AN ABSTRACT OF THE THESIS OF

Lisette Aline Berglund (Name) for the MASTER OF SCIENCE (Degree)

in Botany (Major) presented on June 28, 1972 (Date)

Title: LABORATORY STUDIES OF SUCCESSIONAL PATTERNS IN ASSEMBLAGES OF ATTACHED ESTUARINE DIATOMS

Abstract approved: Redacted for Privacy

Dr. C. David McIntire

Successional patterns of attached estuarine diatoms were investigated using laboratory model ecosystems. Artificial substrates of acrylic plastic were exposed to 0, 4, and 10 hours of desiccation per day. Diatom assemblages that developed under temperatures normal for Yaquina Bay, Oregon (control ecosystem) were compared to assemblages that developed at temperatures elevated 10 C (heated ecosystem).

Continuously submerged substrates were quickly invaded by solitary, motile and attached diatoms. By the end of the experiment, filamentous and tube dwelling colonial diatoms had become established with many motile and epiphytic diatoms interspersed among the colonies. However, planktonic taxa were the first to settle on the substrates exposed to 4 and 10 hours of desiccation. These taxa were gradually replaced in prominence by solitary, motile and attached taxa that had previously colonized the continuously submerged substrates

and by several species that were tolerant of desiccation and high air temperatures. Again, filamentous and tube dwelling forms began to establish colonies at the end of the experiment.

A total of 21,569 diatoms was counted in 42 samples, and 136 species were identified. The most abundant diatoms found in the control ecosystem included Navicula directa, Thalassiosira no. 1, Thalassionema nitzschioides, Nitzschia no. 2, and Navicula diserta. Thalassiosira no. 1, Thalassionema nitzschioides, Nitzschia aerophila, Nitzschia sigma, and Navicula no. 2 were the most abundant species in the heated ecosystem. Of these taxa, Navicula directa and Thalassionema nitzschioides were the most evenly distributed over the samples. Species diversity was higher in the heated ecosystem.than in the control ecosystem.

Laboratory Studies of Successional Patterns in Assemblages of Attached Estuarine Diatoms

by

Lisette Aline Berglund

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

June 1973

APPROVED:

Redacted for Privacy

Associate Professor of Botany
in charge of major

Redacted for Privacy

Chairman of the Department of Botany and Plant Pathology

Redacted for Privacy

Dean of Graduate School

Date thesis is presented June 28, 1972

Typed by Susie Kozlik for Lisette Aline Berglund

ACKNOWLEDGEMENTS

Many people in the department of Botany and Plant Pathology deserve my thanks for their assistance and encouragement in the completion of this study. I wish to make special mention of my appreciation of Dr. C. David McIntire, my major professor, for his guidance during the experiment and patient editorial efforts during the preparation of this thesis. Dr. Harry K. Phinney provided interesting discussions and helpful criticisms throughout all phases of the study.

I would also like to acknowledge my appreciation of technical assistance received from Dr. Stephan P. Main, Sue Carpenter, Kay Fernald, and the staff at the Oregon State University Marine Science Center.

Financial support for this study came from the National Science Foundation in the form of a Research Assistantship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LABORATORY STUDIES OF SUCCESSIONAL PATTERNS IN ASSEMBLAGES OF ATTACHED ESTUARINE DIATOMS

INTRODUCTION

In comparison to work done on planktonic diatoms, research on attached diatoms has been relatively neglected. In the past, most of the studies have involved zonal distribution, substrate preference, associations between taxa, and geographic distributions. In Oregon, studies have been concerned with the effects of salinity on the distribution of diatoms (Martin, 1970); epilithic and episamic diatoms (Riznyk, 1969); distribution of attached diatoms in Yaquina Estuary using artificial substrates (McIntire and Overton, 1971); distribution of epiphytes (Main, 1973); and the effects of grazers, light intensity and daylength, and the vertical distribution of diatoms on concrete (Castenholz, 1961, 1963, 1964). Wulff (1971) used a laboratory model ecosystem to study the effects of light intensity, salinity, tidal cycle, and elevated water temperatures on diatom assemblages. Under more or less normal conditions, the populations found in the model ecosystems closely resembled those assemblages found in Yaquina Bay during field studies. However, Wulff found that, in the laboratory model ecosystem, certain species such as Melosira nummuloides and Nitzschia aerophila maintained much larger populations than normally occurred in the estuary.

The investigation of the patterns of colonization and succession in assemblages of estuarine diatoms also has been neglected. Wilson (1925) followed successional patterns from a colonial diatom community through a kelp community on bare substrates. ZoBell and Allen (1934) and Hendey (1951), both working on the fouling of metals, discovered that the initial colonizers of bare substrates were bacteria rather than colonial diatoms as Wilson had thought. Mucilage secreted by the bacteria was found to enhance the ability of the diatoms to attach to the surface.

The purpose of the experiment reported in this thesis is to detect successional patterns of attached diatoms occurring during the initial colonization of hard, bare, artificial substrates. In addition, the effects of elevated water temperatures on the structure and development of diatom assemblages were observed. The laboratory model ecosystem described by McIntire and Wulff (1969) was implemented in the experiment. Such a system allows the development of natural diatom assemblages and also permits the regulation of temperature and light intensity together with the simulation of a tidal cycle. The structural aspects of the assemblages were evaluated by measures of diversity, niche breadth, and similarity between assemblages. Cluster analyses were performed to determine distributional relationships between species.

LITERATURE REVIEW

Diatoms are one of the initial colonizers of bare substrates in aquatic environments. In addition, they function as primary producers (Mann, 1969) and provide a food source for primary consumer organisms (Castenholz, 1961). Cooke (1956) described techniques commonly used in tracing the colonization of various natural and artificial bare areas by microorganisms. The colonization of wooden blocks, boulders, glass plates, and suspended ropes with iron weights was studied by Wilson (1925) who found similar colonization sequences for all four substrates. The first invaders were colonial diatoms, which then were followed by a hydroid-colonial diatom association, Ectocarpus or an Ectocarpus-hydroid association, a pre-kelp association, and last of all, a kelp association.

Wilson's studies indicated that colonial diatoms were the first sessile organisms to colonize the submerged substrates, but his methods made no provision for the detection of bacteria. ZoBell (1943) and ZoBell and Allen (1934) found bacteria firmly attached to glass slides two to four hours after exposure to seawater. In another experiment, slides that were covered with a bacterial slime had a noticeably greater number of other organisms (including diatoms) attached to them than slides without a well developed bacterial flora.

Hendey (1951) found that several diatoms also produced a slime which is favorable for the attachment of other diatoms. The diatoms that produce the slime are small, are closely associated with the substrate, and are embedded in the film. Motile diatoms must first attach themselves to this slime or the substrate before movement is possible (Drum and Hopkins, 1966).

Neither stalked nor tube dwelling diatoms contribute to the surface slime. Instead, tube dwellers such as Amphipleura rutilans secrete mucopolysaccharide material in the form of a sheath around the colony. This sheath serves both as an active nutrient trap and as a barrier against sudden salinity changes (Drum, 1969). Williams (1965) made observations on the ability of the tube dwellers Nitzschia obtusa and Frustulia asymmetrica to retreat into the sediments in response to a stimulus such as the grazing activities of fiddler crabs. Cells of Nitzschia obtusa moved within a stationary tube. In the case of Frustulia asymmetrica, the tubes moved while the cells remained motionless within the tube.

There are many factors determining the distribution of attached marine diatoms. Photoperiod, light intensity, and salinity are very important factors along with the rate of growth of the organism and its efficiency in attaching to the substrate (Castenholz, 1964; McIntire, 1966; and Wulff and McIntire, 1972). To this list, Reisen and Spencer

(1970) added current velocity, the length of time the substrate was exposed to colonization, and the season of the year.

A substrate periodicially exposed to the air is colonized much more slowly than a continuously submerged substrate (McIntire and Wulff, 1969). Hostetter and Hoshaw (1970) using Stauroneis anceps found that the survival of this species depends on the rate of drying, particle size of the substrate, age of the culture, and perhaps the amount of metabolites in the surrounding area (also see Davis, 1972). However, desiccated vegetative cells had an advantage over hydrated cells in that they survived very high temperatures with little damage (Hostetter and Hoshaw, 1970).

Several investigators have looked at the vertical and horizontal distribution of intertidal diatoms. Aleem (1950) recognized eleven diatom communities on the English coast. The habitats studied included littoral pools, concrete structures, reefs, boulders, and a calcareous shore. Most of these communities were found in more than one habitat. Those diatoms found in the upper littoral region had weakly silicified frustules and were frequently deformed. Hendey (1964) described eight littoral diatom communities and two supra-littoral communities for Dovery estuary and reported seasonal distributions for the most common diatoms. Hopkins (1964b) found that air temperature together with desiccation were important factors in the survival of a diatom community. Survival depended on the water retention

ability of the substrate. The Achnanthes-blue-green algal community found by Aleem grew well on wood while solitary diatoms favored chalk and the thalli of macroalgae. Edsbagge (1965) compared the vertical distribution of diatoms found in the Baltic Sea, on the southern coast of England, and on the west coast of Sweden. The species composition of the lower littoral zone community on the English coast was similar to that of the sublittoral zone on the west coast of Sweden.

