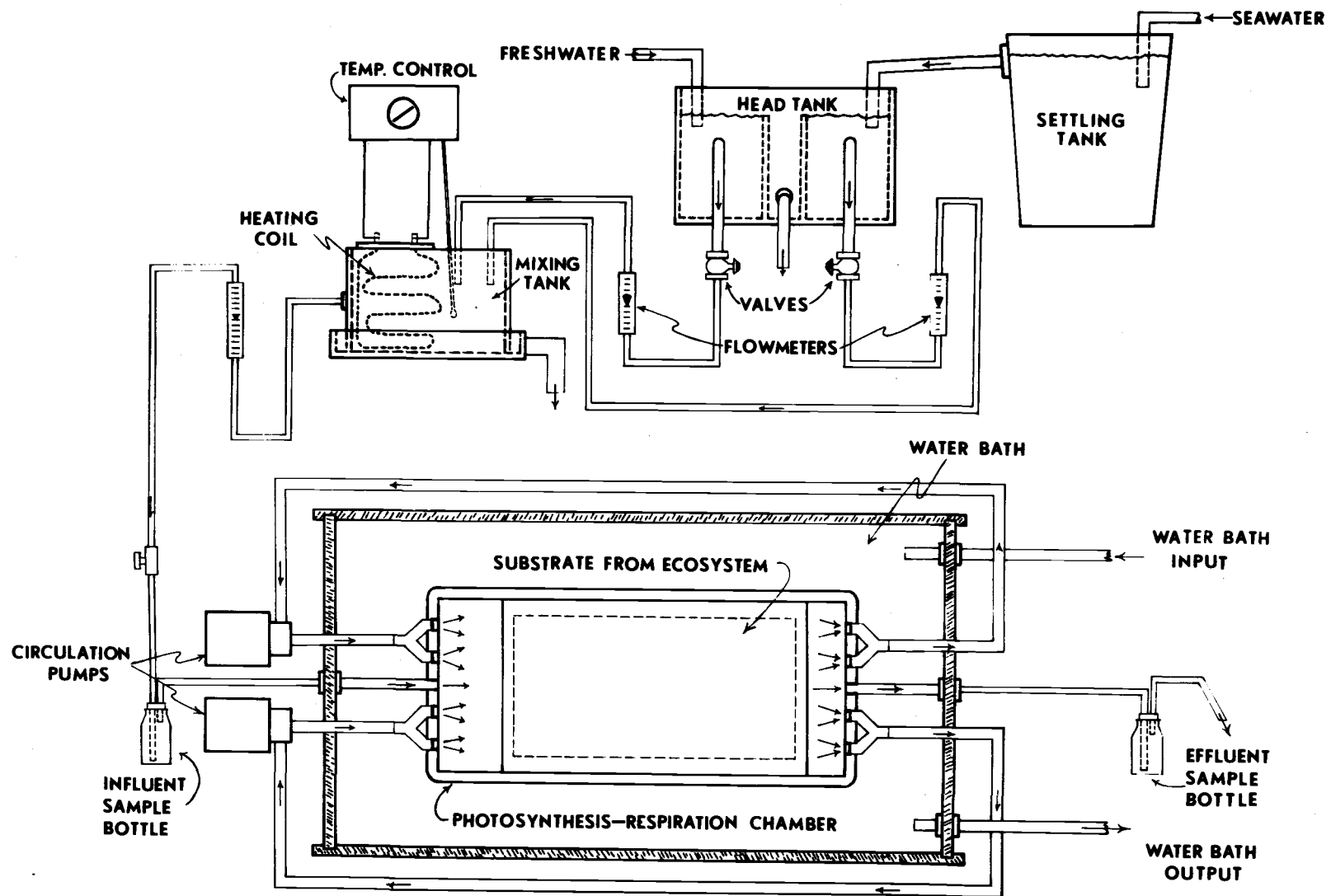


Figure 3. Diagram of the respirometer chamber and associated water supply system.

Illumination for the respirometer chamber was provided by six, 122-cm, cool white, power groove fluorescent lamps and ten, 60 w incandescent lamps on a fixture that could be raised or lowered over the sample. The light quality was similar to that received by the communities in the model ecosystem. Illumination intensities up to 20,000 lux were obtained when the fixture was adjusted to its lowest position. Lower light intensities were obtained by raising the fixture and/or by placing one or more layers of nylon screen over the chamber.

Sampling Methods

Substrates with an established community were removed from the model ecosystem and placed on the base of the respirometer chamber. Next, the top was clamped on, and the chamber was slowly filled with water. Air was evacuated through small holes in the top corners of the main compartment and end chambers. To maintain a stable temperature in the respirometer throughout an experiment, seawater was exchanged in the bath holding the chamber.

Rates of photosynthesis and respiration of the sample community were estimated by measurements of the dissolved oxygen concentration in influent and effluent water of the chamber at 60-min intervals. Details of this procedure were first outlined by McIntire et al. (1964) and McIntire and Phinney (1965). Since the water in the chamber was mixed by pumps, it was assumed that the dissolved oxygen

concentration of the water leaving the chamber was equal to that of water in the chamber at all times. Furthermore, the mean dissolved oxygen concentration of the water either entering or leaving the chamber during a time period was assumed to be equal to the mean of the concentrations obtained at the beginning and end of the period. From this, and knowing the exchange rate and the entire respirometer volume (including ancillary hoses, etc.), net oxygen evolution or consumption in the chamber for a time period was computed by the following formula:

$$O_2 = Ft \left[\frac{E_1 + E_0}{2} - \frac{I_1 + I_0}{2} \right] + V(E_1 - E_0),$$

where

F = exchange rate in l/hr;

t = time in hr;

E_0 = dissolved oxygen concentration in mg/liter of the effluent water at the beginning of the time period;

E_1 = dissolved oxygen concentration in mg/liter of the effluent water at the end of the time period;

I_0 = dissolved oxygen concentration in mg/liter of the influent water at the beginning of the time period;

I_1 = dissolved oxygen concentration in mg/liter of the influent water at the end of the time period; and

V = volume of water in the chamber in liters.

During measurements of community respiration, the chamber was darkened with a black polyethylene sheet. Because the amount of oxygen consumption by the community was usually low, the influent and effluent exchange was curtailed. The closed system afforded more sensitive estimates of community respiration for a time period. The rate of gross oxygen evolution for a time period was estimated by summing the values of net oxygen evolution during illumination and oxygen consumed during respiration in the dark. The time period for determination of oxygen evolution or respiration was one hr.

Dissolved oxygen concentration was measured using the azide modification of the Winkler method (American Public Health Association, 1965). Phenylarsine oxide (PAO) was substituted for the sodium thiosulfate solution.

At the conclusion of an experiment, the established community material was removed from the substrate with a rubber spatula and transferred into a bucket. The total suspension volume was increased to two liters by the addition of distilled water. Subsequently, the sample was placed in a Waring blender (4-liter capacity) and mixed for 20 sec. Subsamples were taken from this suspension for determination of biomass, chlorophyll a concentration and species composition.

To determine biomass, expressed either as g/m^2 of dry weight or ash-free dry weight, the procedure outlined by McIntire (1968) was followed. A 500-ml subsample of the blended suspension from

each substrate was evaporated to dryness at 75 C. The weight of the subsample was multiplied by four to calculate the biomass per substrate, and the latter value multiplied by the appropriate correction factor to express the biomass as g/m^2 . Another smaller subsample of the original suspension was centrifuged, and the pellet was transferred to a small platinum pan and dried at 75 C. This material then was weighed, ignited in a muffle furnace at 550 C, and reweighed. The weight lost on ignition divided by the weight of the material before ashing provided an estimate of the percentage of organic matter (ash-free dry weight) contained in the biomass. The weight of organic matter (g/m^2) was determined by multiplying the corresponding biomass estimate by this percentage.

The concentrations of chlorophyll a were estimated according to the methods recommended by the Scientific Committee on Oceanic Research (1966). A 25-ml subsample was removed from the initial 2-liter suspension. A few drops of saturated MgCO_3 solution were added, and this subsample was kept frozen at -20 C in darkness until the actual extraction was performed. In no instance was the storage period more than seven days. After thawing the subsample, a 10-ml portion was centrifuged and the water supernatant was discarded. The pellet was washed from the centrifuge tube with 90% acetone into a tissue grinder. After grinding, the material then was diluted with acetone to 90 ml and held overnight in closed flasks. The following

day the volume was increased to 100 ml, and the optical density was measured on a Beckman DB-G Grating Spectrophotometer. The equation suggested by the Scientific Committee on Oceanic Research (1966) was used for calculation of the concentration of chlorophyll.

To quantitatively evaluate species composition of the diatom flora, material from the algal suspension was transferred to a beaker and boiled in concentrated nitric acid. After oxidation of the organic matter, the empty diatom frustules were mounted in Hyrax (Patrick and Reimer, 1966). Each slide was examined in detail, and a list of diatom taxa compiled. When a particular diatom was relatively abundant and could not be named, it was assigned a temporary number, which was used for identification during the counting procedure. A mechanical stage was employed to traverse each slide under 1250X magnification. Approximately 500 diatoms were counted in samples obtained from each substrate.

STATISTICAL METHODS FOR ANALYSIS OF COMMUNITY STRUCTURE

When considering multi-species ecological systems in which the total number of species is unknown, the mean species diversity of all possible samples of size N may be estimated by the Shannon-Weaver information function,

$$H'' = - \sum_{i=1}^S \frac{n_i}{N} \log_2 \frac{n_i}{N},$$

where

H'' = the diversity of the community in bits of information per individual;

N = the total number of individuals in the sample;

n_i = the number of individuals belonging to the i^{th} species; and

S = the total number of species observed in N individuals.

Lloyd et al. (1968) discussed the derivation, limitations, and ecological implications of this index and presented a useful table for its calculation. Pielou has commented on the use and misuse of the information measure of diversity for different biological collections (Pielou, 1966a, b, c) and its application to species-diversity and pattern-diversity in the study of ecological succession (Pielou, 1966d).

Diversity of a sample of diatoms is a value ranging from zero (only one species present) to some conditional maximum, which

depends on the total number of species in the sample. For a particular number of species, diversity is relatively low when a large number of individuals belong to a few species. Conversely, diversity is maximum when the individuals are distributed as evenly as possible among the species (i.e., the species are equally common).

Because the magnitude of the information index is affected by both the total number of species and the distribution of individuals among the species, it is useful to separate these two components. If all S species are equally common,

$$H''_{c \max} = -S \left[\frac{1}{S} \log_2 \frac{1}{S} \right] = \log_2 S,$$

where $H''_{c \max}$ is a conditional maximum based on the observed number of species in the sample. It is not the maximum diversity of the community, as the total number of species on any selected substrate is always unknown. Since the sample sizes were approximately equal in this study (ca. 500 individual cells), $H''_{c \max}$ was useful for computing the relative degree of evenness in the communities. A measure of evenness (Pielou, 1966a) is provided by the expression $J'' = H''/H''_{c \max}$. A high value of J'' indicates a relatively even distribution of individuals among the species.

A difference measure developed by MacArthur (1965) was used to compare the structures of any two communities, where

$$D_{jh} = \exp [H''_T - \bar{H}''] ,$$

and

H''_T = the diversity of the combined j^{th} and h^{th} communities
calculated as one community, and

$\bar{H}''$ = the mean diversity of the two communities.

If the two communities were identical, i.e., the species composition and relative abundances were the same, D_{jh} had a value of one, whereas if the communities possessed no taxa in common, D_{jh} had a value of two, the maximum possible value.

Difference values were related to environmental variables by fitting regression surfaces to experimental data. An example of one such model equation in this thesis is

$$\hat{D}_{jh} = b_0 + b_1 \Delta E + b_2 \Delta \bar{S} + b_3 \Delta E \Delta \bar{S},$$

where

ΔE = the difference in the period of exposure to desiccation
during colonization of the j^{th} and h^{th} communities;

$\Delta \bar{S}$ = the difference between the mean salinity during two
experiments; and

$\hat{D}_{jh}$ = the predicted value of D_{jh} .

The computer output included the partial regression coefficients, the corresponding t-values for the coefficients, and the coefficient of

determination (R^2). The t -values were used to test whether or not the regression coefficients were different from zero at some arbitrarily selected significance level. The significance of each coefficient was associated with each corresponding variable when the variable entered last in the stepwise procedure. The R^2 value was of particular interest because it indicated the proportion of variance in the dependent variable that could be associated with variations in the independent variables.

Levins (1966, 1968) suggested that a measure of niche breadth should have the following properties: (1) if a species uses all habitats (or resources) equally, it will have a niche breadth equal to the total number of habitats; (2) if a species uses two habitats unequally, then the niche breadth will fall somewhere between one and two; and (3) if two populations are merged, their combined niche breadth should be equal to the sum of the separate values. In the latter case, the value may be less if they overlap, but never more. One statistic satisfying the above condition is:

$$\log B_i = - \sum_{r=1}^Q \frac{n_{ir}}{N_i} \log_e \frac{n_{ir}}{N_i}, \text{ or}$$

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

where n_{ir} is the number of individuals of the i^{th} species found in the sample from the r^{th} station, and N_i is the summation of individuals of the i^{th} taxon found at all Q stations. Thus, B_i is a measure of how evenly distributed a particular species is over the substrates being considered. In other words, it is an indication of the ability of a species to do equally well at the habitats under consideration. Furthermore, if species 1 is abundant and species 2 is rare, it is still possible for B_1 and B_2 to be equal, providing that N_1 and N_2 have the same proportionment among the samples.

All statistical analyses were performed with a Control Data Corporation 3300 computer at the Oregon State University Computer Center using the *AIDONE, *AIDTWO, and *STEP programs. *AIDONE and *AIDTWO are programs for the analysis of information and diversity for one and two sets of data, respectively. *STEP is a standard step-wise multiple regression program.

DESCRIPTION OF EXPERIMENTS

A total of six experiments were performed using the apparatus described above. Experiment TC-68 extended from 26 June through 3 August 1968, and was designed to examine the effects of exposure to desiccation and direct illumination on the structure and metabolism of diatom communities developed in the ecosystem. Another experiment, LI-68, was started 21 August and terminated on 18 September 1968. In this experiment the effects of light intensity on the communities were investigated. During the winter of 1968-69 each of the two experiments was repeated. Experiments TC-69 and LI-69 extended from 28 November to 8 January and from 9 January to 6 February, respectively. During the winter experiments, the period of illumination per day was less, and the salinity was lower and more variable, than in the summer experiments. A fifth experiment, RS-69, was conducted from 16 May to 22 June 1969, and was designed to determine effects of reduced salinity on the structure of new communities and on communities initially developed under normal salinities. The final experiment, HW-69, which extended from 4 to 21 September 1969, examined the effects of heated water on the development and structure of diatom communities in the ecosystem.

Prior to the initiation of an experiment, one acrylic plastic substrate was secured to each of the seven steps of the trough.

Henceforth, the steps are referred to by number, beginning with step 1 at the deep end and progressing upward to step 7 at the shallow end (Figure 1).

In the experiments designed to determine the effects of exposure to desiccation and direct illumination (TC-68 and TC-69), the effluent stopcock was adjusted so that the water could drain from a level of about ten cm above step 7 to the level of step 2 in six hr. After the 6-hr draining period, a timing device energized the centrifugal pump, and water was pumped into the trough. The influent stopcock was adjusted so that the influent water exceeded the effluent loss and refilled the trough to its original level by the end of the next six hr. At this time the timer stopped the pump, and the cycle restarted. With this cycle steps 1, 2, 3, 4, 5, 6, and 7 were exposed to desiccation for 0, 0, 1.0, 4.5, 8, 11, and 20.5 hr, respectively, each 24-hr day during experiment TC-68. The tidal cycle period was slightly different for experiment TC-69; steps 1 through 7 were exposed 0, 3, 5, 7.5, 10, 13, and 18 hr, respectively, for each 24-hr day. During both experiments illumination intensities at steps 1, 2, 3, 4, 5, 6, and 7 were 2,690, 3,280, 3,660, 4,570, 4,570, 4,840, and 3,660 lux, respectively, when the trough was full ("high tide") and 4,630, 5,380, 6,240, 6,940, 7,370, 7,320, and 6,560 lux, respectively, when the water was at the lowest level ("low tide"). The water temperature varied between 12 and 17 C during experiment TC-68, and

between 8 and 18 C in experiment TC-69. The salinity ranged from 28.1 to 34.6‰ during experiment TC-68 and from 8.0 to 32.5‰ during experiment TC-69 (Figure 4).

In experiments LI-68 and LI-69 the pump operated continuously to maintain water at a constant level of 10 cm above step 7. In this case the influent flow was the same as the effluent flow for the entire experiment. The mean rate of water exchange in the system was about 6 l/min during both experiments. Nylon screens were placed over the top of the system to regulate the light intensity on the different steps. Four layers of screen were mounted directly above step 1, three layers above steps 2 and 3, two layers above steps 4 and 5, one layer above step 6, and step 7 was left unshaded. Illumination intensities at steps 1, 3, 5, and 7 were 1,290, 2,370, 5,490, and 11,300 lux, respectively, during LI-68. At steps 1, 2, 3, 4, 5, 6, and 7 the intensities for LI-69 were 800, 1,070, 2,370, 3,770, 5,380, 10,540, and 17,650 lux, respectively. The salinity varied between 27.8 and 30.5‰ for LI-68 and 11.5 and 32‰ for LI-69 (Figure 5). However, the average salinity for LI-69 was 27.5‰. Water temperature ranged from 13.5 to 15 C during LI-68 and from 8.3 to 14.4 C during LI-69.

At the conclusion of experiments TC-68, TC-69, LI-68, and LI-69, the acrylic substrates with their established communities were transferred from the steps to the respirometer for measurements

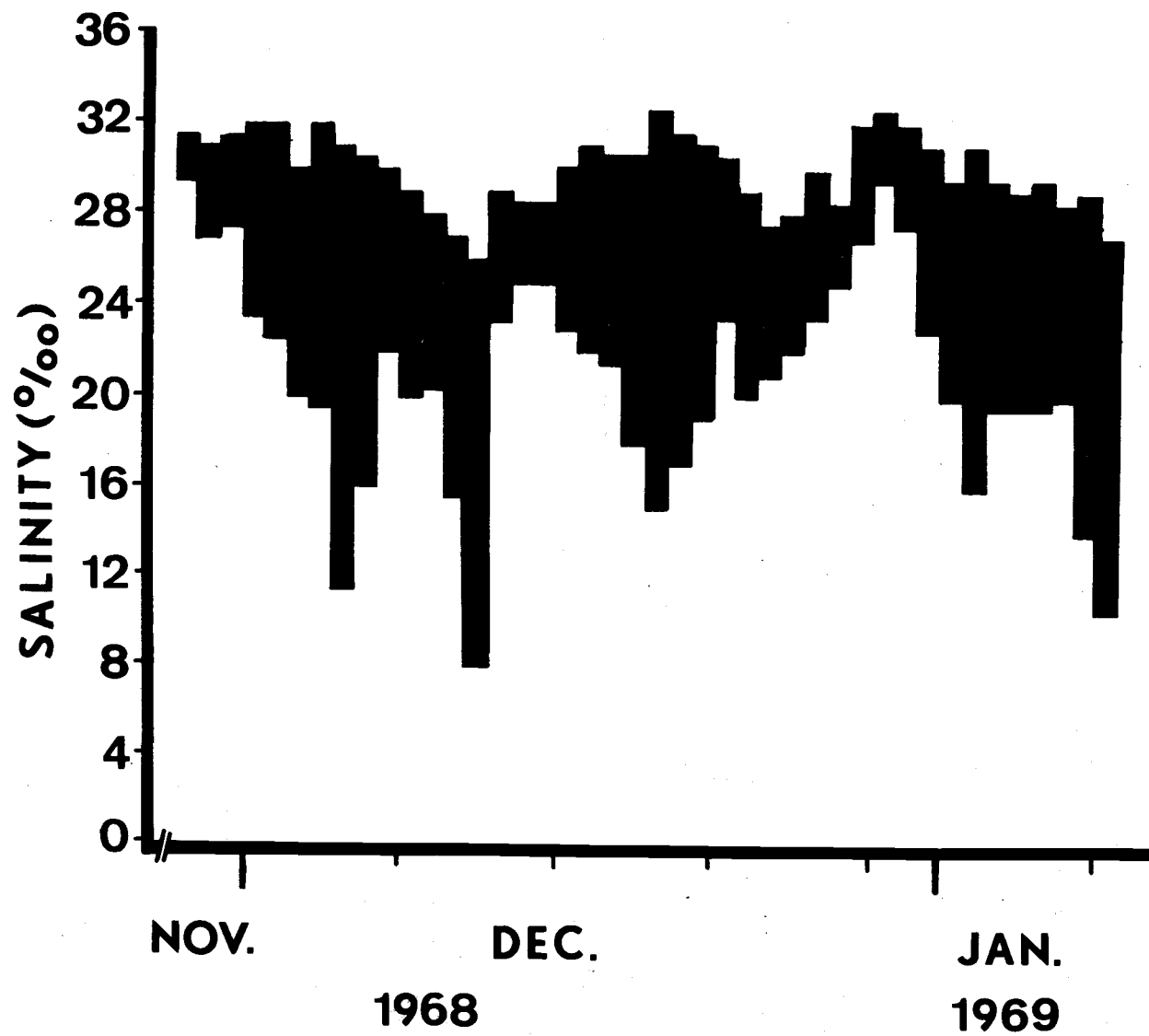


Figure 4. Salinity range during experiment TC-69.

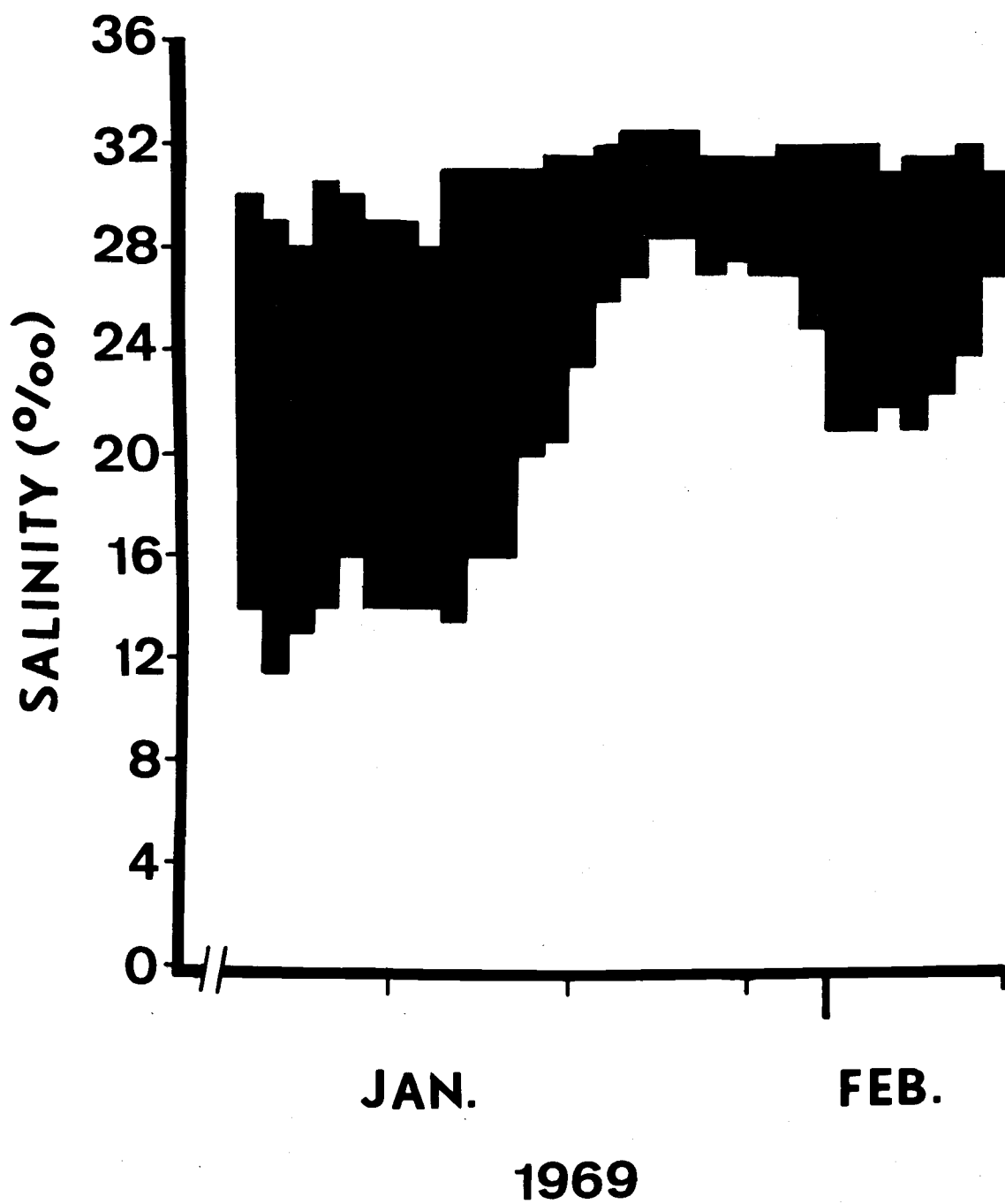


Figure 5. Salinity range during experiment LI-69.

of community metabolism. Colonization of steps 6 and 7 was negligible for TC-68, so the corresponding substrates were not examined. After a substrate was placed in the respirometer, the chamber was covered with a black polyethylene sheet, and community respiration was measured for a period of 2 hr. The next morning the chamber was uncovered, and rates of photosynthesis were measured for 1-hr periods at each of eight different illumination intensities ranging from 590 to 18,450 lux. The time required for the respirometer experiments was one day for each substrate. The species composition of communities from steps 1, 3, and 5 was determined in experiment TC-68; for experiments TC-69, LI-68, and LI-69, samples from steps 1, 3, 5, and 7 were examined for species composition.

The experiment designed to determine the effect of reduced salinity on the development and structure of diatom communities (RS-69) required the use of a control system. For this, the respirometer bath was temporarily modified with the addition of nylon screens and appropriate plumbing. In this experiment, only community structure and biomass were investigated. Seawater was continuously exchanged in both the model ecosystem and the control system, as in experiments LI-68 and LI-69. The lamp fixtures were adjusted so that light intensities at substrates 1, 4, and 7 in the model ecosystem corresponded to those at substrates 1, 2, and 3 in the control system; these intensities were 1,030, 4,710, and 12,270 lux, and 1,030,

4,380, and 12,600 lux, respectively. Each substrate was partitioned into two halves by a piece of black electrical tape. Both systems then were allowed to develop under the normal estuarine salinities (18-33‰) for 19 days, at which time one-half of all substrates were harvested. Subsequently, the salinity in the ecosystem was reduced to 15 ± 2 ‰. After another 18 days, both halves of all substrates were harvested. This permitted the harvesting of substrates subjected to the following conditions: (1) ecosystem with normal salinity for the first 19 days (RSA); (2) ecosystem with normal salinity for the first 19 days followed by reduced salinity for the last 18 days (RSB); (3) control system with normal salinity for the first 19 days (RSC); (4) control system with normal salinity for the entire 37 days (RSD); (5) ecosystem with reduced salinity for the last 18 days (RSE); and (6) control system with normal salinity for the last 18 days (RSF).

For experiment HW-69 the model ecosystem was kept continuously filled with water, and the communities were allowed to develop for 17 days under a temperature of 25 ± 2.5 C. Seawater temperature in the estuary was about 10 C and the salinity varied between 28 and 32‰ during the experiment. Substrates 1, 4, and 7 were sampled and the light intensities were 1,040, 3,950, and 16,880 lux, respectively. A control system was established initially, but later it was necessary to dismantle this system because of difficulties with the

water supply. Therefore, the preliminary information reported in this thesis is intended to serve only as a guide for future experiments.

RESULTS

The Diatom Flora

A list of the diatom taxa identified from samples obtained at the conclusion of the experiments and their relative abundances may be found in Appendices 1 and 2. Where abundance is not indicated, that taxon did not appear during the counting and was observed only during the detailed preliminary examinations of the slides. The identity of some diatoms could not be obtained or was uncertain. In such an event a number was assigned to the morphological form in question. The appendices also represent a new distributional record for several diatoms, as many of these taxa have never been reported from either the estuaries or coastal regions of Oregon.

The diatoms that were among the five most abundant taxa on any one of the three substrates sampled in experiment TC-68 included Achnanthes temperei, Melosira nummuloides, Navicula directa, Nitzschia lanceolata var. minor, N. sigma, N. socialis, N. subhybrida, Synedra fasciculata and Thalassionema nitzschioides. The five most abundant taxa on any one of the four substrates examined in experiment TC-69 included Achnanthes hauckiana, Navicula diserta, N. grevillei, Navicula #2, Nitzschia aerophila, N. apiculata, N. hybrida, N. socialis, N. subhybrida, Nitzschia #1 and Nitzschia #2.

A similar list for the four substrates examined in experiment LI-68 included Amphipleura rutilans, Bacillaria paxillifer, Cocconeis costata, C. scutellum var. parva, Fragilaria striatula var. californica, Melosira nummuloides, Nitzschia longissima, N. aerophila, Nitzschia #5, Synedra fasciculata, and Thalassionema nitzschioides. For experiment LI-69 the five most abundant taxa included Amphipleura rutilans, Navicula diserta, N. grevillei, Nitzschia aerophila, N. hybrida, N. socialis, Nitzschia #1, Nitzschia #3, and Nitzschia #5.

There were 18 diatom taxa that were included among the five most abundant taxa on any one of the six substrates in experiment RS-69. These were Amphipleura rutilans, Fragilaria striatula var. californica, Gyrosigma fasciola, Licmophora paradoxa, Melosira jurgensii, M. nummuloides, Navicula directa, N. diserta, N. grevillei, Navicula #2, Nitzschia subhybrida, Nitzschia #2, Plagiogramma brockmanni, P. vanheurckii, Synedra fasciculata, Thalassionema nitzschioides, Thalassiosira #1, and Pleurosigma #1.

For experiment HW-69 the list of the five most abundant diatom taxa for the four substrates sampled included Amphora #5, Melosira nummuloides, Navicula diserta, Navicula #2, Nitzschia aerophila, N. longissima, Plagiogramma vanheurckii, and Thalassionema nitzschioides.

Some of the smaller specimens of the genus Cocconeis were extremely difficult to sort out taxonomically on the basis of frustule

morphology. These variable forms tended to co-occur and apparently possessed similar physiological and ecological properties. For the purposes of this thesis, they were lumped temporarily under C. scutellum var. parva.

A few very rare diatoms, e. g., Achnanthes lanceolata, A. minutissima, Cymbella ventricosa, Diploneis smithii, Gomphonema subclavatum var. montana, Hannaea arcus, and Stauroneis phoenicenteron f. gracilis were obviously freshwater species that presumably had washed down the estuary from the lower Yaquina River.

Table 1 presents the niche breadths of 107 species that were present on more than one of the 36 substrates sampled. Navicula diserta had the highest niche breadth (28.18), and it was found on 34 substrates. Several species that had high niche breadths were not among the five most abundant taxa on any substrate (e. g., Amphora #1, Melosira sulcata, and Navicula cancellata var. apiculata). Almost all other species exhibiting a relatively high niche breadth were among the five most abundant taxa on one or more substrates. The niche breadths of three species that dominated some communities with a large number of specimens, namely Melosira nummuloides, Navicula grevillei, and Fragilaria striatula var. californica were relatively low because of their uneven distribution over the 36 substrates.

Table 1. The niche breadth B_i for 107 diatom populations, where $B_i = \exp \left[- \sum_{r=1}^Q \frac{n_{ir}}{N_i} \log_e \frac{n_{ir}}{N_i} \right]^*$

Species	B_i	Total number of specimens	Number of substrates
<u>Navicula diserta</u>	28.18	927	34
<u>Amphora #1</u>	24.70	132	29
<u>Melosira sulcata</u>	24.30	141	30
<u>Navicula cancellata</u> v. <u>apiculata</u>	24.18	112	29
<u>Synedra fasciculata</u>	23.72	898	36
<u>Nitzschia subhybrida</u>	22.20	812	33
<u>Plagiogramma brockmanni</u>	21.36	517	34
<u>Navicula #2</u>	21.03	709	27
<u>Amphipleura rutilans</u> .	20.78	615	34
<u>Thalassiosira #1</u>	20.74	287	29
<u>Nitzschia #2</u>	20.70	499	29
<u>Thalassionema nitzschioides</u>	20.53	425	34
<u>Plagiogramma vanheurckii</u>	19.69	1239	34
<u>Amphora #5</u>	19.60	157	28
<u>Navicula abunda</u>	18.89	151	26
<u>Pleurosigma #1</u>	18.64	227	23
<u>Rhaphoneis #1</u>	18.22	47	22
<u>Nitzschia frustulum</u> v. <u>perpusilla</u>	18.15	67	22
<u>Nitzschia aerophila</u>	17.87	322	34
<u>Navicula gregaria</u>	17.60	121	23
<u>Achnanthes hauckiana</u>	16.71	90	24
<u>Nitzschia socialis</u>	16.67	823	31
<u>Amphora #2</u>	16.24	61	23
<u>Gyrosigma fasciola</u>	16.19	228	28
<u>Nitzschia hybrida</u>	15.93	148	21
<u>Rhaphoneis ampiceros</u>	15.92	36	19
<u>Navicula directa</u>	15.13	486	27
<u>Nitzschia longissima</u>	14.75	274	24
<u>Nitzschia #3</u>	14.26	113	21
<u>Biddulphia aurita</u>	13.16	44	16
<u>Amphiprora alata</u>	12.98	22	15
<u>Nitzschia #5</u>	12.06	424	27
<u>Nitzschia sigma</u>	11.40	196	20
<u>Bacillaria paxillifer</u>	11.37	256	26
<u>Cocconeis placentula</u> v. <u>euglypta</u>	10.91	22	12
<u>Achnanthes lanceolata</u>	10.43	28	13
<u>Amphora #3</u>	10.30	30	15
<u>Nitzschia angularis</u>	9.81	37	14
<u>Nitzschia dissipata</u> v. <u>media</u>	9.33	40	11
<u>Navicula #1</u>	9.25	28	11
<u>Nitzschia apiculata</u>	9.04	61	18
<u>Gyrosigma fibergerei</u>	8.99	39	11
<u>Licmophora paradoxa</u>	8.96	178	16
<u>Nitzschia #1</u>	8.80	248	27
<u>Navicula crucigera</u>	8.62	25	11

Table 1. (continued)

Species	B _i	Total number of specimens	Number of substrates
<u>Cocconeis scutellum</u>	8.58	17	10
<u>Melosira nummuloides</u>	8.27	1236	30
<u>Cocconeis #1</u>	8.22	29	11
<u>Thalassiosira aestivalis</u>	7.63	26	10
<u>Navicula secreta v. apiculata</u>	7.56	24	10
<u>Navicula complanata</u>	7.19	11	8
<u>Navicula grevillei</u>	7.12	267	19
<u>Pseudo-Nitzschia #1</u>	7.04	13	8
<u>Pleurosigma angulatum v. aestuarii</u>	7.00	7	7
<u>Achnanthes minutissima</u>	6.73	8	7
<u>Synedra fasciculata v. truncata</u>	6.32	17	8
<u>Actinopterychus undulatus</u>	6.00	6	6
<u>Navicula agnita</u>	5.78	16	7
<u>Navicula auriculata</u>	5.74	10	7
<u>Achnanthes #1</u>	5.74	7	6
<u>Coscinodiscus lineatus</u>	5.67	9	6
<u>Licmophora #1</u>	5.66	8	6
<u>Fragilaria striatula v. californica</u>	5.48	482	21
<u>Cocconeis costata v. pacifica</u>	5.30	8	6
<u>Chaetoceros cinctum</u>	5.28	16	6
<u>Licmophora californica</u>	4.76	8	5
<u>Surirella gemma</u>	4.76	6	5
<u>Navicula cryptocephala</u>	4.71	7	5
<u>Navicula #5</u>	4.64	30	7
<u>Navicula #4</u>	4.46	8	5
<u>Opephora #1</u>	4.37	7	5
<u>Navicula tripunctata v. schizonemoides</u>	4.33	9	5
<u>Cymbella ventricosa</u>	4.00	4	4
<u>Pseudo-Nitzschia sicula v. migrans</u>	3.79	5	4
<u>Navicula tripunctata</u>	3.79	5	4
<u>Navicula viridula v. avenacea</u>	3.79	5	4
<u>Cocconeis scutellum v. parva</u>	3.19	214	23
<u>Navicula diversistriata</u>	3.17	7	4
<u>Navicula mutica</u>	3.14	12	4
<u>Navicula minima</u>	3.00	3	3
<u>Coscinodiscus curvatulus</u>	3.00	3	3
<u>Cyclotella meneghiniana</u>	3.00	6	3
<u>Triceratium alternans</u>	3.00	3	3
<u>Nitzschia dissipata</u>	2.91	23	4
<u>Coscinodiscus excentricus</u>	2.87	5	3
<u>Nitzschis frustulum v. perminuta</u>	2.84	26	6
<u>Achnanthes deflexa</u>	2.83	4	3
<u>Cocconeis placentula v. lineata</u>	2.83	4	3
<u>Thalassiosira #1</u>	2.65	8	3
<u>Aulocodiscus probabilis</u>	2.59	5	3
<u>Stephanopyxis turris</u>	2.38	6	3

Table 1. (continued)

Species	B_i	Total number of specimens	Number of substrates
<u>Navicula</u> #3	2.20	33	5
<u>Achnanthes brevipes</u> v. <u>intermedia</u>	2.09	8	3
<u>Eunotia tenella</u>	2.00	2	2
<u>Surirella ovata</u>	2.00	2	2
<u>Gyrosigma spercerii</u> v. <u>curvula</u>	2.00	2	2
<u>Amphora</u> #4	1.98	9	3
<u>Achnanthes temperei</u>	1.96	123	3
<u>Achnanthes parvula</u>	1.96	37	2
<u>Nitzschia lanceolata</u> v. <u>minor</u>	1.96	137	3
<u>Opephora marina</u>	1.89	3	2
<u>Nitzschia frustulum</u> v. <u>subsalina</u>	1.89	3	2
<u>Coscinodiscus radiatus</u>	1.89	3	2
<u>Navicula seminulum</u>	1.75	4	2
<u>Cocconeis costata</u>	1.70	23	4
<u>Skeletonema costata</u>	1.33	12	2
<u>Melosira jurgensii</u>	1.32	37	2

* The maximum possible value of B_i is 36, the number of substrates sampled.

Effect of Tidal Cycle

Biomasses on substrates 1, 2, 3, 4, and 5 at the conclusion of experiment TC-68 were 453.2, 342.6, 165.8, 120.6, and 71.4 g/m² dry weight, respectively (Table 2). Similarly, the biomasses at the conclusion of experiment TC-69 on substrates 1 through 7 were 904.2, 315.5, 273.1, 233.5, 68.1, 96.7, and 79.3 g/m² dry weight, respectively (Table 3). Thus, there was an inverse relationship between biomass and period of exposure to desiccation. The percentage ash-free dry weight in samples from the five substrates of TC-68 varied between 24 and 29% and was typical of communities dominated by diatoms (McIntire and Phinney, 1965; McIntire, 1968). The percentage ash-free dry weight in samples from the seven substrates in TC-69 varied between 14 and 20%. During the winter a greater proportion of the individual communities was composed of silt and inorganic debris, which probably resulted from a relatively high silt load in the water supply during periods of high freshwater discharge. Concentrations of chlorophyll a for both experiments TC-68 and TC-69 followed a pattern similar to biomass, with values decreasing progressively from the lower to the upper steps. During TC-68 the amount of chlorophyll a was in most instances an order of magnitude greater than that found in TC-69 on comparable substrates.

Rates of gross photosynthesis in experiment TC-68

Table 2. Biomasses and chlorophyll a concentrations for samples obtained from the laboratory ecosystem during experiment TC-68.

Substrate	Exposure to air (hr/day)	Light intensity (lux)		Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		High tide	Low tide	Dry wt	Ash-free dry wt	
1	0	2,690	4,630	453.2	128.2	0.837
2	0	3,280	5,380	342.6	98.7	0.558
3	1	3,660	6,240	165.8	41.1	0.191
4	4-1/2	4,570	6,940	120.6	32.8	0.117
5	8	4,570	7,370	71.4	17.2	0.037

Table 3. Biomasses and chlorophyll a concentrations for samples obtained from the laboratory ecosystem during experiment TC-69.

Substrate	Exposure to air (hr/day)	Light intensity (lux)		Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		High tide	Low tide	Dry wt	Ash-free dry wt	
1	0	2,690	4,630	904.2	179.3	0.018
2	3	3,280	5,380	315.5	43.2	0.014
3	5	3,660	6,240	273.1	41.4	0.007
4	7-1/2	4,570	6,940	233.5	47.1	0.007
5	10	4,570	7,370	68.1	10.9	0.003
6	13	4,840	7,320	96.7	16.2	0.004
7	18	3,660	6,560	79.3	12.3	0.004

were approximately the same for substrates from steps 1, 2, 3, and 4 at illumination intensities below 4,000 lux (Figure 6). At higher intensities, slopes of curves relating illumination intensity to oxygen evolution were much steeper for communities from steps 1 and 2 than those from steps 3 and 4. Maximum rates of photosynthesis for these samples were obtained at the highest illumination intensity (18,450 lux) and ranged from 0.50 g O₂/m² hr (substrate 3) to 1.23 g O₂/m² hr (substrate 2). The curve for the community from step 5 was irregular and the photosynthetic rate never exceeded 0.27 g O₂/m² hr. In TC-69, rates of gross photosynthesis for substrates 1, 2, 3, and 4 approached saturation at 18,450 lux (Figure 7). The maximum rate of photosynthesis was 0.36 g O₂/m² hr (substrate 1), at 11,840 lux. Thus, the maximum photosynthetic rate on steps 1 through 4 under winter conditions was considerably less than that during the summer. Gross photosynthesis on substrate 5 ranged from 0.03 to 0.10 g O₂/m² hr and was nearly a linear function of light intensity.