Castenholz (1963) demonstrated that the directional orientation of the substrate and the period of exposure to insolation and desiccation regulated both the species composition and the density of diatom communities found on concrete blocks at Gregory Point, Oregon. McIntire and Overton (1971), also studying the flora of Oregon, described the distribution of diatoms in Yaquina Bay and estuary. Samples were taken vertically, horizontally, and seasonally across desiccation, insolation, and salinity gradients. They found a distributional continuum of diatom populations along these environmental gradients and only in regions where there were discontinuities in the gradients could discrete assemblages be found. Riznyk (1969), Martin (1970), and Wulff (1971) also investigated various aspects of the physiological ecology of the diatom flora of Yaquina Bay.

Main (1973) found that a number of taxa were likely to occur epiphytically on species of macroalgae and Zostera marina, especially

species of the genus Cocconeis. The influence of the host macrophytes on the epiphytes tended to be masked by salinity and desiccation gradients. However, in the winter, this host-epiphyte relationship was more noticeable because differences in exposure and salinity among the stations of interest were relatively small.

The diatom flora of mud flats has been studied by J. T. Hopkins (1963, 1964a, and 1966), Rees (1940), and Williams (1962). Studies on salt marshes have been done by Williams (1964), Round (1960), and Drum and Webber (1966), while Harper (1969) followed the circadian migrations of diatoms over sand grains. Stockner (1968) found stable patterns in the diatom flora of a hot spring.

As long as a natural environment remains relatively undisturbed, the numbers and relative abundance of populations of taxa change only slightly even though the kinds of diatoms change with time (Patrick, 1961). Unpolluted rivers have a high diversity; as pollution increases, the diversity decreases because of the elimination of sensitive species (Patrick, Holn, and Wallace, 1954). The invasion rate, size of the species pool,and the area of the substrate are all important in determining the degree of diversity of a diatom assemblage (Patrick, 1967). A reduction in any of these three variables reduces the diversity of the community without affecting the biomass. High invasion rates enable the community to adapt to changing conditions by maintaining populations of the rarer species.

A detailed description of the laboratory model ecosystem used in this experiment can be found in a paper by McIntire and Wulff (1969). Also included were the results of experiments done on the effects of light intensity and tidal cycle on summer diatom assemblages. Additional results of these studies together with the effects of heated water and reduced salinity have been discussed in a more recent paper (Wulff and McIntire 1972).

APPARATUS AND METHODS

Description of the Ecosystems

Two laboratory model ecosystems (Figures 1 and 2) are located at the Oregon State University Marine Science Center, Newport, Oregon. Each system consists of a polyester resin coated, plywood trough, 3 m long, 76 cm wide, and 80 cm deep (McIntire and Wulff, 1969). A 12 rpm electric motor (Pynatron 5K934) pivots a board back and forth at one end of each trough to provide water circulation.

Seawater for each system comes from lower Yaquina Bay and has salinities that normally range from 28 to 34 °/oo except during periods of high river flow during the winter months when the salinity may be as low as 8 °/oo for short periods at low tide. Salinity of the seawater supply is monitored with a continuous recording salinometer (Thayer and Redmond, 1969). The seawater enters the laboratory through pipes of polyvinyl chloride, and a plastic garbage can serves as a settling tank for each trough. The influent seawater is transferred from the settling tank to a wooden head tank and subsequently through flowmeters downward to a mixing tank. The water is then pumped from the mixing tank into the trough by a centrifugal pump (Gormann-Rupp Industries, Model 11888). The settling, head, and mixing tanks have overflow outlets to provide a constant head. An effluent line is located near the

Figure 1. The laboratory model ecosystem at "high tide."

Figure 2. The laboratory model ecosystem showing the arrangement of lights.

bottom of each trough, and both the influent and the effluent flow are controlled by glass stopcocks.

Before an experiment, the effluent stopcock is adjusted so that the water drains from a level of about 65 cm to a level of 12.5 cm in six hours. After the six-hour draining period, a timing device energizes the centrifugal pump, and water is pumped into the trough. The influent stopcock is adjusted so that the influent water exceeds the effluent loss and refills the system to its original level by the end of the next six hours. Specifically, influent water enters the system at the rate of 4.65 l/min, and effluent water drains at a rate of 2.85 l/min when the trough is full. In summary, these adjustments allow the simulation of a tidal cycle consisting of two "high tides" and two "low tides" every 24 hours.

At a flow rate of six liters per minute, the seawater for one of the model ecosystems can be heated from a temperature of about 10 C to 33 C with a booster water heater (Abco 309B). The inside of the heater is lined with stainless steel, and the 9000 w element is fabricated from Inconel. For the experiment described here, the temperature in the mixing tank of the model ecosystem was held approximately 10 C higher than that in a control model ecosystem by adjusting the flow of water through the heater and the flow of non-heated water into the mixing tank. Continuous recording of the water temperature in each trough is obtained with a Partlow recording thermometer (Model RFT).

Illumination for each laboratory system is provided by six 244-cm, cool white, power groove, fluorescent lamps (General Electric Corp.) supplemented with sixteen 60 w incandescant lamps mounted on a fixture that can be raised or lowered over the trough (Figure 2). When the fixture is at its lowest level, illumination intensities of about 17,000 lux can be obtained at the water surface when the trough is nearly full. Light intensity is measured with a Weston Sunlight Illumination Meter (Model 756) and photoperiod is controlled by timing devices.

Experimental Procedure

Before initiating the experiment, three boards, each 12 by 75 cm, were wedged between the sides of each laboratory ecosystem. Boards 1, 2, and 3 were oriented 9, 24, and 40 cm from the bottom, respectively. Eight 6.5 by 12.5-cm acrylic plastic plates were attached to each board with rubber bands. To minimize settling of silt and empty diatom frustules, the boards were tilted so that the upper edge was 3 cm above the lower edge (Figure 3). The simulated tidal cycle in each system, exposed the three boards to different periods of desiccation. Board 1 of each trough was continuously submerged during the experiment, while Board 2 and Board 3 were exposed to the air for 4 and 10 hours per day, respectively (Table 1).

Figure 3. Placement of boards and substrates in the laboratory model ecosystem.

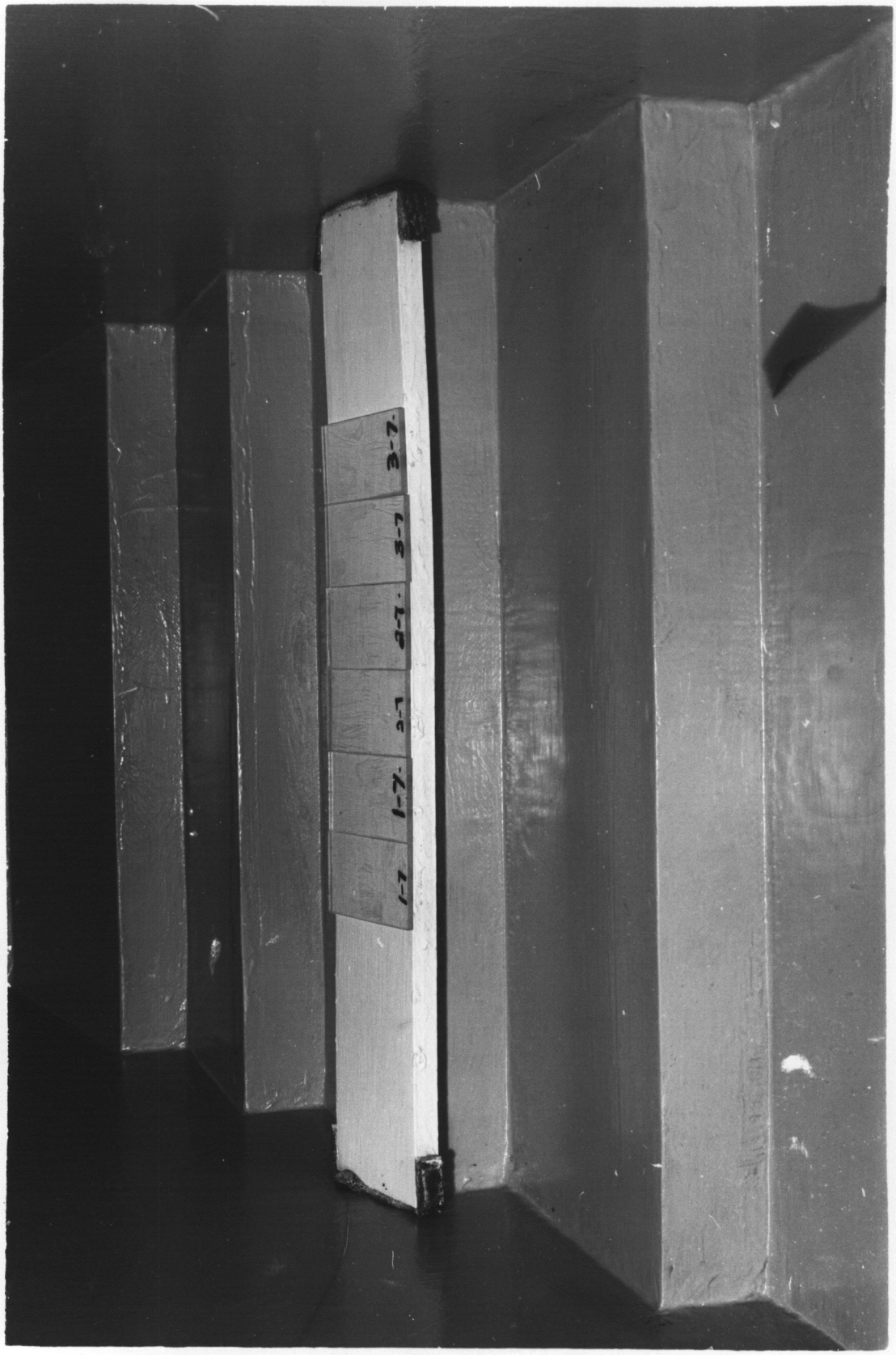
3-7
3-1
2-7
2-1
1-7
1-1

Table 1. Distance of the boards from the bottom of the laboratory ecosystem, length of time the substrates were exposed to dessiccation, and the light intensity on the boards at the end of the experiment when the substrates were exposed to air.