In TC-68 a distinct zonation of the more abundant diatoms clearly was related to period of exposure to desiccation (Figure 8). Navicula directa, Nitzschia socialis, N. subhybrida, Melosira nummuloides, and Synedra fasciculata were more abundant on the substrate with no exposure than on the substrates with 1 or 8 hr exposure per day. Nitzschia lanceolata var. minor and possibly N. sigma were able to

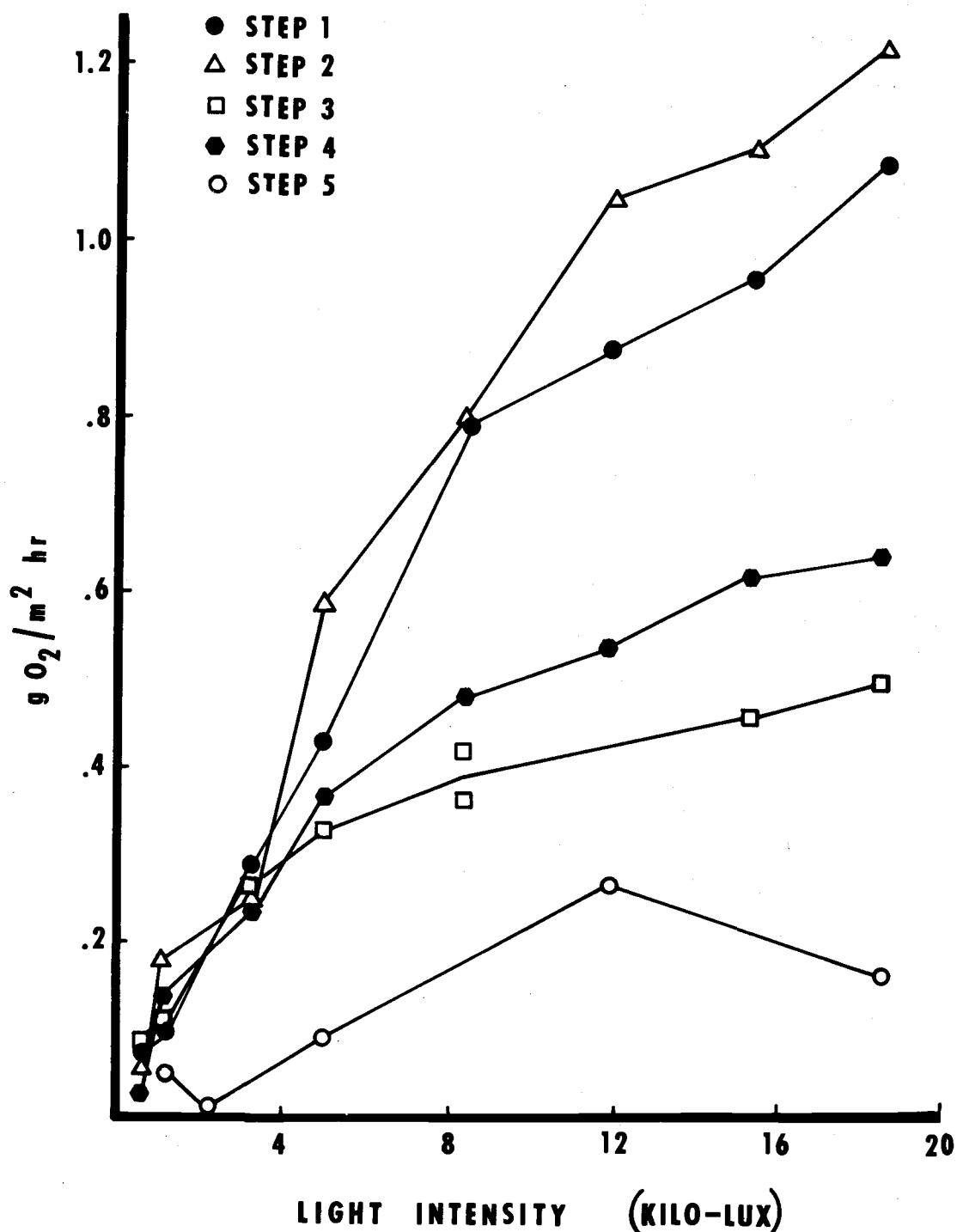


Figure 6. Relationship between illumination intensity and the rate of gross photosynthesis of diatom communities from steps 1, 2, 3, 4, and 5 determined in the respirometer chamber at the conclusion of experiment TC-68.

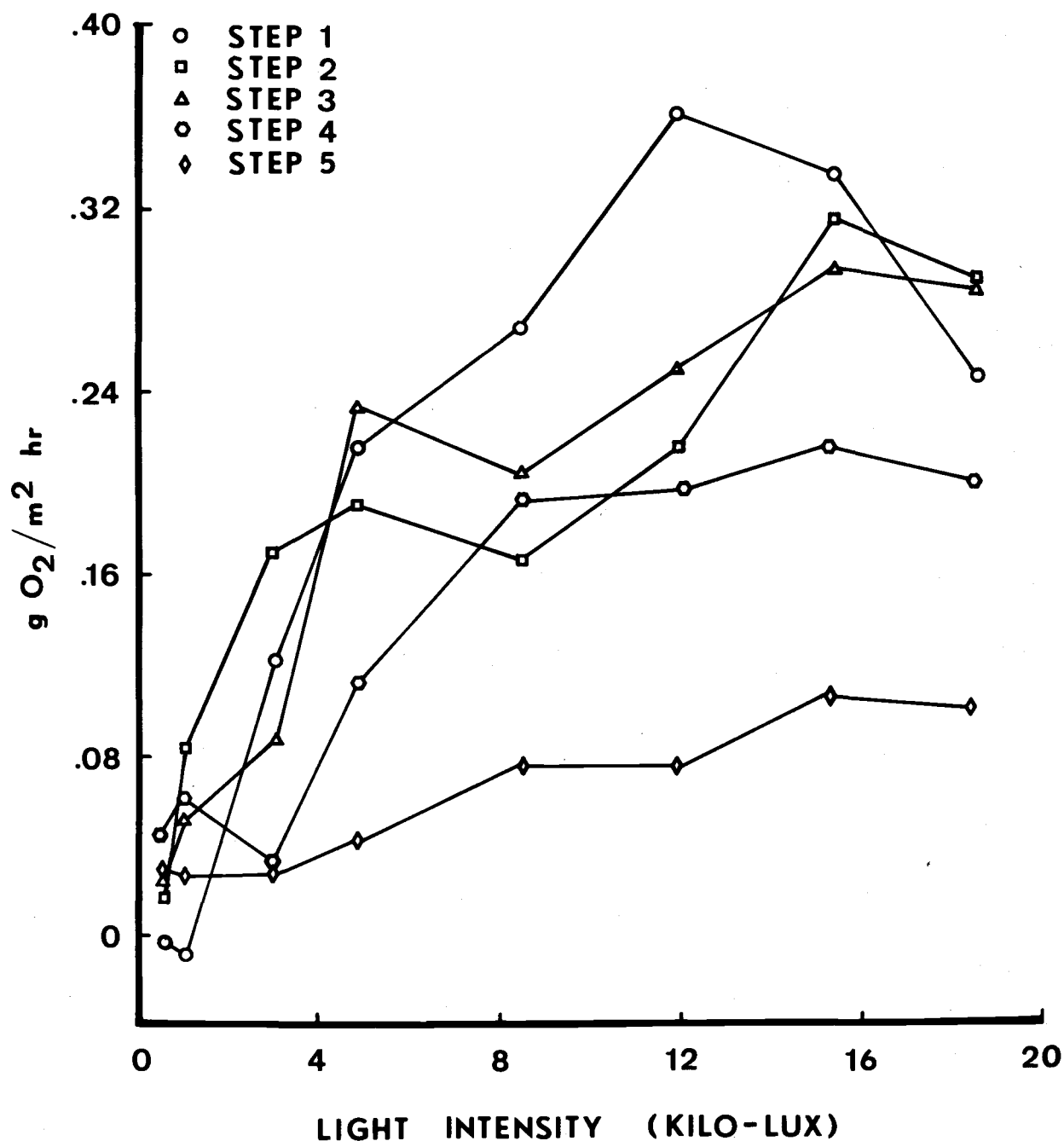


Figure 7. Relationship between illumination intensity and the rate of gross photosynthesis of diatom communities from steps 1, 2, 3, 4, and 5 determined in the respirometer chamber at the conclusion of experiment TC-69.

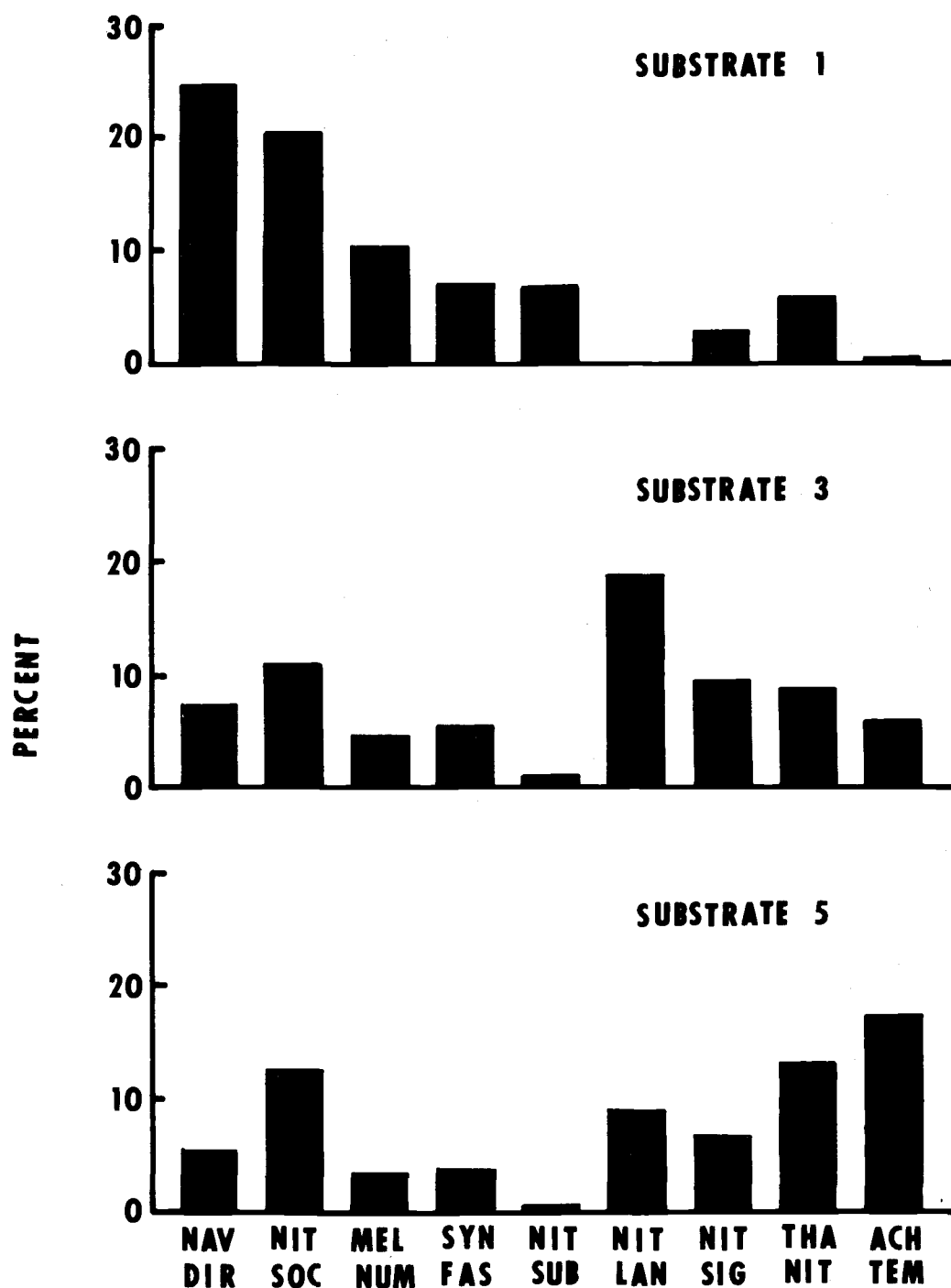


Figure 8. Relative abundance of the five most abundant diatom taxa on substrates 1, 3, and 5 at the conclusion of experiment TC-68. The abbreviations below the horizontal axis correspond to *Navicula directa*, *Nitzschia socialis*, *Melosira nummuloides*, *Synedra fasciculata*, *Nitzschia subhybrida*, *Nitzschia lanceolata* var. *minor*, *Nitzschia sigma*, *Thalassionema nitzschioides*, and *Achnanthes temperi* and varieties, respectively.

compete best on the substrate with an exposure period of 1 hr/day. Achnanthes temperei and Thalassionema nitzschioides were extremely tolerant of desiccation and represented 17.5 and 13.0%, respectively, of the number of individuals counted from substrate 5. The pattern of zonation was not as closely related to period of exposure to desiccation in experiment TC-69 (Figure 9). Nitzschia aerophila was by far the most abundant diatom on all four substrates. On substrates 1 and 5, where exposure was 0 and 8 hr/day, respectively, the relative abundance of N. aerophila was greater than 50%, while on substrate 7 (exposure 20.5 hr/day) it was 29% of the total specimens counted. Nitzschia apiculata, N. hybrida, Nitzschia #2, and Nitzschia #5 were most abundant on substrate 3 (exposure 1 hr/day), whereas Navicula diserta was more abundant on substrate 5 than on the other substrates. Navicula grevillei and Nitzschia #1 were abundant only on the substrate exposed to desiccation for 20.5 hr/day.

The diversity index H'' for communities examined during experiment TC-68 (Table 4) ranged from 3.56 (substrate 1) to 4.18 (substrate 5) bits per individual, and the number of taxa ranged from 32 in 522 individuals counted (substrate 1) to 41 in 511 individuals (substrate 5). In TC-69 H'' ranged from 2.89 (substrate 1) to 3.42 (substrate 7) bits per individual; the number of taxa varied from 32 in 542 individuals on substrate 7 to 41 in 512 individuals on substrate 5. Surprisingly, the index was slightly higher for the communities

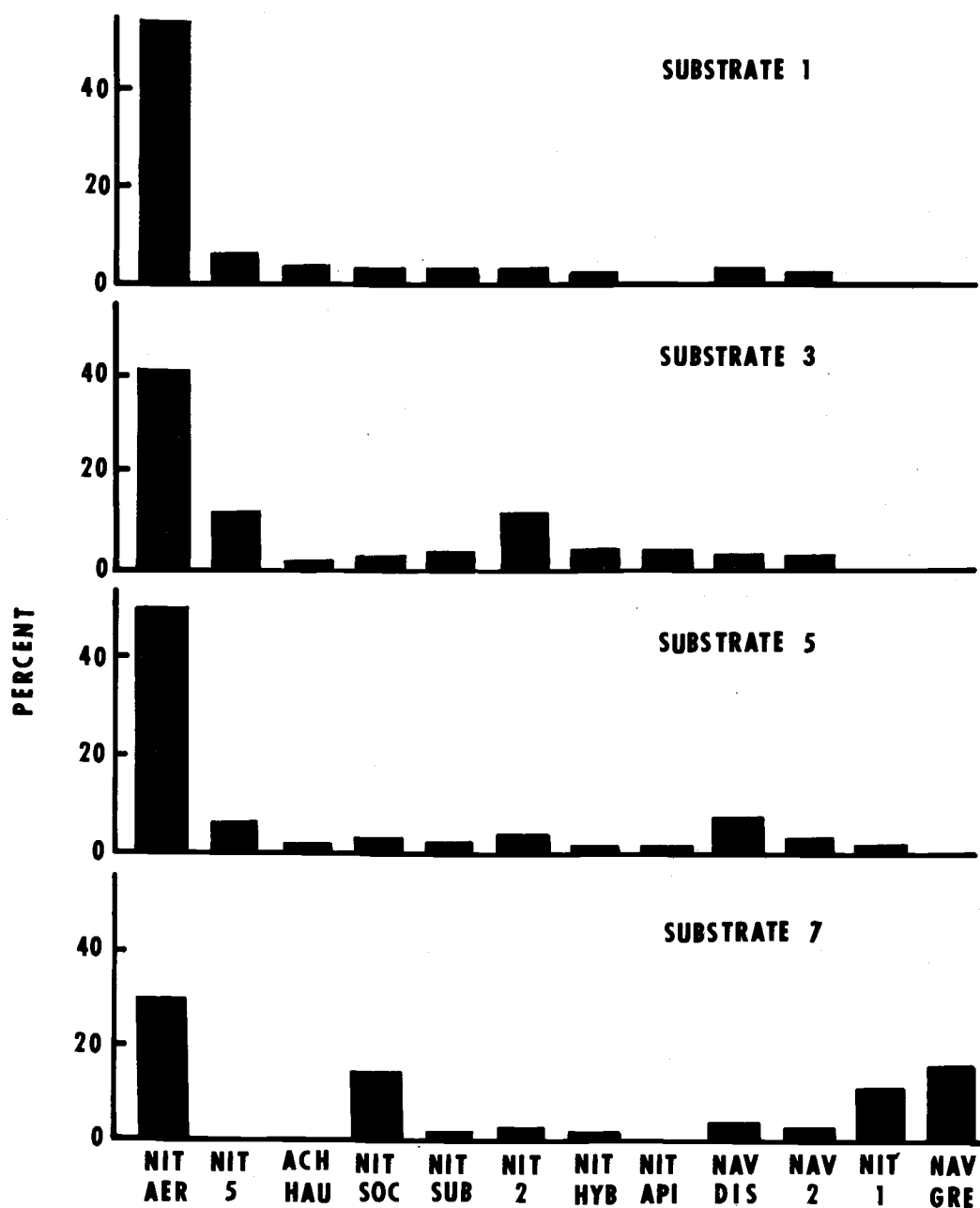


Figure 9. Relative abundance of the five most abundant diatom taxa on substrates 1, 3, and 5 at the conclusion of experiment TC-69. The abbreviations below the horizontal axis correspond to *Nitzschia aerophila*, *Nitzschia* #5, *Achnanthes haukiana*, *Nitzschia socialis*, *Nitzschia subhybrida*, *Nitzschia* #2, *Nitzschia hybrida*, *Nitzschia apiculata*, *Navicula diserta*, *Navicula* #2, *Nitzschia* #1, and *Navicula grevillei*, respectively.

that developed on the upper steps than those from step 1 with less exposure to the atmosphere. The estimated evenness values for substrates 1, 3, and 5 for TC-68 were 0.71, 0.77, and 0.78, respectively. In contrast to TC-68, values of J'' were much lower in TC-69; the estimated values for substrates 1, 3, 5, and 7 were 0.54, 0.63, 0.57, and 0.68.

Table 4. Statistics expressing the structure of diatom communities sampled at the conclusion of TC-68 and TC-69, where N is the number of diatom cells counted, S is the number of species, H'' is the diversity index expressed as bits per individual, and J'' is the evenness component of the diversity index.

Experiment	Substrate	N	S	H''	J''
TC-68	1	522	32	3.56	.71
	3	502	38	4.04	.77
	5	511	41	4.18	.78
TC-69	1	513	40	2.89	.54
	3	544	37	3.27	.63
	5	512	41	3.07	.57
	7	542	32	3.42	.68

Table 5 presents a matrix of difference values and of proportions of co-occurring taxa for comparisons of communities sampled in experiments TC-68 and TC-69. The matrix of difference values is separated into three sectors: (1) the upper left triangle compares the communities within experiment TC-68; (2) the lower right

Table 5. A matrix of difference values D_{jh} (upper right triangle) and of proportions of co-occurring taxa P_{jh} (lower left triangle) for comparisons of communities during experiments TC-68 and TC-69. The values in the table are $(D_{jh} - 1) \times 10^3$ and $P_{jh} \times 10^2$.

		TC-68			TC-69			
		1	3	5	1	3	5	7
TC-68	1		207	234	640	689	590	484
	3	59		66	627	730	630	529
	5	64	70		608	722	622	560
TC-69	1	26	26	28		117	90	272
	3	21	23	22	45		102	309
	5	28	32	34	50	37		230
	7	33	35	37	44	38	55	

triangle compares communities within TC-69; and (3) the upper right rectangle compares communities between the two experiments. The difference values were relatively low for comparisons within an experiment. In comparing communities for experiment TC-68 with those for TC-69, the difference values were relatively high for all comparisons, and the values showed that the lower substrates of TC-68 were most closely related to the upper substrates of TC-69. The matrix of proportions of co-occurring taxa shows that within TC-68 the percentage of species in common ranged from 59-70, while within TC-69 the values ranged from 37-55%. When comparing substrates between TC-68 and TC-69, however, the values were much lower, ranging from 21-37%.

Effect of Light Intensity

The greatest accumulation of biomass during experiments LI-68 and LI-69 occurred on substrate 7, the level that received the highest light intensity. In experiment LI-68 biomasses on substrates 1, 3, 5, and 7 were 103.0, 109.9, 442.0, and 537.5 g/m² dry weight, respectively (Table 6), and the corresponding percentage ash-free dry weight varied between 20 and 32%. For experiment LI-69 biomasses on substrates 1, 2, 3, 4, 5, 6, and 7 were 137.1, 178.3, 212.5, 304.5, 290.6, 165.6, and 588.7 g/m² dry weight, respectively (Table 7). The corresponding values of percentage ash-free dry

Table 6. Biomasses and chlorophyll a concentrations for samples obtained from the laboratory ecosystem during experiment LI-68.

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
1	1,290	103.0	30.0	0.044
3	2,370	109.9	88.7	0.096
5	5,490	442.0	101.0	0.175
7	11,300	537.5	170.6	0.538

Table 7. Biomasses and chlorophyll a concentrations for samples obtained from the laboratory ecosystem during experiment LI-69.

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
1	807	137.1	18.2	0.007
2	1,076	178.3	25.9	0.009
3	2,367	212.5	37.5	0.020
4	3,766	304.5	62.5	0.032
5	5,380	290.6	61.0	0.031
6	10,544	165.6	45.9	0.023
7	17,646	588.7	178.1	0.025

weight for LI-69 varied between 13 and 30%. This percentage value increased progressively from substrates 1 to 7 for experiment LI-69. For experiment LI-68 concentrations of chlorophyll a were greatest on substrate 7 and least on substrate 1. In experiment LI-69 the concentration of chlorophyll a was greatest on substrate 4 and less on upper and lower substrates. The amount of chlorophyll a was much greater in TC-68 than for comparable substrates in TC-69.