Board	Distance from Bottom (cm)	Length of Exposure (hr/day)	Light Intensity Dry Tank (lux)	
			Control	Heated
1	9-11	0	4,736	4,736
2	24-27	4	7,642	7,535
3	40-43	10	10,549	10,226

The light fixture was adjusted over each trough so that the illumination intensity ranged from about 4,700 lux on Board 1 to approximately 10,500 lux on Board 3 (Table 1). These values represent illumination intensities at the middle of each board when the board was not covered with water. A timer regulated the lamps to provide a 15-hour light period followed by a 9-hour period of darkness, a photoperiod that corresponded to the season during which the experiment was in progress.

On 6 July 1971, the boards with their attached substrates were placed in each trough and the experiment was initiated by introducing seawater into the ecosystems. In one of the ecosystems, seawater was heated 10 C above the temperature of the influent water from Yaquina Bay; seawater for the other ecosystem was unheated. Henceforth, the two troughs will be referred to as the heated ecosystem and the control (unheated) ecosystem.

Sampling was initiated on 12 July (sample 1), one week after the beginning of the experiment (Table 2). This allowed enough time for the initial colonization of bacteria and the invasion of diatoms. Each sample consisted of one substrate from each board and a total of three substrates from each trough. Subsequent sets of samples were obtained on 15 July (sample 2), 19 July (sample 3), 22 July (sample 4), 26 July (sample 5), 2 August (sample 6), and 9 August (sample 7). In other words, the substrates were exposed to colonization for 7 days (sample 1), 10 days (sample 2), 14 days (sample 3), 17 days (sample 4), 21 days (sample 5), 28 days (sample 6), and 35 days (sample 7). Samples were obtained at relatively short time intervals early in the experiment when successional changes were rapid. The experiment was terminated after the last sample was taken on 9 August.

Table 2. Sampling dates and the length of time the substrates were exposed to colonization.

Sample	Sampling Date (1971)	Days of Exposure
1	July 12	7
2	15	10
3	19	14
4	22	17
5	26	21
6	Aug 2	28
7	9	35

During the sampling, each substrate was placed on paper towels and allowed to dry. The diatom assemblages were then scraped from the substrates into flasks and were boiled in concentrated nitric acid. After the diatom frustules were cleaned by this procedure, the cell walls were mounted on slides in Hyrax (Patrick and Reimer, 1966). Therefore, each sample was represented by one slide. In this work, the classical criteria of frustule size, shape, and ornamentation were used as a basis for identification of species and varieties. The diatoms not found in the literature were photographed and given a temporary identification number (McIntire and Overton, 1971). In this way, all taxa were uniquely identified during the counting procedure.

Data Analysis

Because the term "species diversity" has been defined in various ways by different ecologists, Hurlbert (1971) recently has criticized the concept and has proposed that statistics calculable on a list of species and their abundances be referred to as "species composition parameters" rather than diversity indices. In the work that follows, four such parameters-- the complement of Simpson's measure of concentration (Simpson, 1949), the Information measure (Shannon and Weaver, 1949), an index of redundancy or dominance, and an index to the similarity between pairs of assemblages--are used to express community structure.

The complement of Simpson's measure of concentration is influenced by the distribution of the proportions of individuals into s categories, or species, and is related to the probability that two individuals encountered at random in an assemblage belong to different species. An estimator of this parameter is

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

where n_i is the number of individuals in the i-th species, N the number of individuals in the sample, and S the total number of species in the sample. SDI increases as the number of species increases or as the individuals become more evenly distributed among the species.

Since many ecologists have used the Information measure of community structure to express species diversity, I also have included this statistic along with SDI in the results section of this thesis. An estimator of the Information measure is

$$H'' = - \sum_{i=1}^{s} \left(\frac{n_i}{N}\right) \log_2 \left(\frac{n_i}{N}\right) . \qquad (2)$$

The magnitude of H'' is influenced by the number of species and the proportionment of individuals among these species in the same way as the value SDI.

McIntire and Overton (1971) found that values of SDI and H'' changed relatively little beyond sample sizes of 300. As a result, I

have selected 500 as a suitable sample size for estimates of the Information and Simpson's species composition parameters. The estimators in equations (1) and (2) are both biased, but consistant, and bias is negligible at the sample size used in the analysis.

A statistic that expresses species redundancy or dominance in the diatom assemblages is given by the equation

$$R' = \frac{H''_{cmax} - H''}{H''_{cmax} - H''_{cmin}} , \tag{3}$$

where R' can vary from 0 when the species are equally common to 1 when all species but one are represented by just one individual. The conditional maximum and minimum values of H'' based on the observed number of species in a sample is calculated from the expressions

$$H''_{cmax} = \log_2 S , \tag{4}$$

and

$$H''_{cmin} = - \left[\log_2 N - \left(\frac{N-S+1}{N}\right) \log_2 (N-S+1)\right] . \tag{5}$$

To compare the structures of selected pairs of diatom assemblages, the Similarity Index SIMI proposed by Stander (1970) is used, where

$$SIMI_{1,2} = \frac{\sum_{i=1}^{s} p_{1i}\, p_{2i}}{\left(\sqrt{\sum_{i=1}^{s} p_{1i}^2}\right)\left(\sqrt{\sum_{i=1}^{s} p_{2i}^2}\right)} \tag{6}$$

In this expression p_{1i} is the proportion of the individuals in the sample of assemblage 1 belonging to the i-th species, and p_{2i} the proportion of the individuals in the sample of assemblage 2 belonging to the i-th species. The value of SIMI can vary from 0 when the two samples have no species in common to 1 when the two assemblages are identical, i. e., the species composition and relative abundances are the same. Differences in structure of the diatom assemblages are related to environmental variables by the regression of SIMI on differences in period of exposure to the air and time of sampling (McIntire and Overton, 1971).

The niche breadth of a selected diatom taxon is measured by the expression

$$B_{cj} \text{ or } B_{hj} = \exp\left[- \sum_{i=1}^{Q} \left(\frac{p_{ij}}{R_j}\right) \log e \left(\frac{p_{ij}}{R_j}\right)\right], \qquad (7)$$

where B_{cj} and B_{hj} are the niche breadths of the j-th species in the control and heated ecosystems, respectively, p_{ij} is the proportion of the j-th species in the i-th sample, Q is the number of samples (i. e., stations), and

$$R_j = \sum_{i=1}^{Q} p_{ij} .$$

The magnitude of B_{cj} or B_{hj} is an indication of a taxon's ability to do equally well at the stations under consideration. The values of B_c or

B_h can range from 1 to Q. In addition it is important to note that 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 the two species are proportioned the same among the stations.

A computer program designed to find "clusters" of observations in multivariate data was used to determine which species in the laboratory system tended to co-occur (i. e., have similar ecological properties) during the experiment. More specifically, this clustering algorithm attempts to determine the minimum variance partition of a set of n observations in q dimensions,

$$\left\{ X_{ij} \mid i = 1, 2, \ldots, n;\ j = 1, 2, \ldots, q \right\},$$

into K clusters. Therefore, the problem is to minimize the sum of squares, SS, around the cluster means, given by

$$SS = \sum_{h=1}^{k} \sum_{i \in S_h} \sum_{j=1}^{q} (x_{ij} - \bar{x}_{hj})^2 , \qquad (8)$$

where S_h is the subset of observations in cluster h, and $\bar{x}_{hj}$ is the mean in the q-th dimension of the observations in cluster h. The general method is an iterative approach which terminates at a local minimum, that is, no observation can be shifted to another group and the sum of squares reduced.

All statistical analyses were performed with a Control Data Corporation 3300 computer at the Oregon State University Computer Center using the *AIDONE, *AIDN, *STEP, and *MACLUS programs.

*AIDONE and *AIDN are programs for the analysis of information and diversity, *STEP is a standard stepwise multiple regression program, and *MAC LUS provides a cluster analysis of multivariate data.

RESULTS

Physical Properties

The daily maximum and minimum water temperatures for both laboratory ecosystems during the experiment are presented in Figure 4. The flow of the water through the booster water heater was adjusted so that the temperature in the heated ecosystem was approximately 10 C higher than that of the control ecosystem when the troughs were full. The lamps over each trough provided some heat but, this source of heat was insignificant at high tide. However, at low tide the lamps warmed the water covering Board 1 in the control ecosystem and increased the rate of desiccation on Board 2 and Board 3 in both ecosystems by heating the boards to approximately 40 C. Unlike the control, the water covering Board 1 in the heated ecosystem decreased in temperature at low tide. In summary, the control ecosystem had a larger range of temperature than the heated ecosystem, and temperature increased as the summer progressed.

Salinity of the influent seawater varied between 29.7 °/oo and 35.9 °/oo during the experiment.

Diatom Flora

Exactly 21,569 diatoms were counted in the 42 samples obtained during the experiment. The diatoms were separated into 136 taxa

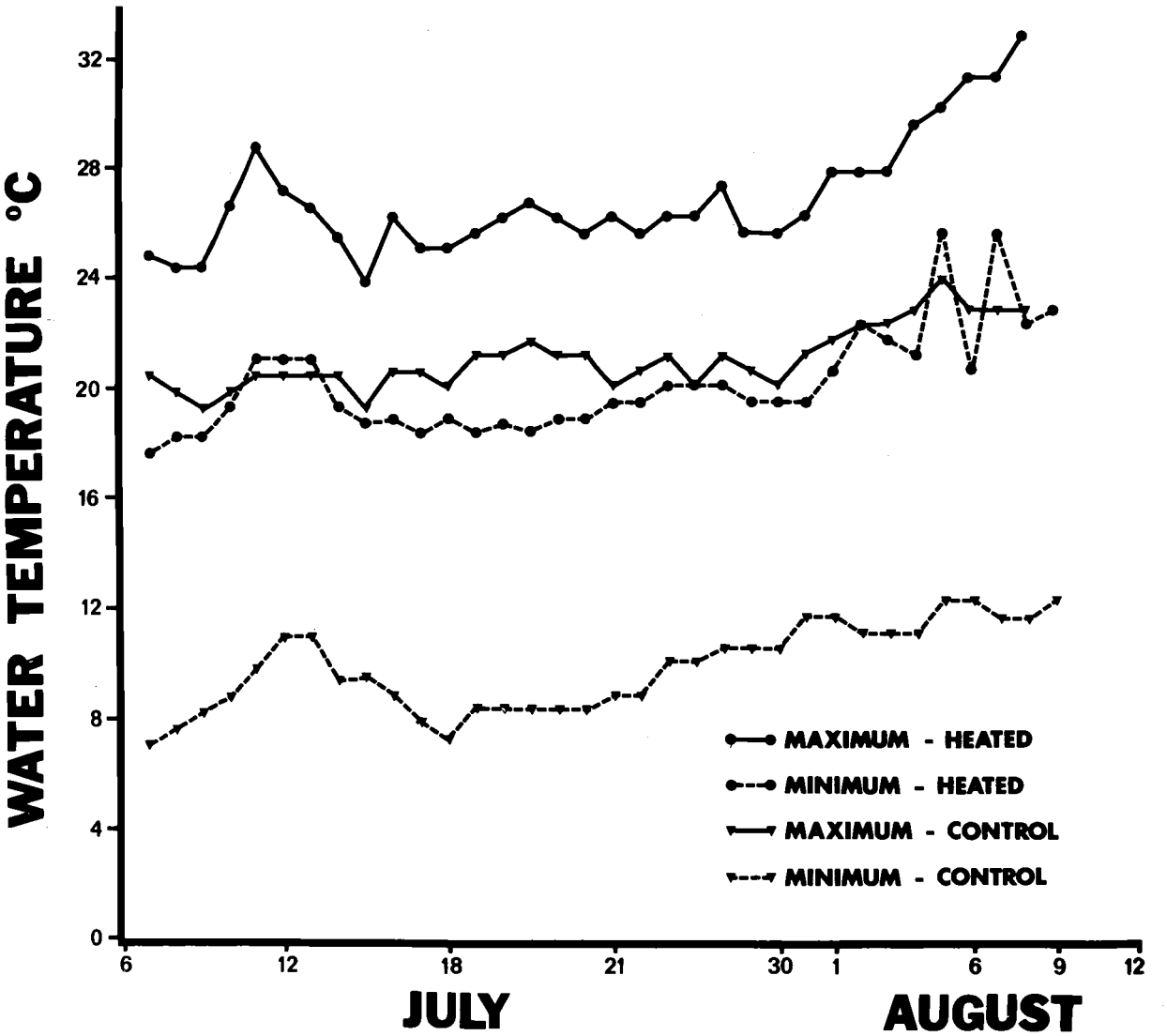

Figure 4. Daily maximum and minimum water temperatures for both the control and heated ecosystems.

(species and varieties of species), of which 35 were found in one sample only, and 25 of these were represented by a single individual (Appendix 1). Thirty-one of the 136 taxa were represented by fifty or more individuals. A list of these taxa along with their abundance, niche breadth, and the number of substrates on which they were found is presented in Table 3.

Several taxa were not found in the literature and are probably new to science. Five of the unknown taxa were represented by over 50 individuals. Nitzschia no. 2, the most abundant unidentified taxon, was similar to Nitzschia laevis Hust. Navicula no. 2 closely resembled five different species of Schizonema found in the Van Heurck collection in the Philadelphia Academy of Natural Sciences (McIntire and Overton, 1971). Amphora no. 5 and Navicula no. 19 were similar to Amphora exigua Greg. and Navicula retusa Bréb., respectively. Amphora no. 1 was not clearly related to any of the taxa found in the literature.

The five most abundant diatoms found in the control ecosystem were Navicula directa, Thalassiosira no. 1, Thalassionema nitzschioides, Nitzschia no. 2, and Navicula diserta (Table 3). Of these, Navicula diserta and Navicula directa had the lowest and highest niche breadth (B_c), 11.03 and 18.10, respectively. A less abundant species, Gyrosigma fasciola, had the highest B_c value (18.56). Of the taxa represented by a total of 50 individuals or more in the 42

Table 3. A list of the 31 most abundant diatom taxa ($N_t \geq 50$), their abbreviations; relative abundance in the control (N_c) and heated (N_h) ecosystems; the number of substrates the particular taxon was observed on in the control (S_c), the heated (S_h), and combined ecosystems (S_t); and their niche breadths for the control (B_c) and heated (B_h) ecosystems.

Taxon	Abbreviations	Number of organisms			Number of substrates			Niche breadth	
		N_C	N_H	N_T	S_C	S_H	S_T	B_C	B_H
Thalassiosira no. 1	Thal 1	1764	2920	4684	21	21	42	15.22	14.30
Navicula directa W. Smith	Nav dir	3002	166	3168	21	19	40	18.10	15.05
Thalassionema nitzschioides Grun.	Tha nit	1287	803	2090	21	21	42	15.69	15.24
Nitzschia no. 2	Nit 2	1083	481	1564	19	17	36	11.52	8.41
Navicula diserta Hust.	Nav dis	988	316	1304	20	21	41	11.03	13.44
Navicula no. 2	Nav 2	540	571	1111	20	21	41	13.73	14.84
Nitzschia sigma (Kütz.) W. Smith	Nit sig	93	782	875	9	18	27	5.74	11.03
Nitzschia aerophila Hust.	Nit aer	3	782	785	3	18	21	2.99	12.41
Melosira sulcata (Ehr.) Kütz.	Mel sul	347	221	568	20	21	41	15.59	16.51
Amphora no. 1	Amp 1	22	530	552	5	19	24	3.68	11.28
Navicula cincta Ehr.	Nav cin	7	498	505	5	20	25	4.46	10.29
Plagiogramma brockmanni Hust.	Pla bro	212	133	345	21	17	38	15.29	12.19
Melosira moniliformis (Mull.) Ag.	Mel mon	16	266	282	5	16	21	3.83	8.36
Amphipleura rutilans (Trent.) Cl.	Amp rut	68	198	266	6	10	16	3.92	5.58
Plagiogramma vanheurckii Grun.	Pla van	149	105	254	21	20	41	17.19	17.26
Gyrosigma fasciola (Ehr.) Griff et Henfr.	Gyr fas	171	53	224	20	15	35	18.56	13.19
Amphora no. 5	Amp 5	33	186	219	10	17	27	6.85	11.87
Achnanthes brevipes var. intermedia (Kütz.) Cl.	Ach bre	6	208	214	2	5	7	1.56	3.23
Synedra fasciculata (Ag.) Kütz.	Syn fas	84	117	201	19	20	39	14.47	17.08
Nitzschia subhybrida Hust.	Nit sub	123	67	190	18	13	31	11.91	6.98
Melosira nummuloides (Dillw.) Ag.	Mel num	6	181	187	5	10	15	4.79	7.47
Nitzschia pseudohybrida Hust.	Nit pse	25	161	187	6	8	14	3.31	3.65
Nitzschia closterium Sm.	Nit clo	5	174	179	3	13	16	2.75	9.58
Navicula gregaria Donk.	Nav gre	46	96	142	15	17	32	12.82	9.84
Fragilaria striatula var. californica Grun.	Fra str	95	35	130	16	9	25	10.11	6.78
Nitzschia frustulum var. perpusilla (Rabh.) Grun.	Nit fru	60	37	97	15	14	29	11.68	11.18

Table 3. Continued.