In experiment LI-68 rates of gross photosynthesis for substrates from steps 1, 3, 5, and 7 were relatively low at 1,180 lux, ranging from 0.019 to 0.055 g O₂/m² hr (Figure 10). The slope of the curve relating gross photosynthesis to illumination intensity for the community from step 7 was much steeper than the corresponding slopes for the communities from steps 1, 3, and 5 at intensities between 4,950 and 18,450 lux. Apparently, communities from the lower steps approached light saturation at a lower intensity than the community developed at the top step. Rates of photosynthesis for communities from steps 1, 3, 5, and 7 at 18,450 lux, the highest intensity, were 0.206, 0.347, 0.446, and 0.921 g O₂/m² hr, respectively. In experiment LI-69 the gross photosynthetic rate for substrate 5 was greater than that for substrate 7 at all intensities measured above 2,000 lux (Figure 11). The maximum rate of gross photosynthesis for substrate 5 was 0.860 g O₂/m² hr at 18,450 lux. The curve for substrate 3 was irregular, and the community on substrate 1 reached its

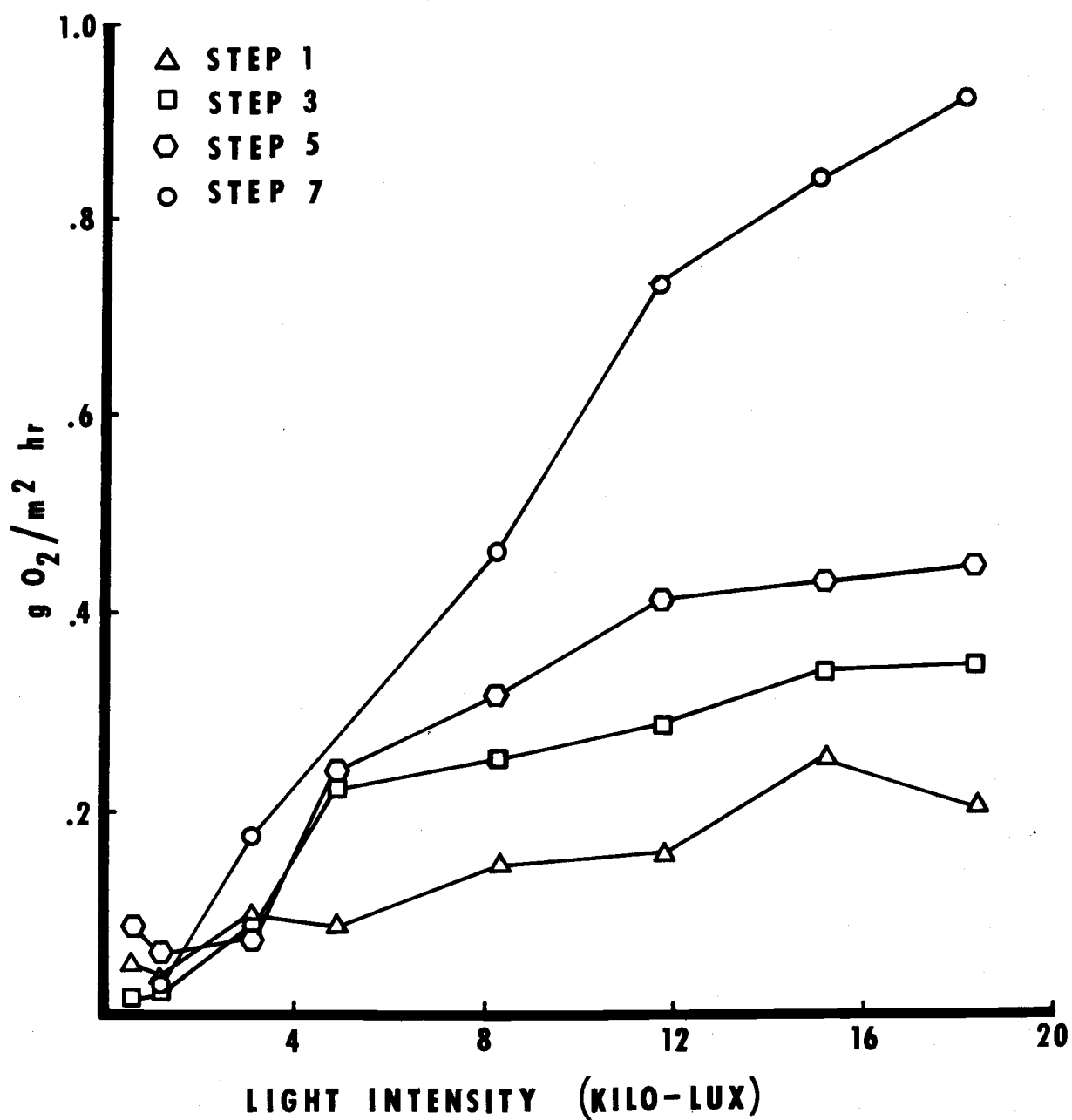


Figure 10. Relationship between illumination intensity and the rate of gross photosynthesis of diatom communities from steps 1, 3, 5, and 7 determined in the respirometer chamber at the conclusion of experiment LI-68.

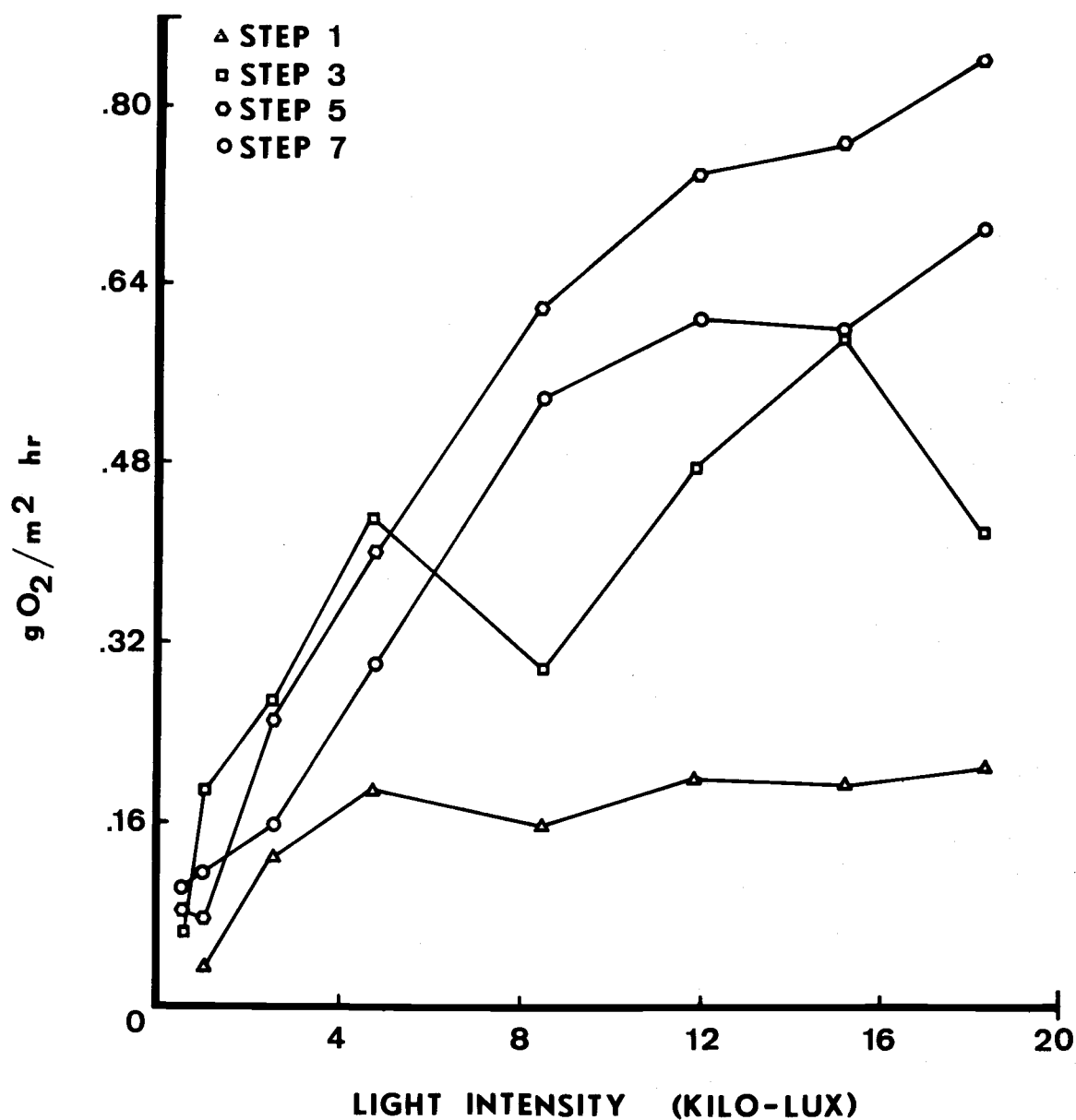


Figure 11. Relationship between illumination intensity and the rate of gross photosynthesis of diatom communities from steps 1, 3, 5, and 7 determined in the respirometer chamber at the conclusion of experiment LI-69.

maximum rate ($0.20 \text{ g O}_2/\text{m}^2 \text{ hr}$) near 4,500 lux. In summary, rates of gross photosynthesis for the two experiments were similar in range, but the corresponding communities did not respond to changes in light intensity in exactly the same way.

Zonation of the more abundant diatoms was closely related to the different light intensities at which the four communities were developed in LI-68. Cocconeis scutellum var. parva represented 33.1% of the community on substrate 1, but was considerably less abundant on the higher substrates (Figure 12). The highest proportions of Synedra fasciculata and Cocconeis costata also were found on substrate 1, the substrate that received the lowest light intensity. The relative abundance of Nitzschia aerophila, Bacillaria paxillifer, and Nitzschia longissima was higher on substrates 3 and 5, than on either substrates 1 or 7. Three species, namely Fragilaria striatula var. californica, Amphipleura rutilans, and Melosira nummuloides, obviously competed best at the highest illumination intensity (11,300 lux). In fact, F. striatula var. californica comprised 52.5% of the total species on substrate 7. The most abundant diatom on all four substrates of LI-69 was Nitzschia aerophila (Figure 13). This was also true in experiment TC-69, and no definite pattern of zonation for this species was apparent in either TC-69 or LI-69. Nitzschia socialis varied in relative abundance from 9.8 (substrate 5) to 20.3% (substrate 1). Nitzschia #5 was more abundant on substrate 3

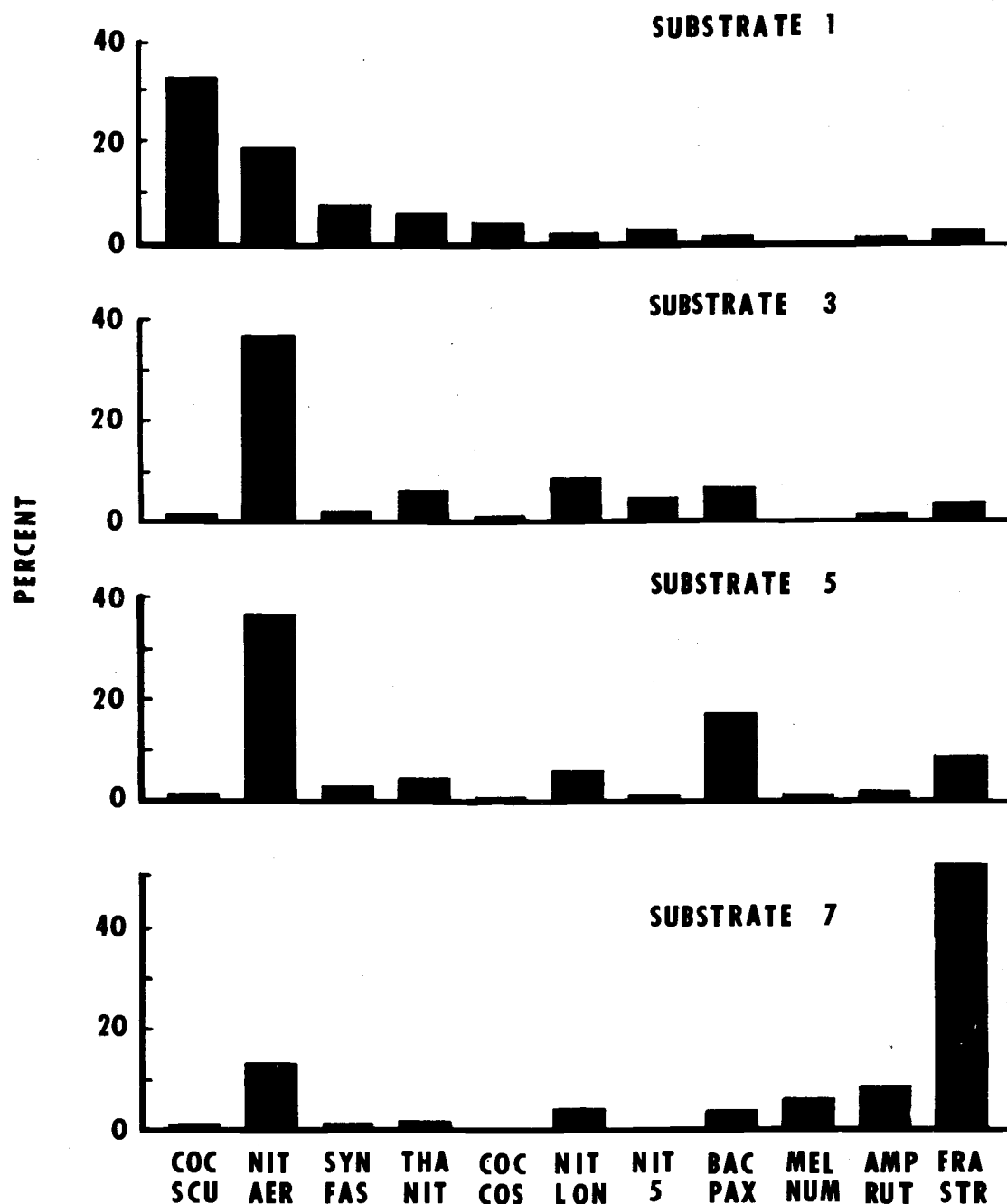


Figure 12. Relative abundance of the five most abundant diatom taxa on substrates 1, 3, 5, and 7 at the conclusion of experiment LI-68. The abbreviations below the horizontal axis correspond to Cocconeis scutellum var. parva, Nitzschia aerophila, Synedra fasciculata, Thalassionema nitzschioides, Cocconeis costata, Nitzschia longissima, Nitzschia #5, Bacillaria paxillifera, Melosira nummuloides, Amphipleura rutilans and Fragilaria striatula var. californica, respectively.

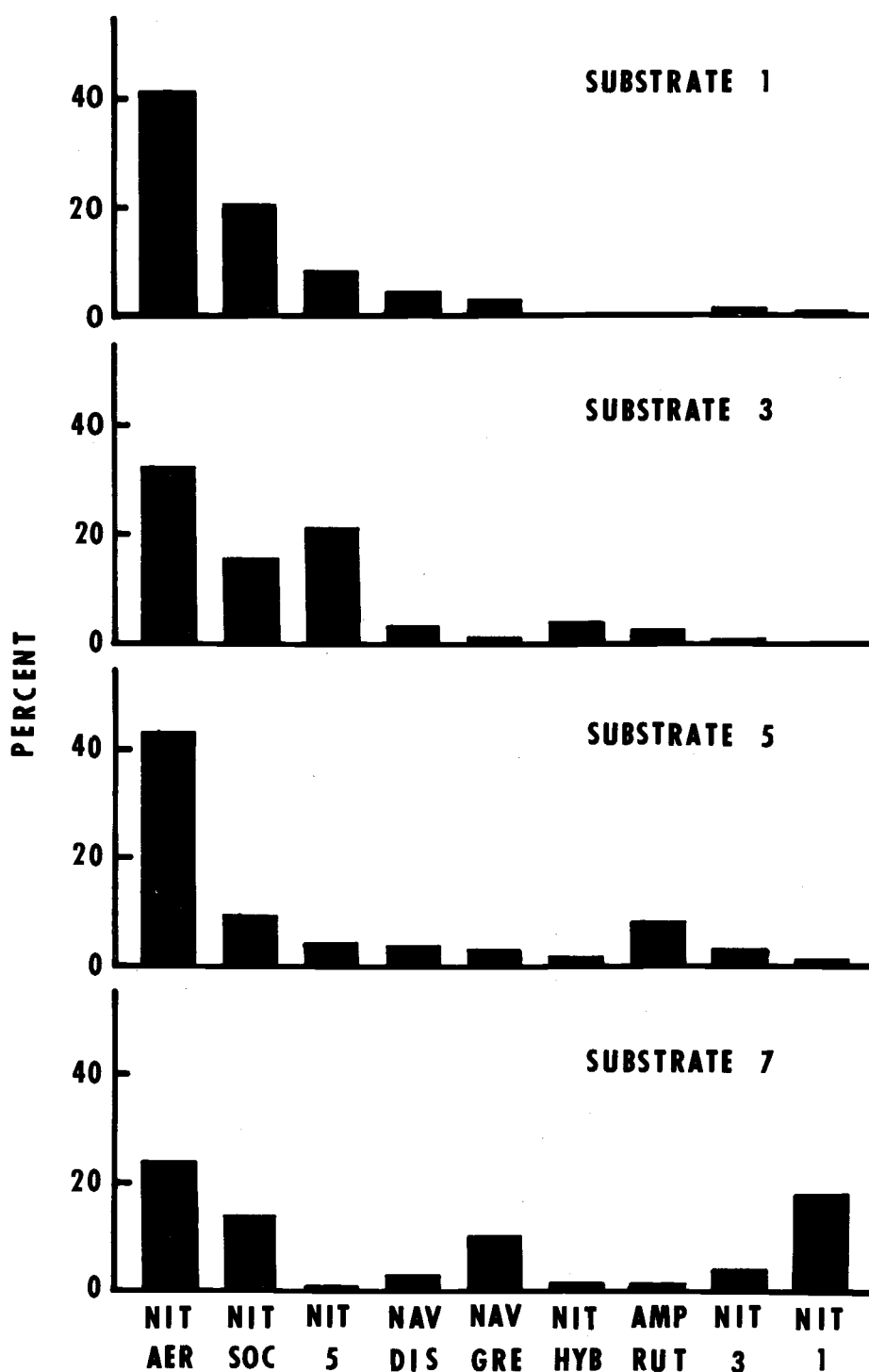


Figure 13. Relative abundance of the five most abundant diatom taxa on substrates 1, 3, 5, and 7 at the conclusion of experiment LI-69. The abbreviations below the horizontal axis correspond to *Nitzschia aerophila*, *Nitzschia socialis*, *Nitzschia* #5, *Navicula diserta*, *Navicula grevillei*, *Nitzschia hybrida*, *Amphipleura rutilans*, *Nitzschia* #3, and *Nitzschia* #1, respectively.

(21.4%) than on substrates at higher or lower light intensities. This species was similarly distributed in LI-68 under summer conditions. Amphipleura rutilans was more abundant on substrate 5 than on other substrates. Navicula grevillei and Nitzschia #1 competed best under conditions of high light intensity and were more abundant on substrate 7 than on any of the lower substrates.

The diversity indices for the four communities examined during experiment LI-68 ranged from 2.59 (substrate 7) to 3.82 (substrate 3), indicating that an illumination intensity of 2,370 lux supported a higher species diversity than intensities of 1,290, 5,490, or 11,300 lux (Table 8). The evenness component J'' was highest (0.69) for the sample from substrate 3 and lowest (0.54) for that from substrate 7. The low diversity value found on substrate 7 was due to the high dominance of Fragilaria striatula var. californica. In experiment LI-69 the diversity index was lowest on substrate 1 (3.17) and highest on substrate 7 (3.78).

Table 9 is a matrix of difference values and proportions of co-occurring taxa comparing communities sampled during LI-68 and LI-69. Within experiment LI-68 the greatest similarity between communities was found between substrates 3 and 5. Furthermore, it is evident that the community from substrate 7 was very different from any other community within LI-68. In LI-69 the difference between communities was generally greater with increasing

Table 8. Statistics expressing the structure of diatom communities sampled at the conclusion of LI-68 and LI-69, where N is the number of diatom cells counted, S is the number of species, H'' is the diversity index expressed as bits per individual, and J'' is the evenness component of the diversity index.

Experiment	Substrate	N	S	H''	J''
LI-68	1	506	41	3.67	.68
	3	497	47	3.82	.69
	5	505	41	3.36	.63
	7	508	28	2.59	.54
LI-69	1	597	39	3.17	.60
	3	502	39	3.29	.62
	5	519	36	3.40	.66
	7	512	33	3.58	.71

Table 9. A matrix of difference values D_{jh} (upper right triangle) and of proportions of co-occurring taxa P_{jh} (lower left triangle) for comparisons of communities during experiments LI-68 and LI-69. Values in the table are $(D_{jh}-1) \times 10^3$ and $P_{jh} \times 10^2$.

		LI-68				LI-69			
		1	3	5	7	1	3	5	7
LI-68	1		205	275	468	385	403	408	500
	3	59		77	332	252	280	261	366
	5	55	60		258	342	383	319	432
	7	57	50	47		581	599	523	611
LI-69	1	30	36	30	31		81	89	175
	3	36	34	36	29	48		96	241
	5	35	32	35	25	56	60		132
	7	32	31	35	30	54	48	58	

differences in light intensity; an exception was the comparison of communities from substrates 1 and 5. When comparing LI-68 and LI-69 differences were greatest between the community on substrate 7 of LI-68 and the communities on all substrates of LI-69. The uniqueness of the community from substrate 7 of LI-68 was attributed to the dominance of Fragilaria striatula var. californica. As in the tidal cycle experiments the proportion of co-occurring taxa was much greater within experiments than between experiments. The percentage of co-occurring taxa within LI-68 and LI-69 ranged from 47-60 and 48-60, respectively, whereas between LI-68 and LI-69 values ranged from 25-35%.

Effects of Reduced Salinity

In experiment RS-69, after the model ecosystem was subjected to 19 days of normal estuarine salinity (RSA), the greatest accumulation of biomass (dry weight) was found on substrate 7 (303.1 g/m^2), the substrate exposed to light intensity of 12,270 lux (Table 10). The biomass on substrate 7 was not appreciably different from that on substrates 1 (279.4 g/m^2) and 4 (285.6 g/m^2), substrates exposed to 1,030 and 4,710 lux, respectively. Biomasses on corresponding substrates in the control system (RSC) after 19 days of normal estuarine salinity were 206.7, 289.9, and 337.8 g/m^2 dry weight. The percentage ash-free dry weight ranged

between 13 and 25% of the total biomass in RSA, while it was only 12 to 18% in the control, RSC. Concentrations of chlorophyll a on the substrates in the ecosystem for RSA corresponded well with those of the substrates in the control system.

Table 10. Biomasses and chlorophyll a concentrations for samples obtained from RSA (normal estuarine salinity for 19 days in the ecosystem) and RSC (normal estuarine salinity for 19 days in the control system).