Taxon	Abbreviations	Number of organisms			Number of substrates			Niche breadth	
		N_C	N_H	N_T	S_C	S_H	S_T	B_C	B_H
Bacillaria paxillifer (Mull.) Hendey	Bac pax	3	83	86	1	13	14	1.00	10.05
Navicula no. 19	Nav 19	52	25	77	13	11	24	11.01	9.66
Pleurosigma angulatum Sm.	Ple ang	14	53	67	6	13	19	4.39	9.80
Biddulphia aurita (Lyngb.) Bréb. et Godey	Bid aur	51	6	57	13	3	16	10.11	2.71
Navicula abunda Hust.	Nav abu	52	4	56	11	1	12	6.76	1.00

samples, Bacillaria paxillifer and Achnanthes brevipes v. intermedia had B_c values less than 2.00, and were found on only one and two substrates, respectively.

Thalassiosira no. 1, Thalassionema nitzschioides, Nitzschia aerophila, Nitzschia sigma, and Navicula no. 2 were the most abundant species in the heated ecosystem. Of these five taxa, the largest niche breadth value (B_h) was found for Thalassionema nitzschioides (15.25), while Nitzschia sigma had the smallest B_h value (11.03). Plagiogramma vanheurckii had the largest B_h value (17.26) for the 31 species in Table 3, and Biddulphia aurita and Navicula abunda had the smallest B_h values, 2.71 and 1.00, respectively.

In the control ecosystem, Navicula directa, Navicula no. 2, Navicula diserta, and Thalassiosira no. 1 were the prominant species on Board 1, representing 18.5%, 24.4%, 22.2% and 5.1% of the cells in 7 days (sample 1), respectively (Figures 5A, 7A, 7C, and 8A). Both Navicula diserta and Navicula no. 2 decreased in relative abundance in 10 and 14 days (samples 2 and 3), and varied between 3.5% and 8.3% and between 2.7% and 7.5% respectively, in subsequent samples. As succession continued, Navicula directa increased in relative abundance and reached a maximum of 47.4% of the total cells in sample 6, 28 days after the experiment was initiated (Figure 7A). Nitzschia no. 2 reached its maximum relative abundance of 41.7% in

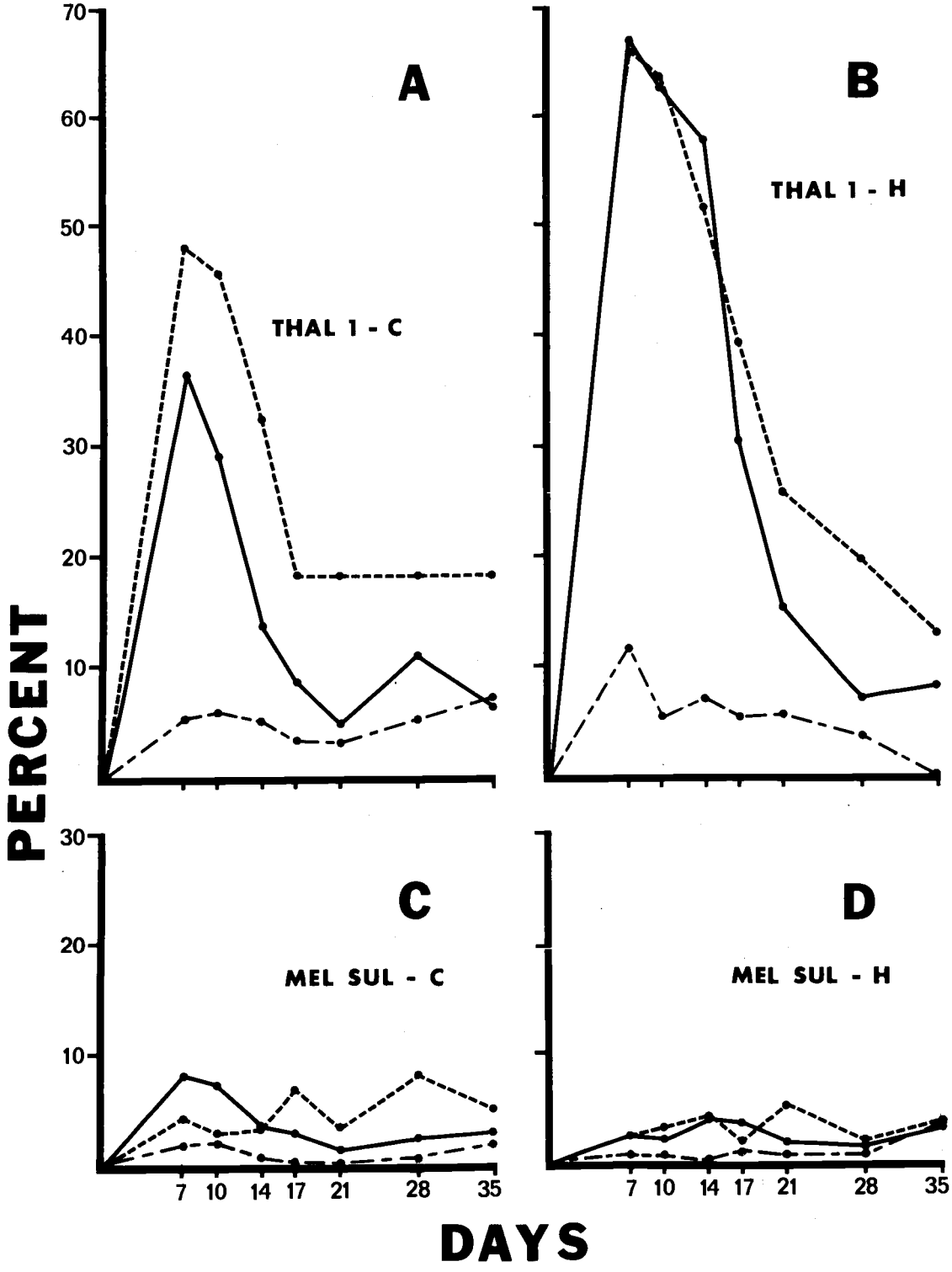

Figure 5. The relative abundance of Thalassiosira no. 1 (A, B) and Melosira sulcata (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line and the dashed line represent Boards 1, 2, and 3, respectively.

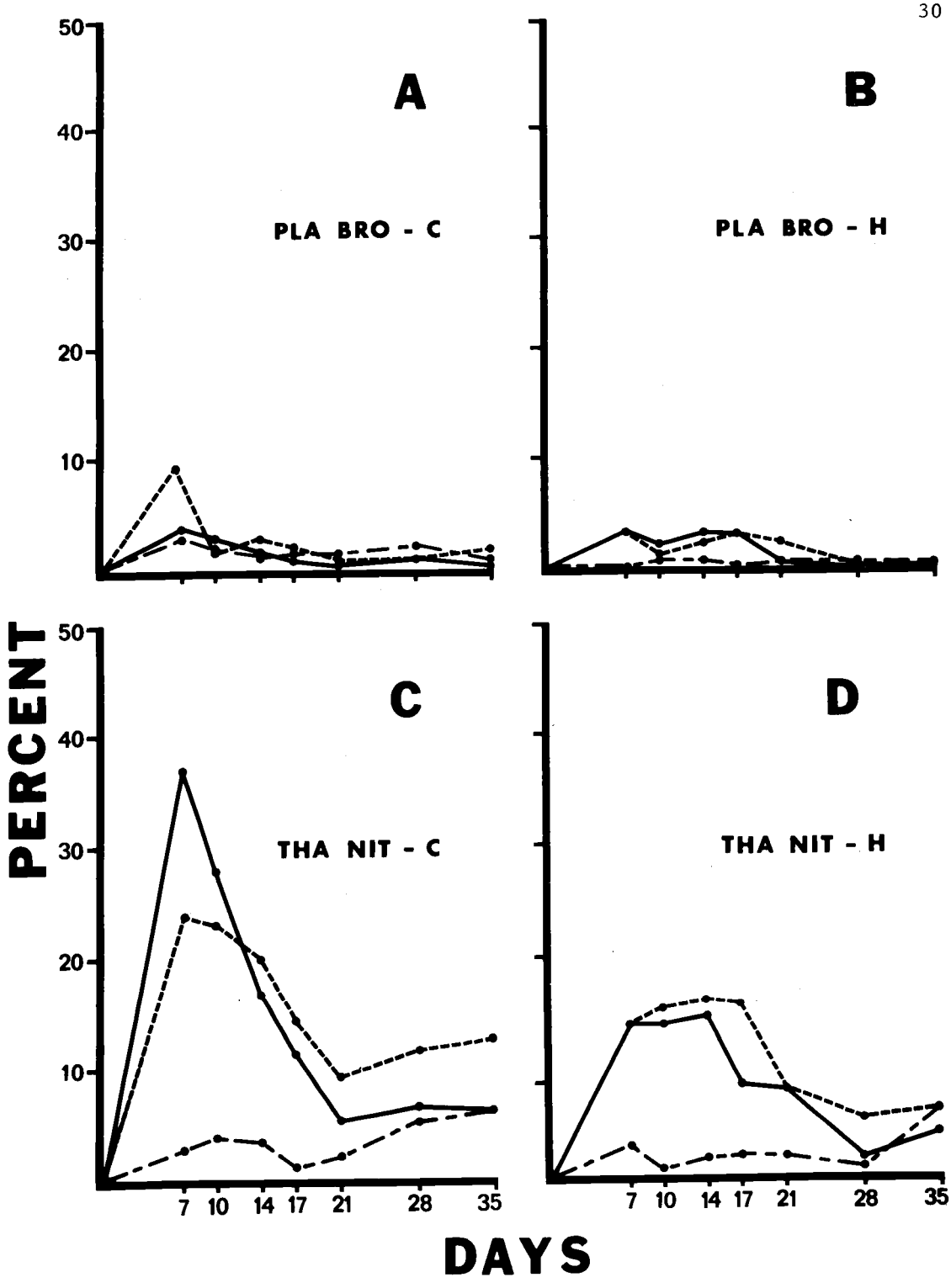

Figure 6. The relative abundance of Plagiogramma brockmanni (A, B) and Thalassionema nitzschioides (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line and the dashed line represent Boards 1, 2, and 3, respectively.

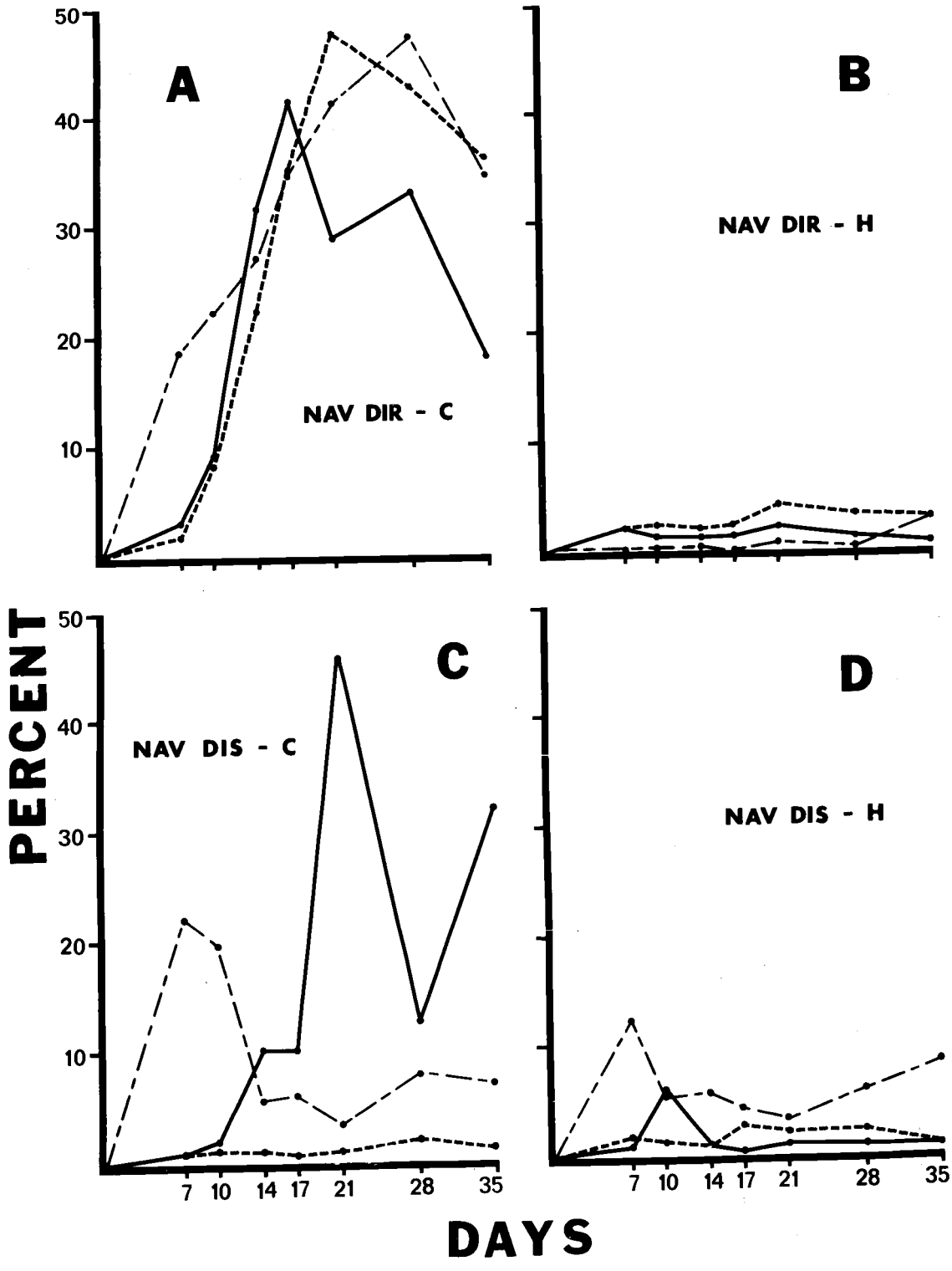

Figure 7. The relative abundance of Navicula directa (A, B) and Navicula diserta (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line and the dashed line represent Boards 1, 2, and 3, respectively.

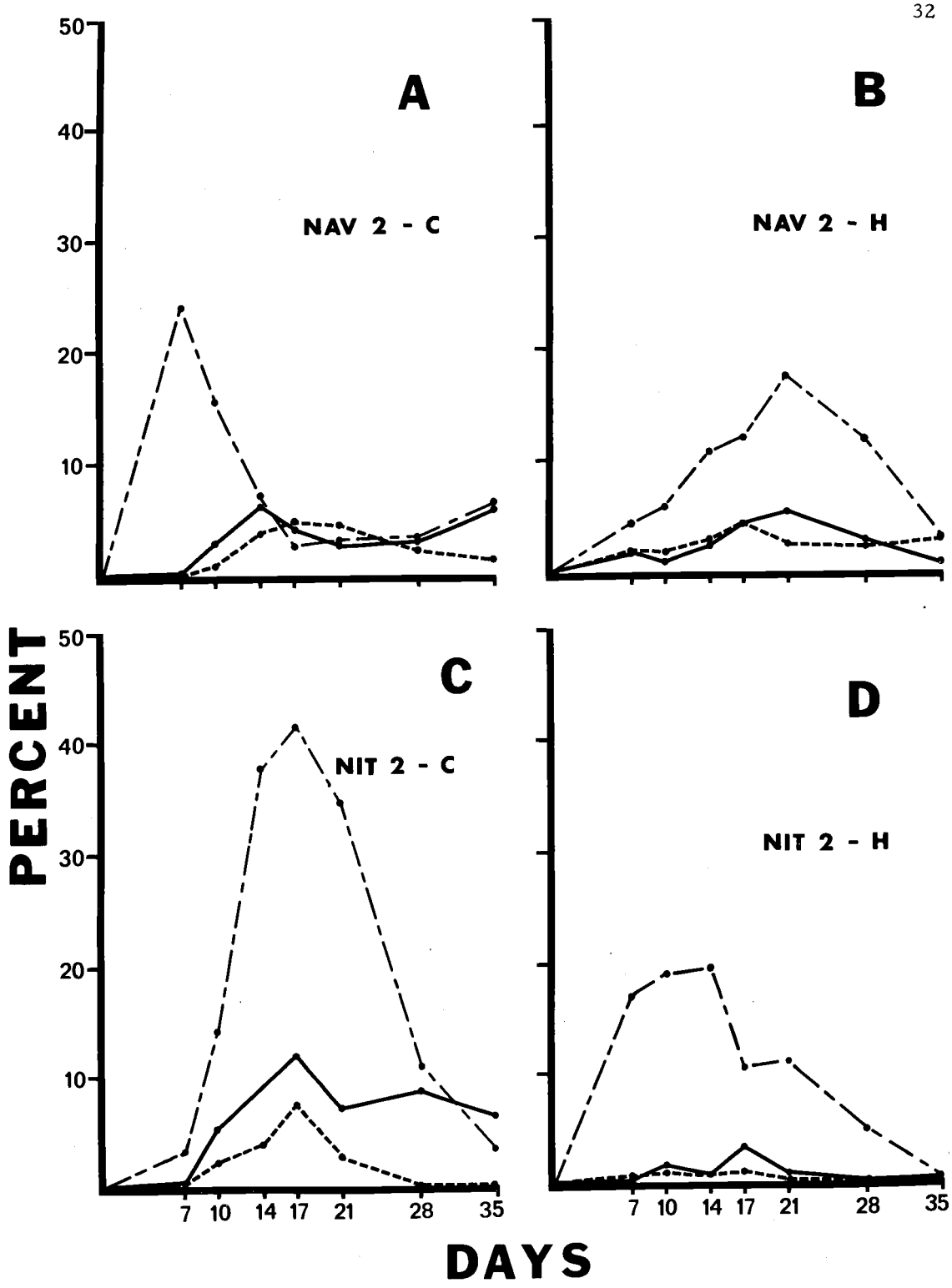

Figure 8. The relative abundance of Navicula no. 2 (A, B) and Nitzschia no. 2 (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line, and the dashed line represent Boards 1, 2, and 3, respectively.