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
RSA - 1	1,030	279.4	37.6	0.046
RSA - 4	4,710	285.6	47.7	0.198
RSA - 7	12,270	303.1	75.5	0.290
RSC - 1	1,030	206.7	31.4	0.021
RSC - 2	4,380	289.9	35.6	0.092
RSC - 3	12,600	337.8	61.8	0.298

In the model ecosystem a total of ten diatom taxa were among the five most abundant species on the three substrates at the conclusion of RSA, and zonation was related to light intensity (Figure 14). Plagiogramma vanheurckii was the most abundant species on substrate 1 (26%), and its relative abundance was 15% on substrate 4 and 8% on substrate 7. P. brockmanni, Thalassiosira #1, and Navicula diserta competed slightly better at the lowest light intensity (1,030 lux). Nitzschia #2, N. subhybrida, and Gyrosigma

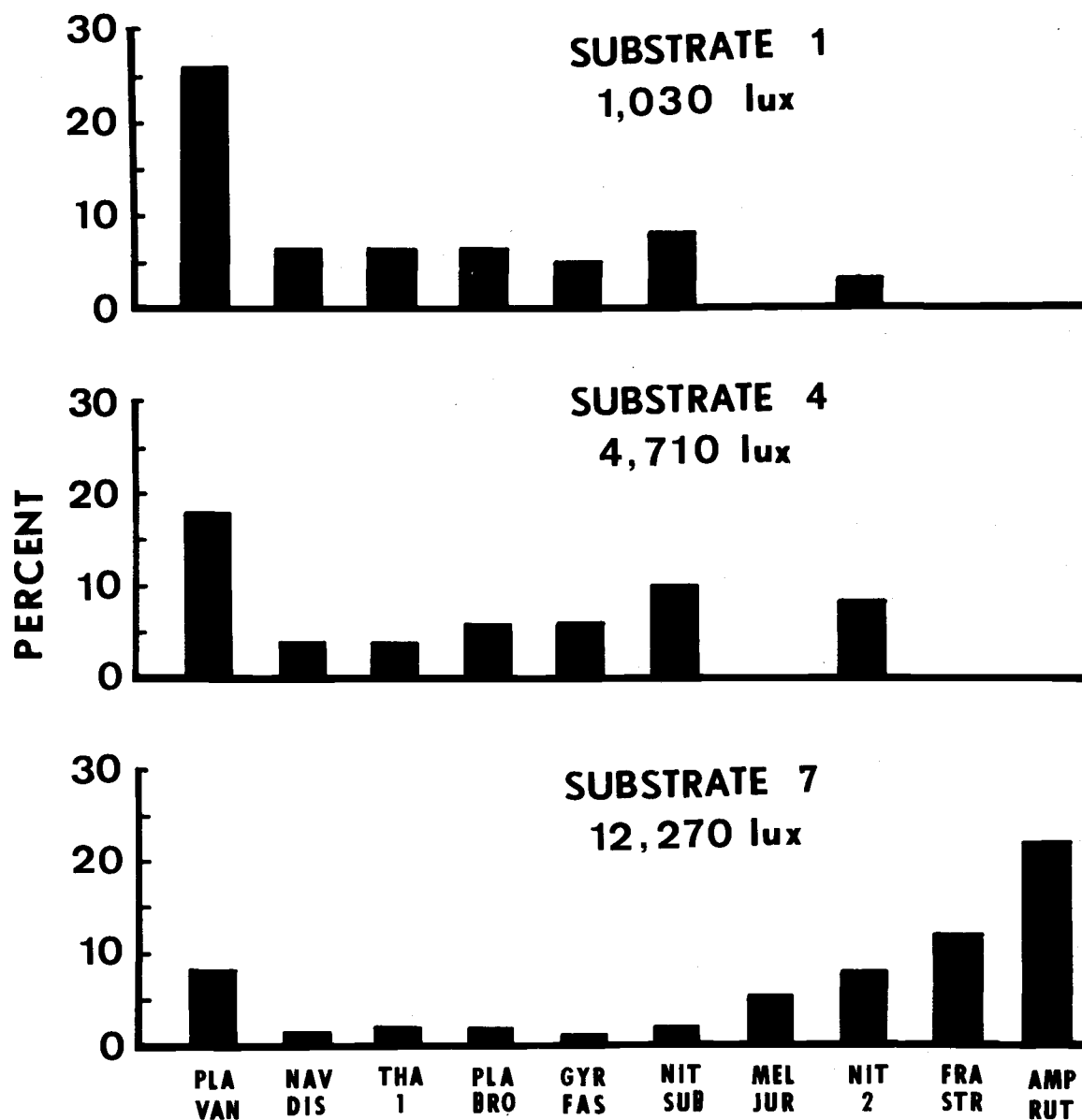


Figure 14. Relative abundance of the five most abundant diatom taxa on substrates 1, 4, and 7 at the conclusion of RSA-69. The abbreviations below the horizontal axis correspond to Plagiogramma vanheurckii, Navicula diserta, Thalassiosira #1, Plagiogramma brockmanni, Gyrosigma fasciola, Nitzschia subhybrida, Melosira jurgensii, Nitzschia #2, Fragilaria striatula var. californica, and Amphipleura ruitlans, respectively.

fasciola were more abundant on substrate 4 (4,710 lux) than on either substrates 1 or 7. Amphipleura rutilans, Fragilaria striatula var. californica, and Melosira jurgensii comprised 22%, 12%, and 6% of the community on substrate 7 (12,270 lux), respectively, while they were either absent or rare on the substrates exposed to lower light intensities. In the control system few distinct zonation patterns were evident (Figure 15). In fact, no species was more abundant than 18% of the total. Plagiogramma vanheurckii and P. brockmanni competed slightly better at the lowest light intensity, whereas Licmophora paradoxa, Synedra fasciculata, Navicula directa, and Navicula #2 favored the highest light intensity (12,600 lux). Navicula diserta and Nitzschia subhybrida competed best at a light intensity of 4,380 lux.

Table 11 shows the diversity indices for communities examined in RSA and RSC. For RSA the diversity index ranged from 4.13 (substrate 7) to 4.50 (substrate 4) bits per individual, and the number of diatom taxa recorded ranged from 44 in 521 individuals (substrate 7) to 51 in 504 individuals (substrate 1). The evenness components for substrates 1, 4, and 7 were 0.76, 0.80, and 0.76, respectively. Diversity indices of corresponding communities in the control (RSC) were 4.25 (substrate 3), 4.36 (substrate 1), and 4.39 (substrate 2). The number of recorded taxa in the control system ranged from 43 in 509 individuals to 50 in 507 individuals. For

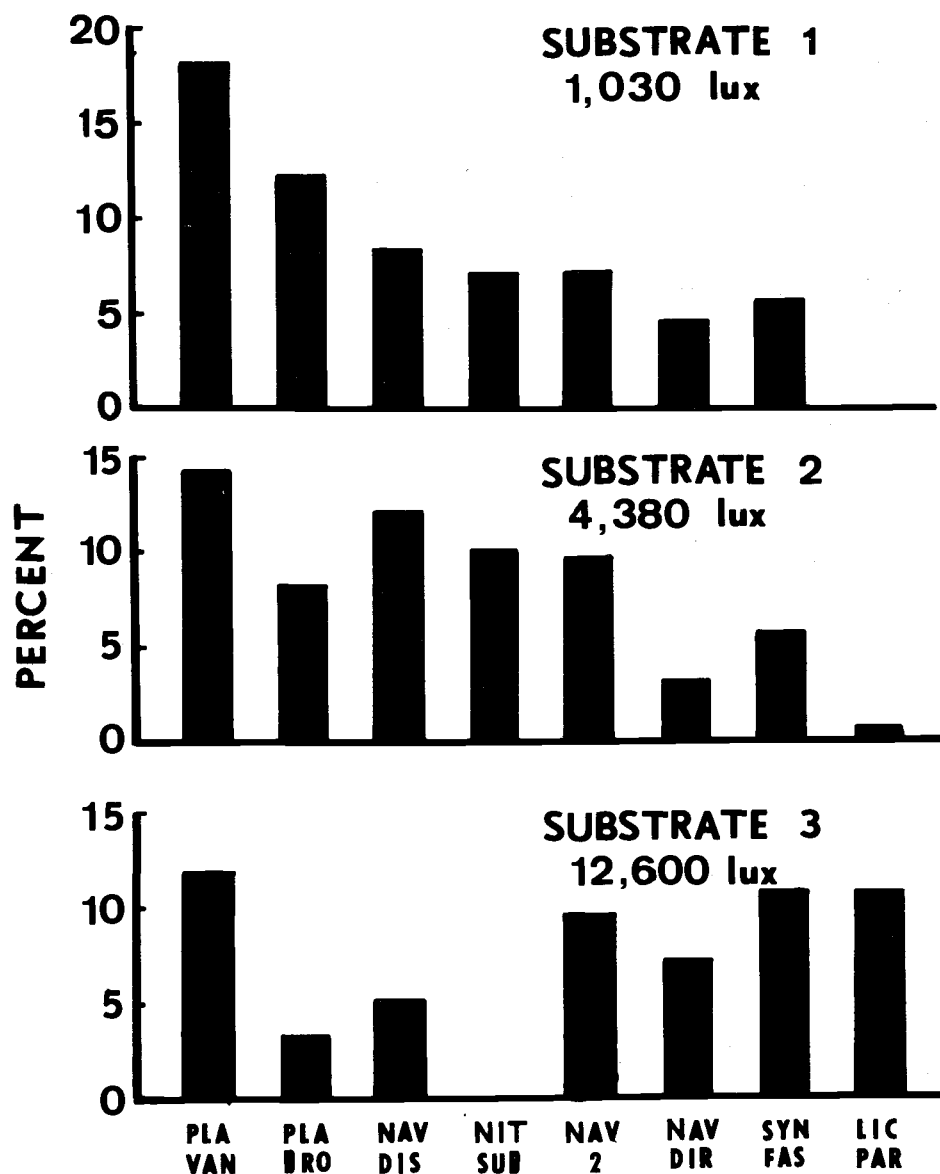


Figure 15. Relative abundance of the five most abundant diatom taxa on substrates 1, 2, and 3 at the conclusion of RSC-69. The abbreviations below the horizontal axis correspond to Plagiogramma vanheurckii, Plagiogramma brockmanni, Navicula diserta, Nitzschia subhybrida, Navicula #2, Navicula directa, Synedra fasciculata, and Licmophora paradoxa, respectively.

RSC the values of evenness were 0.77, 0.79, and 0.78 for substrates 1, 2, and 3, respectively.

Table 11. Statistics expressing the structure of diatom communities sampled at the conclusion of RSA-69 and RSC-69, where N is the number of diatom cells counted; S is the number of species; H'' is the diversity index expressed as bits per individual; and J'' is the evenness component of the diversity index.

Experiment	Substrate	N	S	H''	J''
RSA-69	1	504	51	4.33	.76
	4	506	50	4.50	.80
	7	521	44	4.13	.76
RSC-69	1	507	50	4.36	.77
	2	503	46	4.39	.79
	3	509	43	4.25	.78

Table 12 is a matrix of difference values and proportions of co-occurring taxa for communities developed during RS-69. The difference values for RSA show that communities from substrates 1 and 4 are similar, but the community from substrate 7 is quite different from 1 and 4. The communities on all three substrates of RSC were similar. Values comparing the community from substrate 7 of RSA with communities from substrates 1, 2, and 3 of RSC were greater than all other comparisons between RSA and RSC. Within RSA the proportion of co-occurring taxa ranged from 42-58, within RSC from

Table 12. A matrix of difference Values D_{jh} (upper right triangle) and of proportions of co-occurring taxa P_{jh} (lower left triangle) for comparisons of communities during experiment RS-69. The values in the table are $(D_{jh} - 1) \times 10^3$ and $P_{jh} \times 10^2$.

		RSA			RSB			RSC			RSD			RSE			RSF		
		1	4	7	1	4	7	1	2	3	1	2	3	1	4	7	1	2	3
RSA	1		104	304	55	72	683	72	114	202	133	191	243	95	242	673	180	220	337
	4	58		378	113	67	638	124	107	168	174	210	245	139	263	634	232	233	331
	7	42	49		334	267	966	337	293	235	315	283	223	257	281	500	351	315	298
RSB	1	64	53	46		60	623				134	180	231	101	201	618	175	195	314
	4	63	59	49	68		600				140	168	198	94	201	598	172	186	278
	7	36	37	36	34	39					599	524	396	549	577	50	559	446	470
RSC	1	63	54	49				72	149		98	139	178				127	177	254
	2	52	50	55				55		117	128	134	167				146	178	244
	3	57	48	45				58	62		136	130	125				175	175	182
RSD	1	59	54	51	55	51	34	55	74	52		69	123				80	80	160
	2	51	43	52	49	48	37	53	55	58	63		85				88	84	113
	3	53	52	58	56	55	46	66	62	65	52	58					105	70	103
RSE	1	63	54	52	56	50	34							136	540		131	151	202
	4	59	50	45	58	50	35							67		550	210	193	237
	7	37	40	45	40	45	50							43	47		548	440	448
RSF	1	58	52	47	51	52	37	55	52	61	58	54	55	62	57	42		57	108
	2	56	55	52	58	60	46	62	56	59	64	66	61	60	58	52	66		85
	3	50	55	51	35	48	37	53	49	60	55	59	57	56	57	57	68	69	

55-62, and between RSA and RSC from 48-63%.

Substrates 1, 4, and 7 that were developed under normal estuarine salinity for 19 days followed by 18 days of reduced salinity (RSB) accumulated biomasses of 360.6, 402.5, and 307.2 g/m² dry weight, respectively (Table 13). The values for the corresponding substrates in the control system exposed for the entire 37 days to normal salinity (RSD) were 390.3, 521.3, and 654.8 g/m² dry weight. The percentage ash-free dry weight of the total biomass for RSB varied between 19 and 31%, while in RSD it ranged from 15 to 18%. In general, chlorophyll a concentrations were less on substrates of RSB than on the corresponding substrates of RSD, especially at the higher light intensities.

Table 13. Biomasses and chlorophyll a concentrations for samples obtained from RSB (normal estuarine salinity for 19 days followed by 18 days of reduced salinity) and RSD (normal estuarine salinity for 37 days).

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
RSB - 1	1,030	360.6	13.0	0.121
RSB - 4	4,710	402.5	16.2	0.070
RSB - 7	12,270	307.2	94.4	0.293
RSD - 1	1,030	390.3	60.8	0.061
RSD - 2	4,380	521.3	96.3	0.462
RSD - 3	12,600	654.8	157.4	0.544

In RSB, the community subjected to 12,270 lux (substrate 7) was dominated by Melosira nummuloides, which comprised 68% of the cells in the sample from that substrate (Figure 16). Navicula directa and Amphipleura rutilans showed only a slight competitive advantage on substrate 7 as compared to substrates 1 and 4. Substrates 1 (1,030 lux) and 4 (4,710 lux) were quite similar in proportions of the five most abundant taxa, and Plagiogramma vanheurckii, P. brockmanni, Nitzschia subhybrida, Navicula diserta, and Thalassiosira #1 competed better at 1,030 and 4,710 than at 12,270 lux. In the control system (RSD), where the communities were allowed to develop for 37 days under normal estuarine salinity, no species comprised more than 15% of the cells on any one substrate (Figure 17). Furthermore, few distinct zonation patterns were evident. The relative abundances of Melosira nummuloides and Nitzschia subhybrida were slightly higher on substrate 3 (12,600 lux) than on the other two substrates (1,030 and 4,380 lux). Plagiogramma vanheurckii was relatively more abundant at the lowest light intensity and exhibited a similar distribution to that observed for RSA, RSB, and RSC.

In RSB the diversity index for the community from substrate 7 was much lower than that for communities from either substrates 1 or 4 (Table 14). Also, on substrate 7 there were only 24 species present in 533 individuals counted and the J'' was only 0.47. On substrates 1 and 4 there were 54 and 47 taxa in 500 and 504

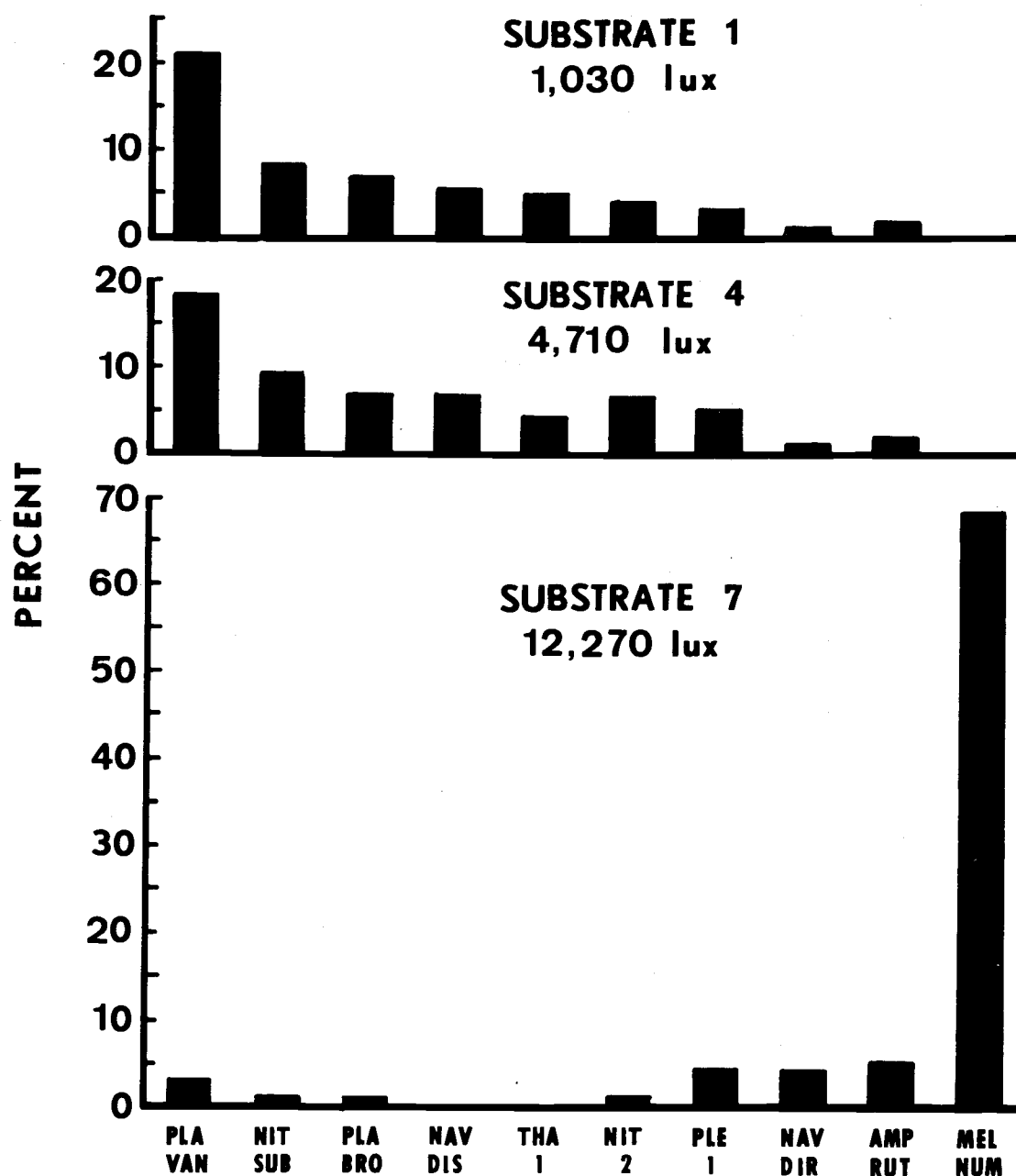


Figure 16. Relative abundance of the five most abundant diatom taxa on substrates 1, 4, and 7 at the conclusion of RSB-69. The abbreviations below the horizontal axis correspond to Plagiogramma vanheurckii, Nitzschia subhybrida, Plagiogramma brockmanni, Navicula diserta, Thalassiosira #1, Nitzschia #2, Pleurosigma #1, Navicula directa, Amphipleura rutilans, and Melosira nummuloides, respectively.

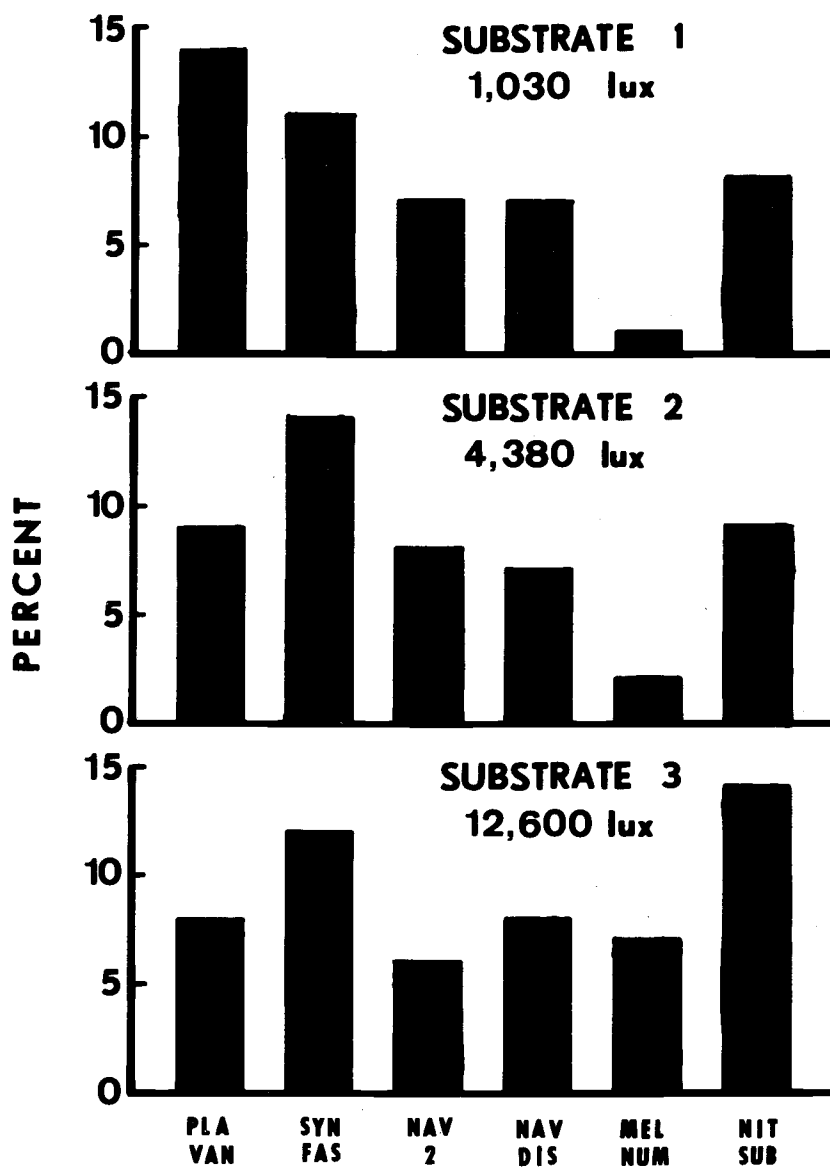


Figure 17. Relative abundance of the five most abundant diatom taxa on substrates 1, 2, and 3 at the conclusion of RSD-69. The abbreviations below the horizontal axis corresponds to Plagiogramma vanheurckii, Synedra fasciculata, Navicula #2, Navicula diserta, Melosira nummuloides, Nitzschia subhybrida, respectively.

individuals, respectively, and the corresponding J'' values were 0.80 and 0.81. In the control system (RSD), the community from substrate 3 had a diversity of 4.33, a value considerably higher than the community from substrate 7 of RSB. The diversity of communities from substrates 1 and 2 of the control system was quite similar to that for the communities from substrates 1 and 4 of the model ecosystem.