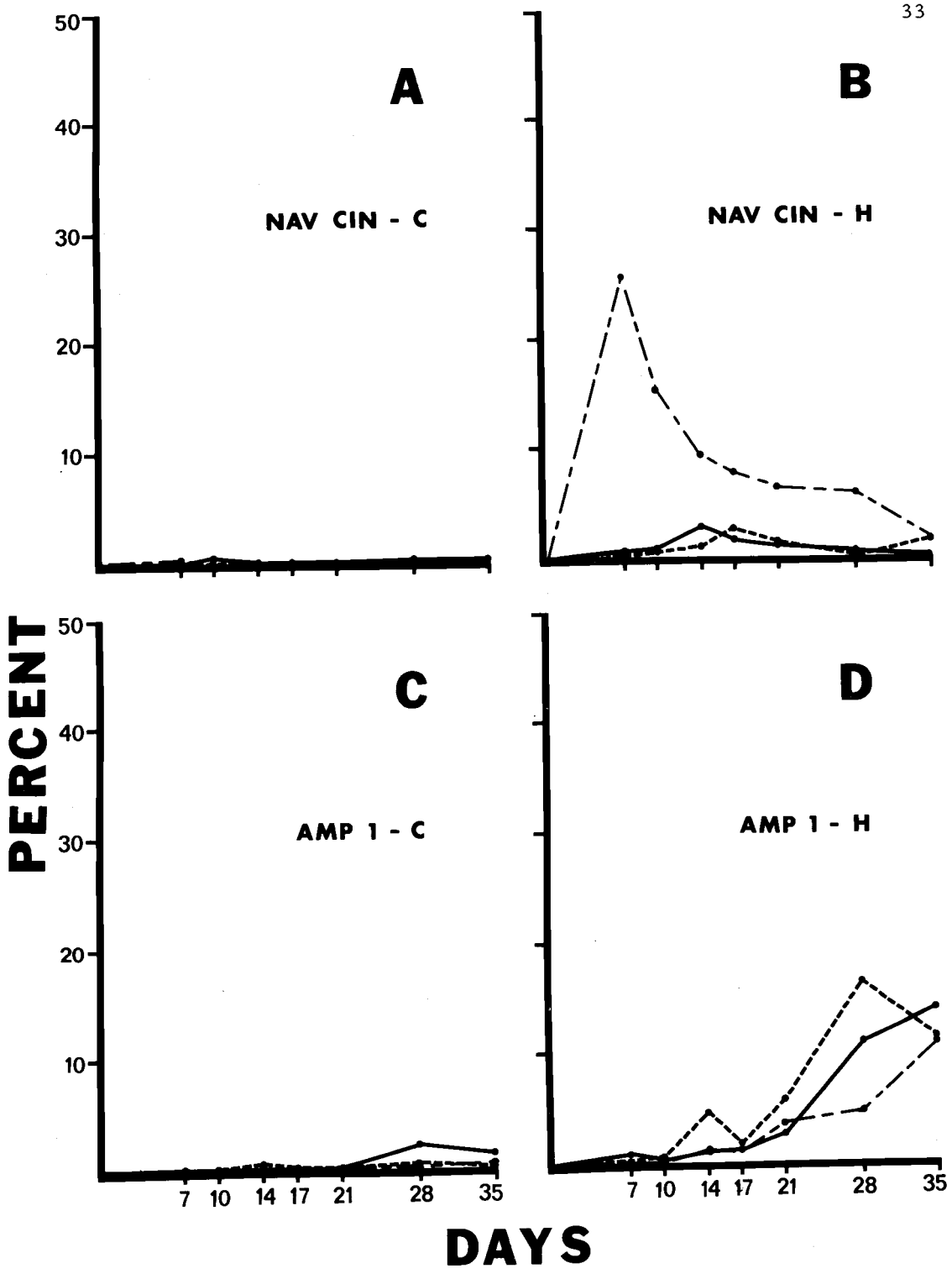

Figure 9. The relative abundance of Navicula cincta (A, B) and Amphora no. 1 (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line, and the dashed line represent Boards 1, 2, and 3, respectively.

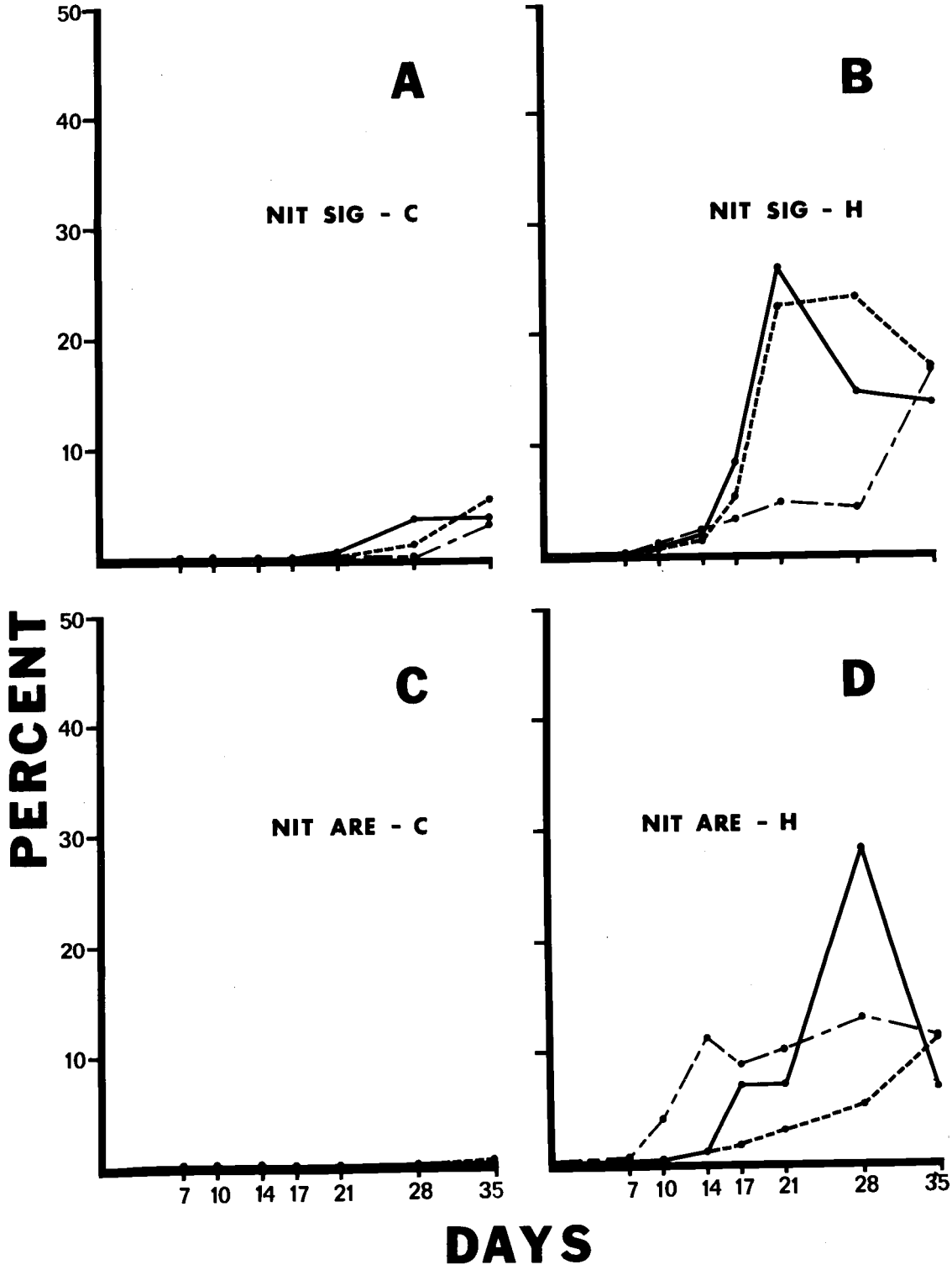

Figure 10. The relative abundance of Nitzschia sigma (A, B) and Nitzschia aerophila (C, D) in the control (c) and heated (h) ecosystems. The long-short dashed line, the solid line and the dashed line represent Boards 1, 2, and 3, respectively.

sample 4 (17 days) and then decreased to 3.3% in sample 7 (Figure 8C).

Colonization on Board 2 of the control ecosystem, the board exposed to the air for four hours per day, was slower than that on Board 1. Samples 1 (7 days) and 2 (10 days) were dominated by planktonic diatoms, namely Thalassiosira no. 1 and Thalassionema nitzschioides (Figure 5A and 6C). These taxa decreased in relative abundance from the 14th day to the 21st day as typical attached forms invaded the substrates. Navicula directa and Nitzschia no. 2 reached maximum relative abundances in sample 4 of 41.4% and 11.8%, respectively; while in sample 5, Navicula diserta reached a relative abundance of 45.5% and replaced Navicula directa as the most abundant diatom. Amphipleura rutilans and Nitzschia sigma were beginning to invade substrates on Board 2 when the experiment was terminated (Figure 10A).

Colonization on Board 3 of the control ecosystem, the board exposed to the air for 10 hours per day, was slower than that on either Board 1 or Board 2. Thalassiosira no. 1 and Thalassionema nitzschioides dominated the assemblages in samples 1, 2, and 3 (Figures 5A and 6C). Navicula directa increased in relative abundance from 1.8% in sample 1 to a maximum of 47.6% in samples 5 (Figure 7A).