Table 14. Statistics expressing the structure of diatom communities sampled at the conclusion of RSB-69 and RSD-69, where N is the number of diatom cells counted, S is the number of species, H'' is the diversity index expressed as bits per individual, and J'' is the evenness component of the diversity index.

Experiment	Substrate	N	S	H''	J''
RSB-69	1	500	54	4.64	.80
	4	504	47	4.50	.81
	7	533	24	2.14	.47
RSD-69	1	513	59	4.79	.81
	2	509	47	4.57	.82
	3	504	43	4.33	.80

The difference values for communities within RSB showed the communities on substrates 1 and 4 to be similar but both were very different from the community on substrate 7 (Table 12). Within the control system (RSD) all three substrates were relatively similar.

Communities on substrates 1 and 4 of RSB were quite similar to the three communities of RSD; however, the community from substrate 7 of RSB was very different from all communities in RSD. When comparing communities of RSA with those of RSB, difference values showed that the community on substrate 7 of RSB had the greatest change in structure after the salinity reduction in the model ecosystem. The communities in the control system in RSD were very similar to those in the model ecosystem for RSA, and difference values ranged from 1.133 to 1.315. Also, communities in RSD were similar to those of RSC, indicating that community structure did not change much in the control during the experiment. Within RSB the proportion of co-occurring taxa was high between substrates 1 and 4 (68%), but low between substrate 7 and substrates 1 and 4 (34 and 39%, respectively). The proportion of co-occurring taxa between RSB and RSD ranged from 34 to 56%. Within the control the values ranged from 52 to 63%.

Communities in the ecosystem that had developed for 18 days at reduced salinity (RSE) had biomasses of 44.8, 108.0, and 145.0 g/m^2 dry weight on substrates 1, 4, and 7, respectively (Table 15). Corresponding communities in the control system that developed for the last 18 days of the experiment under normal salinity (RSF) had biomasses of 384.2, 469.3, and 372.9 g/m^2 dry weight, respectively. The percentage ash-free dry weight varied between 15.5 and 24% in

the control system and 21 and 38% in the ecosystem. Concentrations of chlorophyll a were much higher on comparable substrates in the control system (RSF) except for the substrates receiving 1,030 lux.

Table 15. Biomasses and pigment concentrations for samples obtained from RSE (reduced salinity for 18 days) and RSF (normal estuarine salinity for 18 days).

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
RSE - 1	1,030	44.8	9.4	0.035
RSE - 4	4,710	108.0	31.1	0.032
RSE - 7	12,270	145.0	54.8	0.119
RSF - 1	1,030	384.2	57.3	0.070
RSF - 2	4,380	469.3	72.9	0.354
RSF - 3	12,600	372.9	66.3	0.309

Communities from substrates that developed in the model ecosystem for the last 18 days under reduced salinity (RSE) showed zonation patterns similar to those of corresponding communities in RSB (Figures 16 and 18). In RSE, Plagiogramma vanheurckii, P. brockmanni, and Thalassiosira nitzschoides competed best at the lowest light intensity, while Navicula diserta, Navicula #2, Synedra fasciculata, and Amphipleura rutilans competed better at 4,380 lux than at the higher or lower intensity. Melosira nummuloides completely dominated substrate 7. The control system that developed

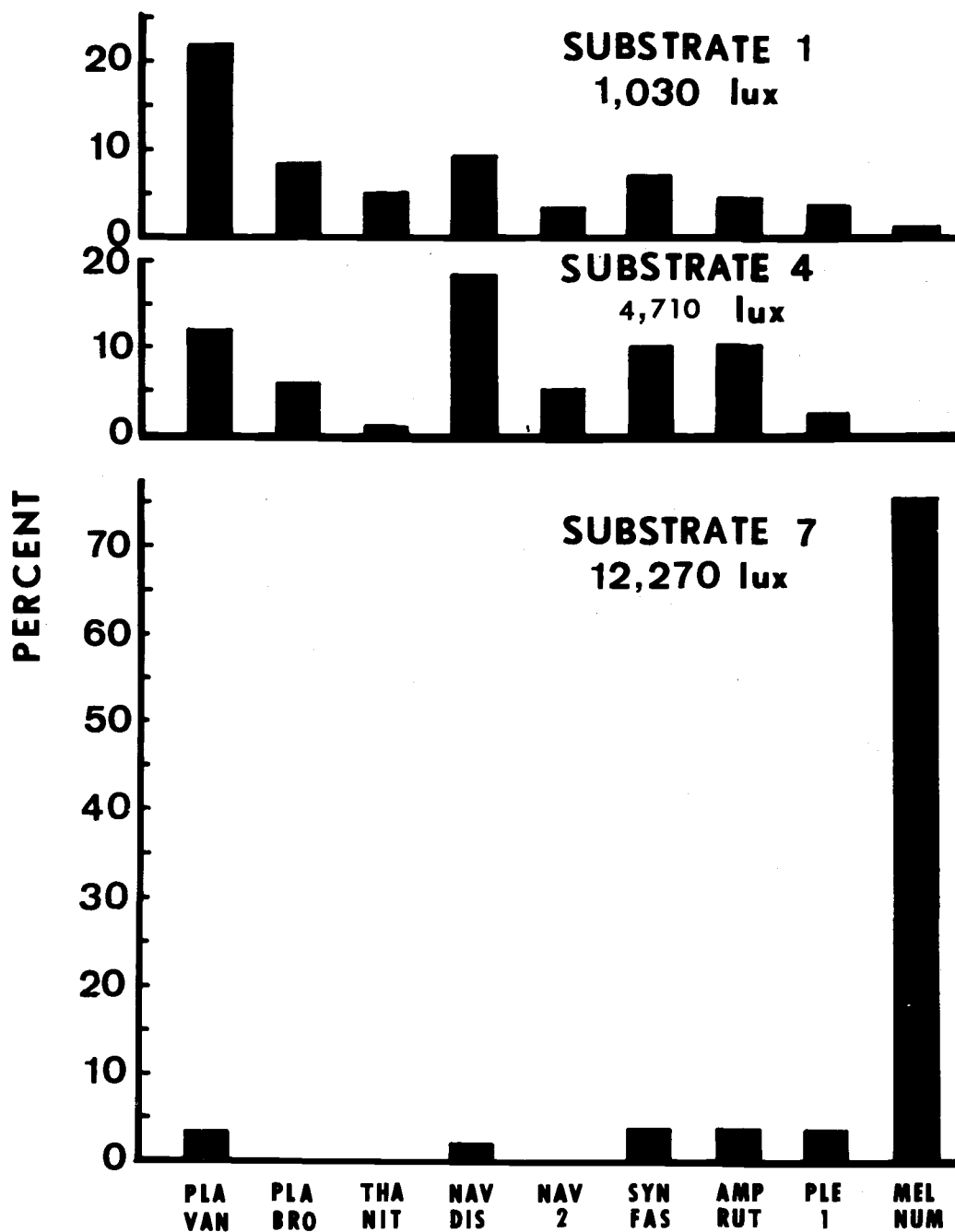


Figure 18. Relative abundance of the five most abundant diatom taxa on substrates 1, 4, and 7 at the conclusion of RSE-69. The abbreviations below the horizontal axis correspond to Plagiogramma vanheurckii, P. brockmanni, Thalassionema nitzschioides, Navicula diserta, Navicula #2, Synedra fasciculata, Amphipleura rutilans, Pleurosigma #1, and Melosira nummuloides, respectively.

under normal estuarine salinity (RSF) for the latter 18 days had few species with a distinct zonal pattern, and no species accounted for more than 20% of the cells on any one substrate (Figure 19).

Diversity indices for communities of RSE showed a pattern similar to that of RSB (Table 16). The number of taxa recorded from substrate 7 was only 27, while 49 and 58 were found on substrates 4 and 1, respectively. The evenness component (J'') was also much less for substrate 7 (0.38) than for substrates 1 (0.79) and 4 (0.79). In the control system (RSF), communities had similar diversity and evenness values and the numbers of taxa on the substrates were approximately equal.

Table 16. Statistics expressing the structure of diatom communities sampled at the conclusion of RSE-69 and RSF-69, where N is the number of diatom cells counted, S is the number of species, H'' is the diversity index expressed as bits per individual, and J'' is the evenness component of the diversity index.

Experiment	Substrate	N	S	H''	J''
RSE-69	1	510	58	4.62	.79
	4	505	49	4.44	.79
	7	507	27	1.81	.38
RSF-69	1	508	47	4.42	.79
	2	502	49	4.39	.78
	3	511	42	4.21	.78

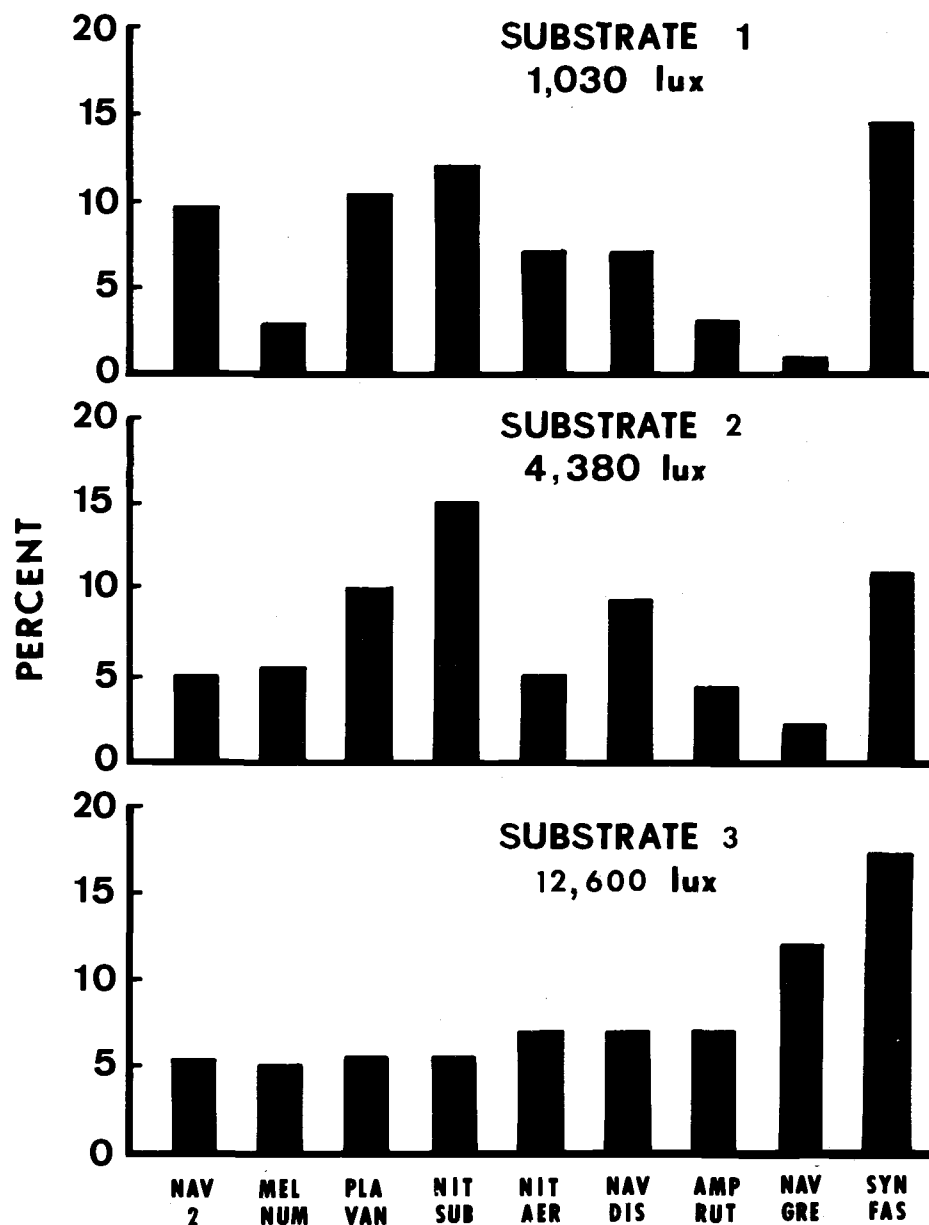


Figure 19. Relative abundance of the five most abundant diatom taxa on substrates 1, 2, and 3 at the conclusion of RSF-69. The abbreviations below the horizontal axis correspond to Navicula #2, Melosira nummuloides, Plagiogramma vanheurckii, Nitzschia subhybrida, Nitzschia aerophila, Navicula diserta, Amphipleura rutilans, Navicula grevillei, and Synedra fasciculata, respectively.

Difference values within RSE (Table 12) indicated that community 7 was quite different from communities 1 and 4, while the difference values within the control system (RSF) were comparatively small. Corresponding communities from substrates 1 and 4 of RSE and 1, 2 and 3 of RSF were similar, but substrate 7 of RSE was different from the others. The communities of RSF were all similar to those of RSA, RSC, and RSD. In comparing RSB with RSE, communities developed on substrate 7 showed the greatest similarity and were different from communities developed at lower light intensities. Communities on the lower substrates were relatively similar to each other. The proportion of co-occurring taxa within RSE was highest between substrates 1 and 4 (67%); within RSF the proportion was relatively high, ranging from 66 to 69%. In comparing the proportion of taxa in common between experiments, the values varied between 42 and 62%.

Effects of Heated Water

The growth of diatoms on substrate 7 during HW-69 was so rapid that mats of Melosira nummuloides and associated taxa floated to the surface and reduced light penetration to the substrates below. Consequently, much of the algal growth was dislodged by the action of the wave board, and biomass accumulation was inhibited on substrate 7 (Table 17). The greatest accumulation of biomass during

the experiment was on substrate 4. The percentage ash-free dry weight was relatively high in the three communities, ranging from 30 to 50%. The concentration of chlorophyll a was greatest on substrate 7.

Table 17. Biomasses and chlorophyll a concentrations for samples obtained from the laboratory ecosystem during HW-69.

Substrate	Light intensity (lux)	Biomass (g/m ²)		Chlorophyll <u>a</u> (g/m ²)
		Dry wt	Ash-free dry wt	
1	1,040	100.0	50.5	0.106
4	3,950	202.4	61.4	0.326
7	16,880	147.9	68.6	0.359

Nitzschia aerophila, N. longissima, Navicula #2, and N. diserta competed best at 3,950 lux, and Nitzschia aerophila was the dominant taxon numerically on all substrates (Figure 20). Plagiogramma vanheurckii and Thalassionema nitzschioides were relatively more abundant at 1,040 lux than at the higher intensities. Melosira nummuloides competed much better at 16,880 lux than at the lower light intensities; it dominated the biomass of substrate 7 and the mats floating at the surface of the system.

The diversity index for the three communities examined in

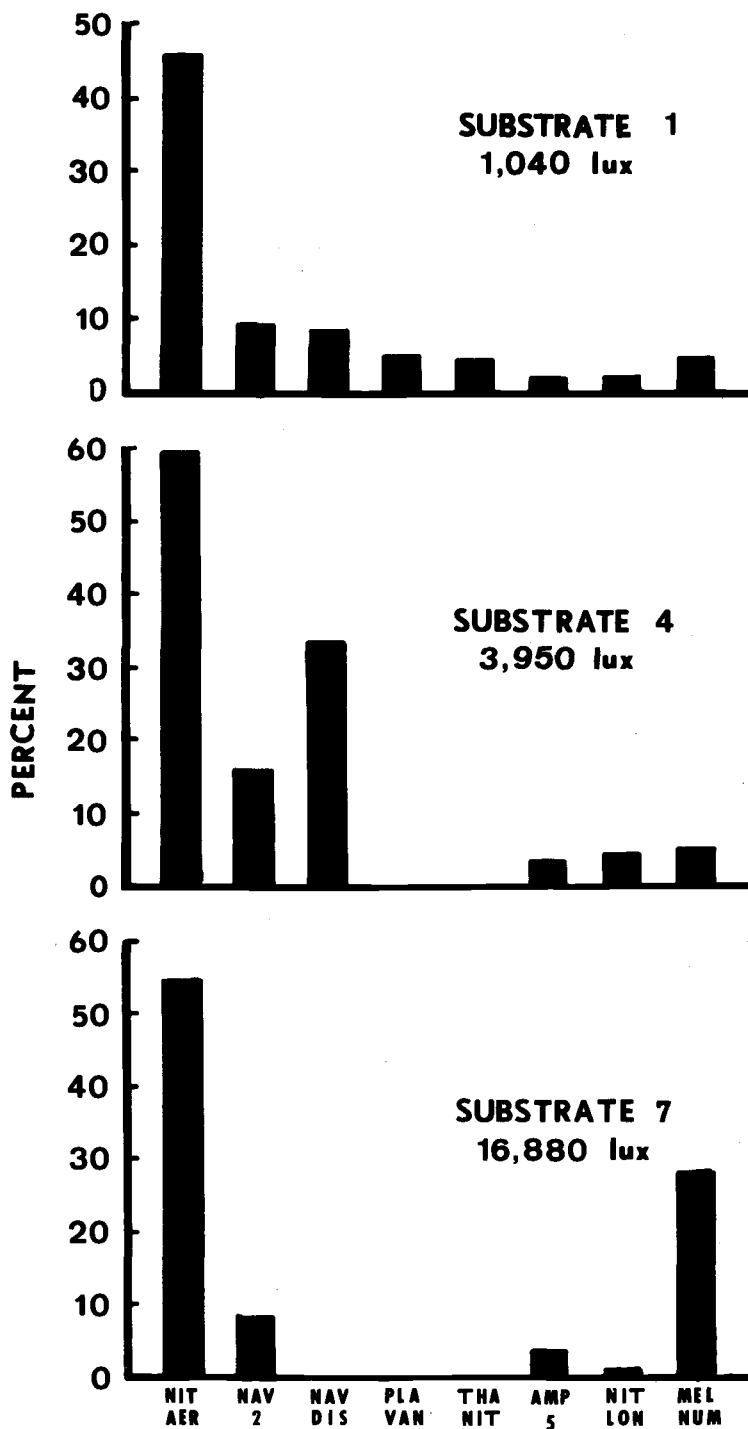


Figure 20. Relative abundance of the five most abundant diatom taxa on substrates 1, 4, and 7 at the conclusion of experiment HW-69. The abbreviations below the horizontal axis correspond to Nitzschia aerophila, Navicula #2, Navicula diserta, Plagiogramma vanheurckii, Thalassionema nitzschioides, Amphora #5, Nitzschia longissima, and Melosira nummuloides, respectively.

HW-69 (Table 18) ranged from 3.19 (substrate 1) to 2.02 (substrate 7). The number of species found in samples from substrates 1 and 7 were 35 and 19 in 506 and 512 individuals, respectively, and J'' ranged from 0.47 (substrate 7) to 0.62 (substrate 1).

Table 18. Statistics expressing the structure of diatom communities sampled at the conclusion of HW-69, where N is the number of diatom cells counted, S is the number of species, H'' is the diversity index expressed as bits per individual, and J'' is the evenness component of the diversity index.

Substrate	N	S	H''	J''
1	506	35	3.19	.62
4	503	26	2.27	.48
7	512	19	2.02	.47

Table 19 is a matrix of difference values comparing communities from HW-69 and RSA of RS-69. RSA was selected because it was believed to be the most representative of the type of community that would develop under normal conditions (i.e., unheated water) at that time. The values are comparatively low within HW-69, ranging from 1.094 to 1.167. In comparing HW-69 with RSA, the values are much larger for all comparisons. The proportion of co-occurring taxa within HW-69 ranged from 35 to 58%, while between HW-69 and RSA the range was between 25 and 46%.

Table 19. A matrix of difference values D_{jh} (upper right triangle) and of proportions of co-occurring taxa P_{jh} (lower left triangle) for comparisons of communities during experiments HW-69 and RSA-69. The values in the table are $(D_{jh} - 1) \times 10^3$ and $P_{jh} \times 10^2$.

		HW-69			RSA-69		
		1	4	7	1	4	7
HW-69	1		94	165	384	448	542
	4	45		89	599	615	652
	7	35	55		731	748	711
RSA-69	1	46	35	27		104	304
	4	39	33	25	58		378
	7	38	37	31	42	49	

DISCUSSION

Communities developed under different regimes of exposure to desiccation in the laboratory model ecosystem responded differently to changes in light intensity in the respirometer chamber. Those substrates that were exposed to the atmosphere and direct light for more than 10 hr per 24-hr day failed to produce sufficient biomass for measurement of physiological activity in the respirometer. Substrates receiving less exposure to desiccation supported dense mats of combined living and detrital organic material. The substrates from the winter experiments showed consistently greater dry weights of material than the corresponding substrates from the summer experiments. However, the percentage of organic material was greater during the summer, as indicated by the greater proportion of ash-free dry weights and higher concentrations of chlorophyll a in samples from TC-68. In TC-68 diatoms accumulated much more rapidly on substrates from steps 1 and 2 than on those from steps 3, 4, and 5. Step-wise increases in illumination intensity in the respirometer allowed light to penetrate deeper into the lower, shaded layers of cells on substrates with high biomasses. Consequently, the photosynthetic rates of the communities from steps 1 and 2 continued to increase as light penetrated deeper into the algal mat. On the substrates from steps 3, 4, and 5 and all five substrates from TC-69, the living mat was thinner

and the communities approached their maximum rate of oxygen evolution at lower light intensities.

Communities adapted to different light intensities during LI-68 and LI-69 also responded differently in the respirometer. Communities developed at the higher light intensities approached their maximum rates of photosynthesis at higher intensities than the other communities. This may have been the result of the greater biomass and concentrations of chlorophyll a on the upper substrates. Moreover, physiological adaptation of individual cells to low light intensities could have been involved. Physiologists have long recognized that shade adapted plants reach their maximum photosynthetic rates at lower light intensities than light adapted plants (Rabinowitch, 1951).

In the reduced salinity experiment the effectiveness of the control system may be determined by comparison of RSA with RSC. For this portion of the experiment, the biomass, number of species, and diversity were similar for the control system and ecosystem, but there was a difference in species composition. This difference may have resulted from a difference in current speed or turbulence over the substrates in the control system.

The effects of reduced salinity or heated water on community development and composition were most dramatic at high light intensities. There was an interaction between high light intensity and either reduced salinity or heated water which promoted very rapid

reproduction in some diatoms. Ruth Patrick (1969) has noted that increases in temperature within the range tolerated by the existing species, provided other factors are suitable, may increase productivity, especially by one or two species. If the natural temperature ranges are exceeded, however, cell division, formation of reproductive cells and photosynthesis will be repressed. Phinney and McIntire (1965) have demonstrated in short term experiments in freshwater communities that an increase in water temperature was accompanied by an increase in gross oxygen evolution at 22,000 lux, but not at 11,100 lux. Both the reduced salinity and heated water experiments reflect Dr. Patrick's observations. In this case, algal mats, primarily of Melosira nummuloides, developed and quickly spread over the substrate receiving the highest light intensity. Soon, bubbles formed under the mat, causing the community to rise to the surface. The higher light intensity at the surface promoted further growth within the floating community, which became so dense that the light penetrating to the substrate surface below was severely reduced. Such communities developed in a natural open area would probably have the floating mat broken-up and dispersed by waves and currents. The relatively low biomass recorded on substrate 7 at the conclusion of RSB and RSE in the reduced salinity experiment and the heated water experiment was partially due to a sloughing off of material during sampling.

Differences in the general nature of the diatom floras between experiments were probably the result of both changes in the laboratory conditions and seasonal changes in the properties of the water in the lower estuary. Many of the diatoms found in the laboratory ecosystem also have been reported to occur in estuaries and coastal regions in other parts of the world (Aleem, 1949, 1950; Castenholz, 1967; Chohnoky, 1968; Edsbagge, 1966; Hustedt, 1939, 1955).

Zonation of some of the more abundant taxa in the ecosystem was clearly similar to the vertical distribution observed by Castenholz (1963) on a concrete substrate at Gregory Point near Coos Bay, Oregon. For example, he found that Achnanthes brevipes was present in the greatest numbers near the uppermost limit of the diatom cover. A. brevipes is very similar to the taxon A. temperei found in these experiments, the principal difference being the presence of polar nodules on the pseudoraphe valve of the latter. In this case it is probable that we are speaking of the same taxon. In experiment TC-68 A. temperei was the most abundant diatom species (21% of the community) on substrate 5, the level exposed to desiccation for 8hr/day. On the substrate with no exposure period this diatom represented less than 1% of the community, and it was not found at all during TC-69, nor in any of the subsequent experiments. The niche breadth of this species was only 1.96, indicating a very uneven distribution. A. brevipes is common in lower estuaries

in other areas of the world and is found almost exclusively in the upper intertidal or supralittoral (Aleem, 1949, 1950; Castenholz, 1967; Edsbagge, 1966; Hendey, 1964). McIntire (personal communication), Riznyk (1969) and Martin (1970) found A. temperei in the lower Yaquina estuary, but not restricted to upper intertidal areas.

Castenholz (1963) concluded that Fragilaria striatula var. californica grew poorly at low light intensities and was abundant principally during the spring and summer, observations which were supported by these experiments. Furthermore, Castenholz (1964) has demonstrated that the doubling rate of F. striatula var. californica was significantly lower during short days than long days. However, its tolerance for desiccation was not demonstrated by our experiments. The niche breadth for F. striatula var. californica was 5.48, a reflection of its uneven distribution. Although McIntire (personal communication) found this species commonly on artificial substrates in Yaquina Bay, Martin (1970) found only a few specimens and Riznyk (1969) failed to find any cells on intertidal sand- or mud-flats. Apparently this taxon grows best on solid surfaces, and is much like the nominate variety (Aleem, 1949; Castenholz, 1967).

Although Melosira nummuloides was present on most substrates sampled, it competed best on substrates receiving high light intensities and a minimum exposure to desiccation. High light intensity, especially under conditions of reduced salinity or thermal elevation,

promoted the growth of this diatom almost to the exclusion of other species. The fact that M. nummuloides was present in varying numbers during all experiments and most of the year in various intertidal regions on the Oregon coast suggested that interactions with other marine organisms may have been more important than physical factors in the determination of the distribution and abundance of this diatom. The relatively low niche breadth value for M. nummuloides (8.27) is a manifestation of its high competitive advantage in adverse environments, but it is actually a ubiquitous taxon.

Amphipleura rutilans had a niche breadth of 20.78, indicating a relative evenness in its distribution under the laboratory conditions. In general, it required a rather high light intensity for maximal growth and was intolerant of desiccation. The finding of this species by Aleem (1950) in high intertidal pools is consistent with the data reported here. McIntire (personal communication), during summer 1968, found A. rutilans mostly in the lower intertidal areas of Yaquina estuary; a similar distributional position was reported by Castenholz (1963) at Gregory Point. Thus, desiccation, not light intensity, appears to limit the distribution of A. rutilans in intertidal areas.

Navicula directa, common only during the summer, was moderately tolerant of desiccation. No consistent pattern was evident with regard to light intensity. However, under conditions of reduced

salinity it competed better at the lower light intensities. This does not necessarily implicate the reduced salinity as the causal factor directly; Melosira nummuloides and Nitzschia aerophila may have inhibited the growth of Navicula directa and other species. Its niche breadth of 15.13 indicated an average evenness of distribution under the laboratory conditions.

The tube dwelling form Navicula grevillei showed no apparent zonation in TC-68, but in TC-69 it was limited to substrate 7 with 18 hr/day exposure to the atmosphere. It was found in greater abundance on substrates receiving high light intensity under normal salinity conditions. The growth of this taxon was negligible under conditions of reduced salinity and elevated temperatures at all light intensities. The niche breadth of N. grevillei was 7.12, indicating a rather uneven distribution under the laboratory conditions. These results are consistent with available field data (Castenholz, 1963; Aleem, 1950; Riznyk, 1969).

The cosmopolitan species Plagiogramma vanheurckii competed best under low light intensities and continuous submergence. Reduced salinity did not appear to affect its distribution severely, while thermal elevation reduced its competitive advantage at all light levels. P. brockmanni was not found in either experiment designed to determine the effect of exposure to desiccation. However, Riznyk (1969) and McIntire (personal communication) both found this species in the

lower intertidal areas in Yaquina estuary. P. brockmanni followed a distributional pattern similar to that of P. vanheurckii under conditions of submergence; that is, it was a better competitor at the lower light levels.

Synedra fasciculata was the only species found on all 36 substrates, and its niche breadth was relatively high (23.72). This species did not compete favorably under conditions of extended exposure to desiccation nor high light intensity. This was in contrast to the findings of Riznyk (1969). Although this species is common in brackish water, reduced salinity had no effect on its abundance in these experiments.

The species having the highest niche breadth was Navicula diserta (28.18). Like Synedra fasciculata, it tolerated a wide range of environmental conditions and was rather equitably distributed on the substrates in each experiment. Hustedt (1955) has remarked that N. diserta is probably cosmopolitan, and Cholnoky (1960) has determined that this species could not tolerate changes in osmotic pressure, i.e., salinity. Thus, N. diserta is most likely a marine species having populations with different tolerances for brackish water.

Nitzschia aerophila had a niche breadth of 17.87, and was one of the most abundant taxa found during the experiments. It was not very tolerant of reduced salinity, but competed extremely well at an elevated water temperature. Light intensity did not appear to have

any effect on controlling distribution. It is exceptionally rare in Yaquina estuary (McIntire, personal communication). Thus, N. aerophila is a taxon that is always present, but under certain laboratory conditions it can develop sizable populations.

Amphora #1, Melosira sulcata and Navicula cancellata var. apiculata exhibited relatively high niche breadths. In spite of their rarity during the experiments, they were found to survive under a wide range of environmental conditions. Several other species with slightly lower niche breadths, namely Thalassiosira #1, Thalassionema nitzschioides, Amphora #5, and Navicula abunda, were also widely distributed.

It is of interest to know whether the more abundant species have higher niche breadths. Several attempts were made to fit a linear regression model to the data. The most satisfactory model was

$$B = \beta_0 + \beta_1(\log_e N) + \epsilon.$$

Figure 21 is a graph of the data and regression line. The parameters β_0 and β_1 were estimated by a weighted regression of B_i on $\log_e N_i$, where it was assumed that the variance σ^2 was a function of N_i , that is, $E(\epsilon_N^2) = N\sigma^2$.

The graph indicates that the niche breadth B is a linear function of the logarithm of N , although variability around the fitted line increases as N increases. A similar distributional spread has been

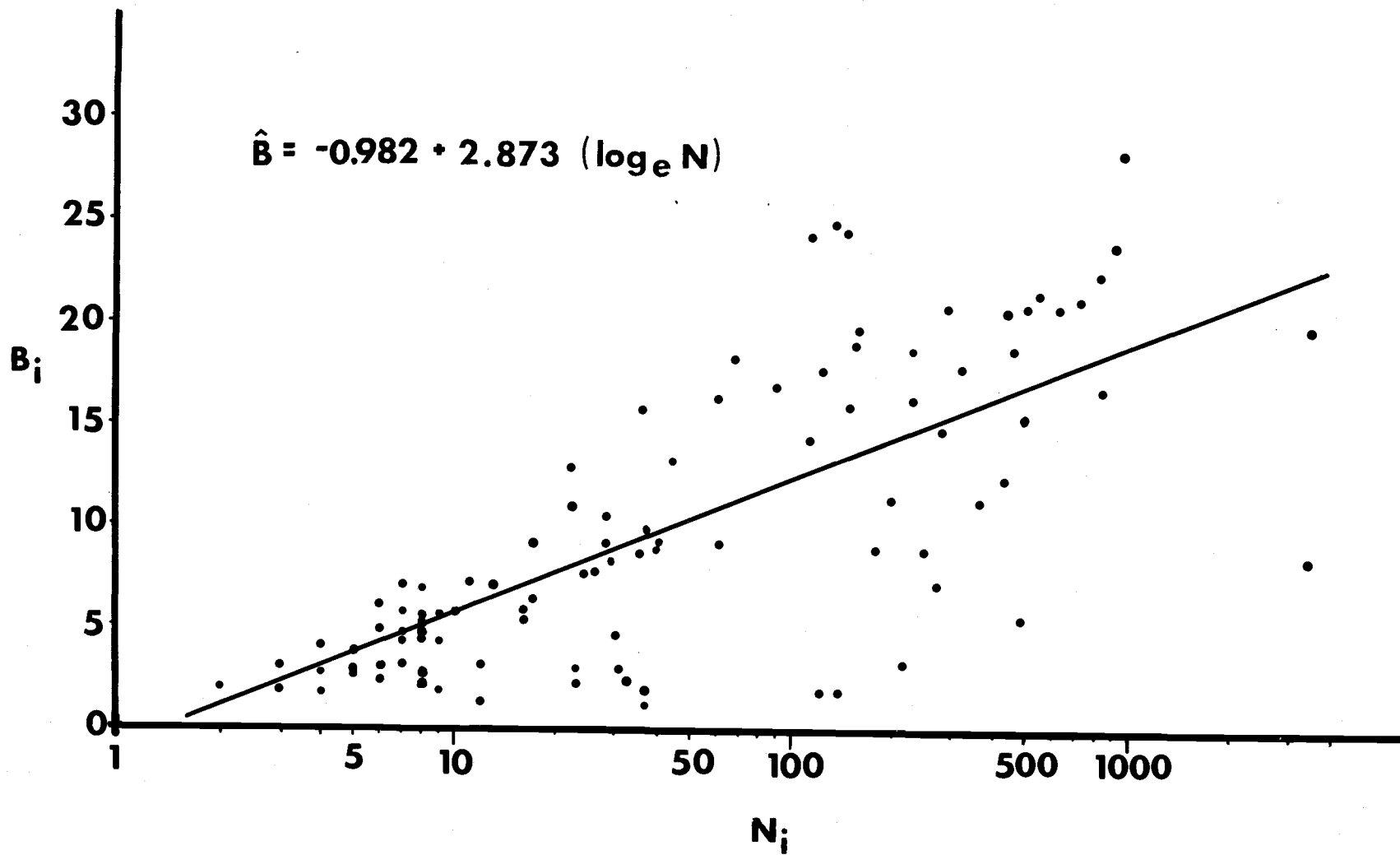


Figure 21. Regression of B_i on the logarithm of N_i .

found for data collected from the estuary (McIntire, personal communication).

In general, the diatom communities were characterized by a relatively large number of taxa represented by one individual. For example, on substrate 3 during experiment LI-68, 26 of the 65 taxa (40%) were represented by only one specimen. There was a strong possibility that many of the specimens representing rare taxa were simply non-living, empty frustules that had washed down from the lower Yaquina River and lodged in the growing community. The presence of a few rare specimens of freshwater species supported this possibility. Therefore, it appeared that a diversity index that de-emphasized the importance of very rare species, such as the H'' value, was the most appropriate for this study.

The relatively high diversity on substrates exposed to long periods of desiccation was difficult to explain. Observations of samples taken from substrates at seven field stations in the Yaquina estuary definitely indicated that diversity was relatively low in the upper littoral zones, areas exposed to long periods of desiccation and direct insolation (McIntire, personal communication). Some of the diversity pattern may have resulted from empty frustules settling on the substrates, but as mentioned above these were rare species in the community and probably would not appreciably influence the magnitude of H'' . If the experiments had been continued for a period longer

than 39 days, perhaps substrates 6 and 7 would have been colonized sufficiently to show lower diversity. In any event, the question of how diversity is related to tidal cycle and degree of desiccation needs clarification by additional experiments.

In experiments designed to determine the effects of light intensity on the communities (LI-68 and LI-69), diversity increased with increasing light intensity in winter, while during the summer the opposite was true. However, in both experiments the smallest number of taxa was found on the substrate with the highest light intensity. In the summer Fragilaria striatula var. californica became extremely abundant, and this species appeared competitively to exclude other species. During the winter this species was not abundant nor was there an ecologically equivalent species that could be associated with the low diversity recorded.

Communities that were developed at 30‰ and later subjected to 15‰ salinity exhibited a significant decrease in diversity at the highest light intensity. A relatively low diversity was also observed in the community developed on the uppermost substrate at 15‰ when seeded with diatoms surviving in 30‰ water. Although many estuarine benthic diatoms are euryhaline, there is evidence that their reproductive maxima occur in a narrow salinity range (Williams, 1964). It is interesting that the introduction of freshwater into marine communities led to extreme dominance in biomass at high light intensities of the

filamentous species, Melosira nummuloides. This same species was dominant in the heated water experiment. Fragilaria striatula var. californica, another filamentous species, was dominant in biomass during the summer under normal salinity conditions.

The introduction of heated water into an aquatic system is an acknowledged pollution problem. Not only is it effective in eliminating some species, but it promotes the growth of others, e.g., Melosira nummuloides. A change in the diversity and species composition sometimes will alter the stability of aquatic systems through time. Furthermore, this often has the effect of disrupting the food chain and consequently secondary production.

Regression equations relating the difference index D_{jh} to environmental variables were calculated for data obtained from the tidal cycle and light intensity experiments. A preliminary analysis indicated that the most satisfactory model for the tidal cycle experiments (TC-68 and TC-69) was

$$\hat{D}_{jh} = b_0 + b_1 \Delta E + b_2 \Delta \bar{S} + b_3 \Delta E \Delta \bar{S}$$

where $\hat{D}_{jh}$ was the predicted value of $\exp [H''_T - \bar{H}'']$, ΔE was the difference in the period of exposure to the air between the j^{th} and h^{th} communities, and $\Delta \bar{S}$ was the difference in the mean salinity between the two experiments. Table 20 is a summary of partial regression coefficients, t-values, and the order of the variable entry

Table 20. A summary table of the partial regression coefficients, t-values, and the order of variable entry for the regression model of the tidal cycle experiments

Independent Variable	b	t(17 d.f.)	Step
ΔE	8.97×10^{-3}	1.99	3
$\Delta \bar{S}$	1.77×10^{-1}	11.21	1
$\Delta E \Delta \bar{S}$	-5.71×10^{-3}	-3.40	2

Intercept = 1.105

$$R^2 = 0.94$$

Table 21. A summary table of the partial regression coefficients, t-values, and the order of variable entry for the regression model of the light intensity experiments.

Independent Variable	b	t(24 d.f.)	Step
ΔL	4.73×10^{-5}	4.57	2
$\Delta \bar{S}$	9.92×10^{-2}	6.93	1
$\Delta L \Delta SR$	-4.19×10^{-6}	-3.82	3

Intercept = 1.091

$$R^2 = 0.72$$

for the model.

The most satisfactory model for the light intensity experiments (LI-68 and LI-69) was

$$\hat{D}_{jh} = b_0 + b_1 \Delta L + b_2 \Delta \bar{S} + b_3 \Delta L \Delta SR,$$

where $\hat{D}_{jh}$ was the predicted value of $\exp [H''_T - \bar{H}'']$, ΔL was the difference in light intensity between the j^{th} and h^{th} communities, $\Delta \bar{S}$ was the difference in mean salinity between the two experiments, and ΔSR was the difference in salinity range between the two experiments. A summary of partial regression coefficients, t-values, and the order of the variable entry for the model is presented in Table 21.

The models generated for both cases fit the data remarkably well. The model for the tidal cycle experiments fit the data better ($R^2 = 0.94$) than the model for the light intensity experiments ($R^2 = 0.72$). In the tidal cycle experiments most of the differences between communities could be attributed to the difference in mean salinity between the summer and winter seasons. In the light intensity experiment the difference in mean salinity between the seasons and the difference in light intensity were strongly associated with differences in communities, and there was a strong negative interaction between light intensity and salinity range.

The response of individual species in the absence of normal

biological interactions may have little relevance to the natural situation. Therefore, this system was constructed to permit normal community development and still maintain some regulation of the physical parameters. Results of these experiments demonstrate the potential of the laboratory model ecosystem as a tool for the investigation of simplified communities. It must be emphasized that all such systems are a simplification of nature, and some reality is usually sacrificed in the process of gaining control over the environment. Thus, interpretation of the data must be made with this in mind. In my opinion, laboratory ecosystems are best used to gain information that can supplement and help understand concurrent field observations.

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APPENDICES

Appendix Table 1. Diatom taxa identified from samples of the laboratory ecosystem for experiments TC-68, TC-69, LI-68, and LI-69. Relative abundance * is expressed as dominant (d), abundant (a), frequent (f), present (p), rare (r), and exceptional (e).

Taxon	TC-68			TC-69				LI-68				LI-69			
	1	3	5	1	3	5	7	1	3	5	7	1	3	5	7
<i>Achnanthes brevipes</i> Ag.	e	p	f												
<i>Achnanthes brevipes</i> var. <i>intermedia</i> (Kütz.) Cl.		e	r												
<i>Achnanthes brevipes</i> var. <i>parvula</i> (Kütz.) Cl.		r	r												
<i>Achnanthes deflexa</i> Reim.								e						e	
<i>Achnanthes hauckiana</i> Grun.				r	r			e	e		e	e	e		
<i>Achnanthes lanceolata</i> (Bréb.) Grun.				e	e	e		e				e			
<i>Achnanthes longipes</i> Ag.			e												
<i>Achnanthes minutissima</i> Kütz.								e	e				e		
<i>Actinopterychus senarius</i> Ehr.		e	e					e			e				
<i>Actinopterychus undulatus</i> (Bail.) Ralfs												e			
<i>Amphipleura rutilans</i> (Trent.) Cl.	r	r	r	e	e	r	r	e	e	r	p	e	r	p	r
<i>Amphiprora alata</i> Kütz.					e	e	e						e	e	e
<i>Amphora angusta</i> Greg.				e											
<i>Amphora ovalis</i> Kütz.								r		e					
<i>Amphora</i> #1	e	e	r	r	e	r	e	r	e	r		r	e	e	
<i>Amphora</i> #2	e	e	e	e		e	e	r	e	e		e	e	e	e
<i>Amphora</i> #3	r		e	e					e	e	e				
<i>Amphora</i> #5					e	r	r					r	r	r	r
<i>Asteromphalus heptactis</i> (Bréb.) Ralfs															
<i>Aulacodiscus probabilis</i> A. S.			e							e					
<i>Bacillaria paradoxa</i> Grmelin				e			r							e	e
<i>Bacillaria paxillifer</i> (Mull.) Hendey	r	r	r					r	p	f	r				
<i>Biddulphia aurita</i> (Lyngb.) Bréb. et Godey	e		e					e							
<i>Caloneis westii</i> (W. Smith) Hendey															
<i>Chaetoceros cinctus</i> Grun.					e			e	e	e	e		e		
<i>Cocconeis costata</i> Greg.				e		e		r	e	e					
<i>Cocconeis californica</i> Grun.															
<i>Cocconeis placentula</i> var. <i>euglypta</i> (Ehr.) Cl.				e		e									
<i>Cocconeis scutellum</i> Ehr.						e		e		e				e	
<i>Cocconeis scutellum</i> var. <i>parva</i> Grun.	e	e	e	e	e	e	e	d	r	e	e	e	e		

Appendix Table 1. (continued)

Taxon	TC-68			TC-69				LI-68				LI-69			
	1	3	5	1	3	5	7	1	3	5	7	1	3	5	7
<u>Cocconeis decipiens</u> Cl.															
<u>Coscinodiscus excentricus</u> Ehr.								e							
<u>Coscinodiscus lineatus</u> Ehr.	e							e	e		e				
<u>Coscinodiscus radiatus</u> Ehr.	e								e						
<u>Cymbella ventricosa</u> Kütz.				e								e			e
<u>Dimmerogramma marinum</u> (Greg.) Ralfs															
<u>Dimmerogramma minor</u> var. <u>nana</u> (Greg.) V. H.										e					
<u>Diploneis bombus</u> Ehr.			e												
<u>Diploneis smithii</u> (Bréb.) Cl.						e									
<u>Eunotogramma marinum</u> (W. Smith) Per.									e						
<u>Fragilaria striatula</u> var. <u>californica</u> Grun.	r	r	r			e		r	r	p	d				e
<u>Frustulia vulgaris</u> (Thwaites) DeT.															
<u>Gomphonema subclavatum</u> var. <u>montana</u> Schum.								e							
<u>Grammatophora angulosa</u> Ehr.															
<u>Grammatophora marina</u> (Lyngb.) Kütz.															
<u>Gyrosigma fasciola</u> (Ehr.) Griff. & Henfr.	e			r	r	e	e	e				e	r	e	e
<u>Gyrosigma febigerii</u> (Grun.) Cl.						e									
<u>Gyrosigma nodiferum</u> (Grun.) Reim.															
<u>Hannaea arcus</u> (Ehr.) Patr.				e											
<u>Licmophora californica</u> Grun.															
<u>Melosira nummuloides</u> (Dillw.) Ag.	f	r	r	e		r	e		e	e	p	r	e	e	r
<u>Melosira sulcata</u> (Ehr.) Kütz.	r	e	r	e		e	e	e	e	e	e	r	e	e	
<u>Meridion circulare</u> (Grev.) Ag.					e					e					
<u>Navicula abunda</u> Hust.	r	e	e		e			r	r	e	e			e	
<u>Navicula agnita</u> Hust.															
<u>Navicula angularis</u> W. Smith															
<u>Navicula auriculata</u> Hust.														e	
<u>Navicula cancellata</u> var. <u>apiculata</u> Greg.	e	e	e		e	r	r	e	e	e		r	r	r	r
<u>Navicula clavata</u> Greg.															
<u>Navicula comoides</u> (Ag.) Per.			e												
<u>Navicula complanatula</u> Hust.	e	e	e					e	e	e	e				

Appendix Table 1. (continued)

Taxon	TC-68			TC-69				LI-68				LI-69			
	1	3	5	1	3	5	7	1	3	5	7	1	3	5	7
<u>Navicula crucigera</u> (W. Smith) Cl.	e	e	e					e	e	e				e	
<u>Navicula cryptocephala</u> Kütz.	e							e	e	e	e				
<u>Navicula directa</u> W. Smith	a	p	p					e		e	e			e	e
<u>Navicula diserta</u> Hust.	r	e	r	r	r	p	r	r	r	r	r	r	r	r	r
<u>Navicula diversistriata</u> Hust.			e						e						
<u>Navicula gregaria</u> Donk.				e		r						e	e	e	e
<u>Navicula grevillei</u> (Ag.) Heib.	e		e				f	e	e	e	e	r	r	r	f
<u>Navicula lyra</u> f. <u>denudata</u> Grun.															
<u>Navicula minima</u> Grun.				e	e										
<u>Navicula mutica</u> Kütz.		r	r				e	e							
<u>Navicula palpebralis</u> Bréb.															
<u>Navicula punctata</u> (Kütz.) Donk.					e										
<u>Navicula punctata</u> var. <u>coarctata</u> Grun.															
<u>Navicula ramosissima</u> Ag.										e					
<u>Navicula secreta</u> var. <u>apiculata</u> Patr.				r	e							e			e
<u>Navicula seminulum</u> Grun.						e									
<u>Navicula tripunctata</u> (Mull.) Bory					e										
<u>Navicula</u> #1														e	
<u>Navicula</u> #2				r	r	r	r					r	e	r	r
<u>Navicula</u> #4							e								
<u>Navicula</u> #5				r	e	e						e		e	
<u>Nitzschia aerophila</u> Hust.	r	r	r	d	d	d	a	f	d	d	f	d	d	d	a
<u>Nitzschia angularis</u> W. Smith				e		e								e	
<u>Nitzschia apiculata</u> (Greg.) Grun.		e		e	r	e	e					e	r	e	
<u>Nitzschia dissipata</u> (Kütz.) Grun.								r	r	e	e				
<u>Nitzschia dissipata</u> var. <u>media</u> Hantz.					r								r	r	
<u>Nitzschia frustulum</u> Kütz.					e										
<u>Nitzschia frustulum</u> var. <u>perminuta</u> Grun.						e	e								
<u>Nitzschia frustulum</u> var. <u>perpusilla</u> (Rabb.) Grun.		e	e					e	r	e			e	e	e
<u>Nitzschia hybrida</u> Grun.				r	r	e	r					r	r	r	r
<u>Nitzschia lanceolata</u> var. <u>minor</u> V. H.	e	p	f												
<u>Nitzschia longissima</u> (Bréb.) Ralfs	e	r						r	p	p	r				

Appendix Table 1. (continued)

Taxon	TC-68			TC-69				LI-68				LI-69			
	1	3	5	1	3	5	7	1	3	5	7	1	3	5	7
<u>Nitzschia sigma</u> (Kütz.) W. Smith	r	p	p					e		e					
<u>Nitzschia socialis</u> Greg.	a	f	f	r	r	r	f	r	r	e		a	f	p	f
<u>Nitzschia subhybrida</u> Hust.	p	r	r	r	r	r	r	e	r	e	e	r	r	r	r
<u>Nitzschia</u> #1		r	e			e	f	e	r	e	e	e		r	f
<u>Nitzschia</u> #2				r	f							e	e	r	r
<u>Nitzschia</u> #3	e	e	r		e			e	r	e		r	r	r	r
<u>Nitzschia</u> #5	e	e	e	p	f	p	e	r	r	e		p	a	r	r
<u>Opephora marina</u> (Greg.) Petit					e										
<u>Plagiogramma brockmanni</u> Hust.				r	e	e	e					e			e
<u>Plagiogramma staurophorum</u> (Greg.) Heib.															
<u>Plagiogramma vanheurckii</u> Grun.		e	e	r		e	r	r	r	r	e	e	e	e	e
<u>Pleurosigma angulatum</u> var. <u>aestuarii</u> (Bréb.) V.H.								e		e					
<u>Pleurosigma decorum</u> W. Smith															
<u>Pleurosigma pergalli</u> Brun															
<u>Pleurosigma</u> #1							r					r	e	e	r
<u>Pseudo-Nitzschia sicula</u> var. <u>migrans</u> Cl.								e	e	e	e				
<u>Rhaphoneis ampiceros</u> Ehr.	e		e						e	e		e			
<u>Rhaphoneis</u> #1		e	e	e	r	e		r	e	e	e	e			
<u>Rhoicosphenia curvata</u> (Kütz.) Grun. ex Rabh.		e	e	e		e		e					e		
<u>Skeletonema costatum</u> (Grev.) Cl.									e	r	e				
<u>Stauroneis phoenicenteron</u> f. <u>gracilis</u> Ehr.												e			
<u>Stephanopyxis turris</u> (Grev. et Arn.) Ralfs												e			
<u>Surirella gemma</u> Ehr.	e						e	e	e	e					
<u>Surirella ovata</u> Kütz.				e	e										
<u>Synedra fasciculata</u> (Ag.) Kütz.	p	p	r	r	r	e	r	p	r	r	r	e	r	e	e
<u>Synedra fasciculata</u> var. <u>truncata</u> (Grev.) Patr.					e										e
<u>Thalassionema nitzschioides</u> Grun.	r	p	f	e		e	e	p	p	r	r	e	e		e
<u>Thalassiosira</u> #1	e	e	r	e	e		e		r	r	r	e	e	e	
<u>Trachyneis aspera</u> Ehr.															

Appendix Table 1. (continued)

Taxon	TC-68			TC-69				LI-68				LI-69			
	1	3	5	1	3	5	7	1	3	5	7	1	3	5	7
<u>Trachysphenia australis</u> Petit			e												
<u>Triceratium alternans</u> Bailey						e									e
<u>Tropidoneis lepidoptera</u> var. <u>minor</u> Cl.															
<u>Tropidoneis maxima</u> var. <u>gracilis</u> Grun.															

* Relative abundance is expressed as:

- dominant (d) = 30% or over of the total number counted;
- abundant (a) = 20 to 30% of the total number counted;
- frequent (f) = 10 to 20% of the total number counted;
- present (p) = 5 to 10% of the total number counted;
- rare (r) = 1 to 5% of the total number counted;
- exceptional (e) = less than 1% of the total number counted.

Appendix Table 2. Diatom taxa identified from samples of the laboratory ecosystem for experiments RS-69 and HW-69. Relative abundance * is expressed as dominant (d), abundant (a), frequent (f), present (p), rare (r), and exceptional (e).

Taxon	RSA			RSB			RSC			RSD			RSE			RSF			HW		
	1	4	7	1	4	7	1	2	3	1	2	3	1	4	7	1	2	3	1	4	7
<u>Achnanthes deflexa</u> Reim													e								e
<u>Achnanthes hauckiana</u> Grun.	r	e	e	r	e		r	e	e	e		r	r	e		e		e	e		
<u>Achnanthes lanceolata</u> (Breb.) Grun.	e	e		r	e					e			e	r	e			e	e		
<u>Achnanthes minutissima</u> Kütz.	e			e	e				e												
<u>Amphipleura rutilans</u> (Trent.) Cl.	e		a	r	r	p		e	r	r	r	p	r	p	e	r	r	p	e	e	e
<u>Amphiprora alata</u> Kütz.		e	e	e	e		e					e			e		e	e			
<u>Amphora</u> #1		e	e	e	r		r	e	e	r	r		r	e		r	e	e	r		
<u>Amphora</u> #2	e		e	r	e		e			e	r		e				e		r		
<u>Amphora</u> #3			e							e	e	e	e		e	e	e	r	e		
<u>Amphora</u> #4										e				e					e		
<u>Amphora</u> #5	e	r		r	e	e	e	e	e	e	r	e	e	r	e	e	e	e	r	r	r
<u>Aulacodiscus probabilis</u> A. S.								e													
<u>Bacillaria paradoxa</u> Gmelin	e	e	r	e		r	e	e		e	e	r	e	e			e			r	e
<u>Bacteriastrium delicatulum</u> Cl.			e																		
<u>Bacteriastrium varians</u> Laud.			e																		
<u>Biddulphia aurita</u> (Lyngb.) Breb. et Gody	r	e	e	e	e		e	r		e	r	e	e			r				e	e
<u>Cocconeis costata</u> var. <u>pacifica</u> (Grun.) Cl.								e			e										
<u>Cocconeis placentula</u> var. <u>euglypta</u> (Ehr.) Cl.	e	e		e			e			e		e	e	e		e			e		
<u>Cocconeis placentula</u> var. <u>lineata</u> (Ehr.) Cl.				e	e			e													
<u>Cocconeis scutellum</u> Ehr.	e			e			e						e	e					e		
<u>Cocconeis scutellum</u> var. <u>parva</u> Grun.				e	e		e	e	e	e	e	e		r					e	e	
<u>Cocconeis</u> #1								r	e		e		e	e		e		e			
<u>Coscinodiscus curvatus</u> Grun.			e	e						e											
<u>Coscinodiscus excentricus</u> Ehr.		e								e											
<u>Coscinodiscus lineatus</u> Ehr.									e				e	e							
<u>Coscinodiscus radiatus</u> Ehr.													e								
<u>Cyclotella meneghiniana</u> Kütz.							e	e	e												
<u>Cymbella ventricosa</u> Kütz.				e																	
<u>Diatoma hiemale</u> var. <u>mesodon</u> (Ehr. Grun.)						e															
<u>Dimmerogramma minor</u> Greg.																					

Appendix Table 2. (continued)

Taxon	RSA			RSB			RSC			RSD			RSE			RSF			HW		
	1	4	7	1	4	7	1	2	3	1	2	3	1	4	7	1	2	3	1	4	7
<u>Diploneis elliptica</u> (Kütz.) Cl.	e																				
<u>Eunotia tenella</u> (Grun.) Cl.		e											e								
<u>Eunotogramma marinum</u> (W. Smith) Per.																					
<u>Fragilaria construens</u> var. <u>venter</u> (Ehr.) Grun.									e												
<u>Fragilaria striatula</u> var. <u>californica</u> Grun.			f			r	e	e				r	e		e	e	e	e	e		
<u>Frustulia vulgaris</u> (Thwaites) DeT.		e																			
<u>Gomphonema parvulum</u> Kütz.					e																
<u>Grammatophora marina</u> (Lyngb.) Kütz.	e																				
<u>Grammatophora oceanica</u> var. <u>macilenta</u> f. <u>subtillissimum</u> W. Smith	e																				
<u>Gyrosigma angulatum</u> Griff. et Henf.		e																			
<u>Gyrosigma balticum</u> (Ehr.) Rabh.							e														
<u>Gyrosigma fasciola</u> (Ehr.) Griff. et Henfr.	p	p	r	r	p	e	r	r	r	e	r	e	r	r	e	e	e	e			
<u>Gyrosigma febigerii</u> (Grun.) Cl.		e		e	e	r		e				e		r	r		e				
<u>Gyrosigma peisoneis</u> (Grun.) Cl.			e																		
<u>Gyrosigma nodiferum</u> (Grun.) Reim.																					
<u>Licmophora californica</u> Grun.										e	e					e	e	e			
<u>Licmophora gracilis</u> (Ehr.) Grun.										e											
<u>Licmophora paradoxa</u> (Lyngb.) C. Ag.	e	r	r		e	e	e		f	r	r	p	r		e	e	r	r			
<u>Licmophora</u> #1							e		e			e				e	e	e			
<u>Melosira jurgensii</u> C. Ag.			p		e																
<u>Melosira nummuloides</u> (Dillw.) C. Ag.			r	e		d	e	e	e	e	r	p	r	e	d	r	p	p	r	p	a
<u>Melosira sulcata</u> (Ehr.) Kütz.	r	r	e	r	e	e	r	e	e	r	r	e	e	e		r	r	e	r		
<u>Navicula abunda</u> Hust.	r	r	e	r	e		e	r	e	r	r	r	e	e		e	e	e	e		
<u>Navicula agnita</u> Hust.				e							e		e	r	e		e	e			
<u>Navicula auriculata</u> Hust.	e			e			e			e						e		e			
<u>Navicula cancellata</u> var. <u>apiculata</u> Greg.	r	r	e	r	e		r			r	r	e	e	e	e	e	r	e	e		e
<u>Navicula clavata</u> var. <u>subconstricta</u> Hust.											e										
<u>Navicula complanatula</u> Hust.											e										e
<u>Navicula crucigera</u> (W. Smith) Cl.										e	r					e	e		e		
<u>Navicula cryptocephala</u> Kütz.		e																			

Appendix Table 2. (continued)

Taxon	RSA			RSB			RSC			RSD			RSE			RSF			HW		
	1	4	7	1	4	7	1	2	3	1	2	3	1	4	7	1	2	3	1	4	7
<i>Navicula directa</i> (W. Smith) Ralfs	e	r	r	r	r	r	r	r	p	r	r	p	r	r	e	r	r	r		e	
<i>Navicula diserta</i> Hust.	p	r	r	p	p		p	f	p	p	p	p	p	f	r	p	p	p	p	r	e
<i>Navicula diversitriata</i> Hust.		e											e								
<i>Navicula finmarchica</i> (Cl. et Grun.) Cl.							e														
<i>Navicula granulata</i> Bréb.		e																			
<i>Navicula gregaria</i> Donk.	r	r	e	r	r		r	r	e	r	e	e	r	r	e		e			e	e
<i>Navicula grevillei</i> (C. Ag.) Heib.		e	e					e	e	e	e	e	e	e		e	r	f			
<i>Navicula minima</i> Grun.					e																
<i>Navicula secreta</i> var. <i>apiculata</i> Patr.	e									e	e		e	e							
<i>Navicula tripunctata</i> (Müll.) Bory							e						e			e					
<i>Navicula tripunctata</i> var. <i>schizonemoides</i> (V. H.) Patr.								e		e							e				
<i>Navicula viridula</i> var. <i>avenacea</i> Cl. et Grun.											e		e								
<i>Navicula</i> #1	e	e		e	r	e	e	r		e						e	e				
<i>Navicula</i> #2	p	r	r	r	p	e	p	p	p	p	p	p	r	p		p	p	p	p	f	p
<i>Navicula</i> #3	e								e					e		e		e			
<i>Navicula</i> #4	e	e											e			e					
<i>Navicula</i> #5													e								
<i>Nitzschia aerophila</i> Hust.	e	e	e	r	r		r	r	r	r	r	r	r	e		p	p	p	d	d	d
<i>Nitzschia angularis</i> W. Smith	e			e				e	e	r	r	e	r	r			e	e			
<i>Nitzschia apiculata</i> (Greg.) Grun.	e			e	e		e		e	r	e		e	e		e	e				
<i>Mitzzschia dissipata</i> var. <i>media</i> Hantz	e	r		r	e		e										e		e	e	
<i>Nitzschia frustulum</i> var. <i>perminuta</i> Grun.				e							e			e	r						
<i>Nitzschia frustulum</i> var. <i>perpusilla</i> (Rabh.) Grun.	r			e	r		e	e	e			e	r	e		e	e	e	r	e	e
<i>Nitzschia frustulum</i> var. <i>subsalina</i> Hust.		e	e																		
<i>Nitzschia hybrida</i> Grun.	e	e		e	e		e		e	r			r	r	e	e	r	e			
<i>Nitzschia longissima</i> (Bréb.) Ralfs	e	p	r	e	r		e	r	p	e	e	e	e	e	e	e	e	e	r	r	e
<i>Nitzschia sigma</i> (Kütz.) W. Smith	e	e	r		r	r	e		r	e	e	r	e	r	e		e	e		e	
<i>Nitzschia socialis</i> Greg.	e	e		e	e	e	e		e	r	r	e	e	r	e	r	p	r	e		
<i>Nitzschia subhybrida</i> Hust.	p	f	r	p	p	e	p	f	p	p	p	f	r	r	e	f	f	p	e		
<i>Nitzschia</i> #1	e	r	e	e	r		r	r	r	e	e	e	e	e		e	e	e			
<i>Nitzschia</i> #2	r	p	p	r	p	r	r	p	p	r	e	r	r	r	r	e	r	r	r	e	

Appendix Table 2. (continued)

Taxon	RSA			RSB			RSC			RSD			RSE			RSF			HW		
	1	4	7	1	4	7	1	2	3	1	2	3	1	4	7	1	2	3	1	4	7
<u>Nitzschia</u> #3	e	r					e	e		r			r	e		r	e	e			
<u>Nitzschia</u> #5	r			r	r	e			e	e			e	r		r	e		e	e	r
<u>Nitzschia</u> #7										e											
<u>Nitzschia</u> #8			e																		
<u>Opephora</u> #1							e					e	e	e							
<u>Plagiogramma brockmanni</u> Hust.	p	p	r	p	p	r	f	p	r	r	p	r	p	r	e	r	r	r	r	r	e
<u>Plagiogramma vanheurckii</u> Grun.	a	f	p	a	f	r	f	f	f	f	p	p	a	f	r	p	f	p	p	e	e
<u>Pleurosigma angulatum</u> var. <u>aestuarii</u> (Bréb.) V. H.										e	e			e		e	e				
<u>Pleurosigma</u> #1	e	p	r	r	r	r	r	r	r	e	r	r	e	r	r	e	r	r			
<u>Pseudo-Nitzschia australis</u> Freng.										e											
<u>Pseudo-Nitzschia</u> #1		e	e					e		e			e						e	e	e
<u>Rhaphoneis amphiceros</u> Ehr.	e	e	e	r	e		e	e	e	e	e		e			e	e	e			
<u>Rhaphoneis</u> #1	e	e		e	e	e	e	r	e	e	e	e	e				e		e		
<u>Rhoicosphenia curvata</u> (Kütz.) Grun. ex Rabh.					e																
<u>Stephanopyxis turris</u> (Grev. et Arn.) Ralfs			e	e																	
<u>Surirella gemma</u> Ehr.																e					
<u>Synedra fasciculata</u> (C. Ag.) Kütz.	r	r	r	r	r	r	p	p	f	f	f	f	p	p	r	f	f	f	r	e	e
<u>Synedra fasciculata</u> var. <u>truncata</u> (Grev.) Patr.	e	e		e	e			e	e												
<u>Thalassionema nitzschioides</u> Grun.	r	r	e	r	r	e	p	r	r	r	r	e	r	e	e	r	r	e	r	e	e
<u>Thalassiosira aestivalis</u> Gran et Angst	e		e				r	e	e		e	e	e	e							
<u>Thalassiosira</u> #1	p	r	r	r	r		p	r	r	r	r	r	r	r	e	r	r	r	r	r	
<u>Triceratium alternans</u> Bailey										e										e	

* Relative abundance is expressed as:

- dominant (d) = 30% or over of the total number counted;
 abundant (a) = 20 to 30% of the total number counted;
 frequent (f) = 10 to 20% of the total number counted;
 present (p) = 5 to 10% of the total number counted;
 rare (r) = 1 to 5% of the total number counted;
 exceptional (e) = less than 1% of the total number counted.