In summary, colonization in the control ecosystem varied in both rates and species of organisms, depending on the time the substrate was exposed to the air. Colonization of the continually

submerged substrate was relatively rapid, as compared to the substrates exposed to periods of dessiccation. The substrates on Boards 2 and 3 initially were invaded by planktonic diatoms (Thalassiosira no. 1 and Thalassionema nitzschioides), while both motile species and typical attached forms (Navicula directa, Navicula diserta, Navicula no. 2 and Thalassiosira no. 1) were abundant in the early samples from Board 1 (Figures 5A, 6C, 7A, 7C, and 8A). As succession continued, Navicula directa became very abundant on all three boards while Nitzschia no. 2 and Navicula diserta did well on Board 1 and Board 2, respectively (Figures 7A, 8C, and 7C).

In contrast to the control ecosystem, the substrates on Board 1 in the heated ecosystem were never dominated by any one particular species during the experiment. Navicula cincta, Navicula diserta, Thalassiosira no. 1 and Nitzschia no. 2 were prominant in sample 1 (Figures 9B, 7D, 5B, and 8D). However, Nitzschia no. 2 was the only species of this group that increased in relative abundance in subsequent samples reaching a maximum of 19.7% of the total cells in sample 3. Nitzschia pseudohybrida, Nitzschia aerophila, Amphipleura rutilans, and Navicula no. 2 (Figures 10D, and 8B) reached their maximum relative abundances in sample 2 (18.6%), sample 3 (11.1%), sample 4 (14.6%), and sample 5 (17.6%), respectively. Amphora no. 1, Nitzschia aerophila, Navicula no. 2, and Navicula cincta were the most

abundant diatoms on Board 1 at the conclusion of the experiment (Figures 9D, 10D, 8B, and 9B).

The planktonic diatoms, Thalassiosira no. 1 and Thalassionema nitzschioides, dominated the diatom flora in samples 1, 2, 3, and 4 on Boards 2 and 3. This pattern was similar to that observed in the control ecosystem, although colonization of Boards 2 and 3 was slower in the heated ecosystem than in the control ecosystem. On Board 2, Nitzschia sigma and Nitzschia aerophila exhibited prominent maxima of 26.8%, and 28.0% in sample 5 and sample 6, respectively (Figures 10B and 10D); Amphora no. 1 (Figure 9D), Melosira nummuloides and Achnanthes brevipes v. intermedia were abundant in sample 7 at the end of the experiment with relative abundances of 14.3%, 7.7%, and 22.2%, respectively. On Board 3, the benthic diatoms abundant in sample 6 were Nitzschia sigma (23.1%), Amphora no. 1 (16.5%), and Achnanthes brevipes v. intermedia (4.1%), and other species abundant in sample 7 at the conclusion of the experiment included Nitzschia aerophila (11.3%), and Melosira nummuloides (3.5%).

In general, Navicula cincta, Amphora no. 1, Nitzschia sigma, and Nitzschia aerophila were relatively tolerant of the heated water. Of these species, Nitzschia cincta did best on Board 1, while all four did relatively well on Boards 2 and 3. Although Nitzschia no. 2, Thalassionema nitzschioides, Navicula directa, and Navicula diserta

were all present in the heated ecosystem, they all were much more prominant in the control ecosystem.

Cluster Analysis

A cluster analysis of the species-number data obtained for each laboratory ecosystem was designed to indicate the extent to which species tended to co-occur in the different samples. Only the species listed in Table 3 were included in the analysis. Presumably, species that co-occur have similar ecological properties as long as their presence is not the result of fortuitous circumstances. First, a cluster analysis was run on data from each ecosystem alone. The data then were combined into one set, and a similar analysis was run on the pooled data set. If the relative within cluster sum of squares is plotted against the number of clusters, the slope of the resulting curve provides information about distributional patterns of the species under consideration. A steep slope indicates that there are relatively tight clusters present and that the species tend to be distributed in well defined groups. On the other hand, if the reduction of within cluster sum of squares with increasing number of clusters is gradual, the clusters are not as well defined and the species tend to over-lap more in distribution.

In general, clusters of species for the heated ecosystem were better defined than those for the control ecosystem (Figure 11). The division of data from the heated ecosystem into two clusters reduced

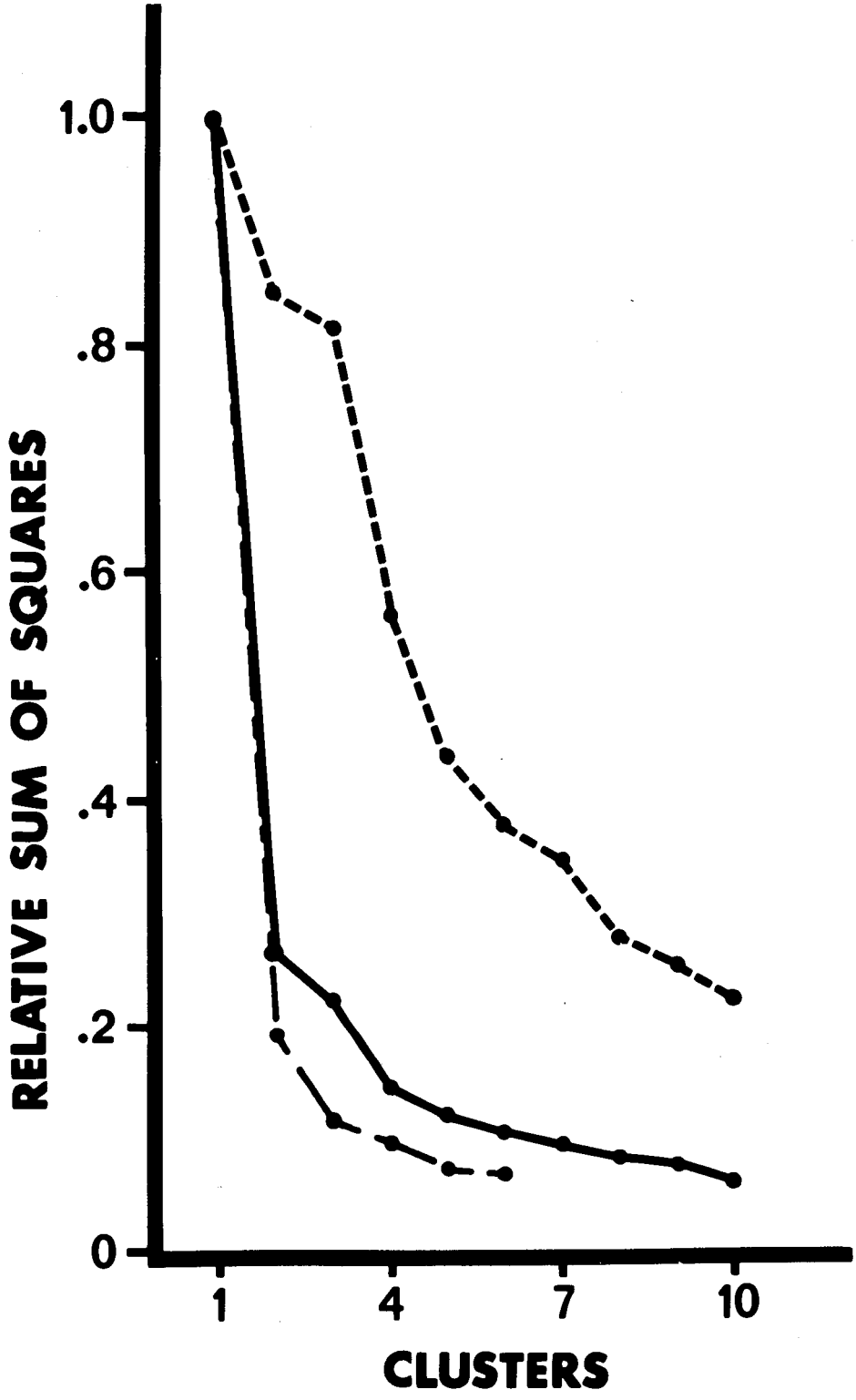

Figure 11. Relationship between the relative sum of squares and the number of clusters in the control (dashed line), heated (solid line), and combined ecosystems (long-short dashed line).

the relative within cluster sum of squares from 1.00 to 0.26 while similar division of data from the control ecosystem only reduced the value from 1.00 to 0.85. In both cases, division of the data into two clusters was based primarily on temporal patterns rather than spatial patterns of the species under consideration. Further partitioning of each set of data was influenced by vertical distributional patterns along the desiccation gradient.

Results of the analysis of the pooled data set emphasized differences in temperature between the two ecosystems and the desiccation gradient within each ecosystem and did not take into account the temporal patterns of the diatom flora. Six clusters were well defined and considered to have biological significance. The within cluster sum of squares was reduced from 1.00 to about 0.19 with a division of the data into two clusters (Figure 11). These two clusters were separated primarily on the basis of the temperature differences between the two ecosystems. Additional partitioning divided the diatom species into groups more closely related to the desiccation gradient within each ecosystem.

A clustering diagram of the 31 diatom species listed in Table 3 is presented in Figure 12. Clusters A, B, and C were groups of species that were prominant in the control ecosystem, while clusters D, E, and F represented species that, in general, were more abundant in the heated ecosystem than in the control ecosystem. A division of

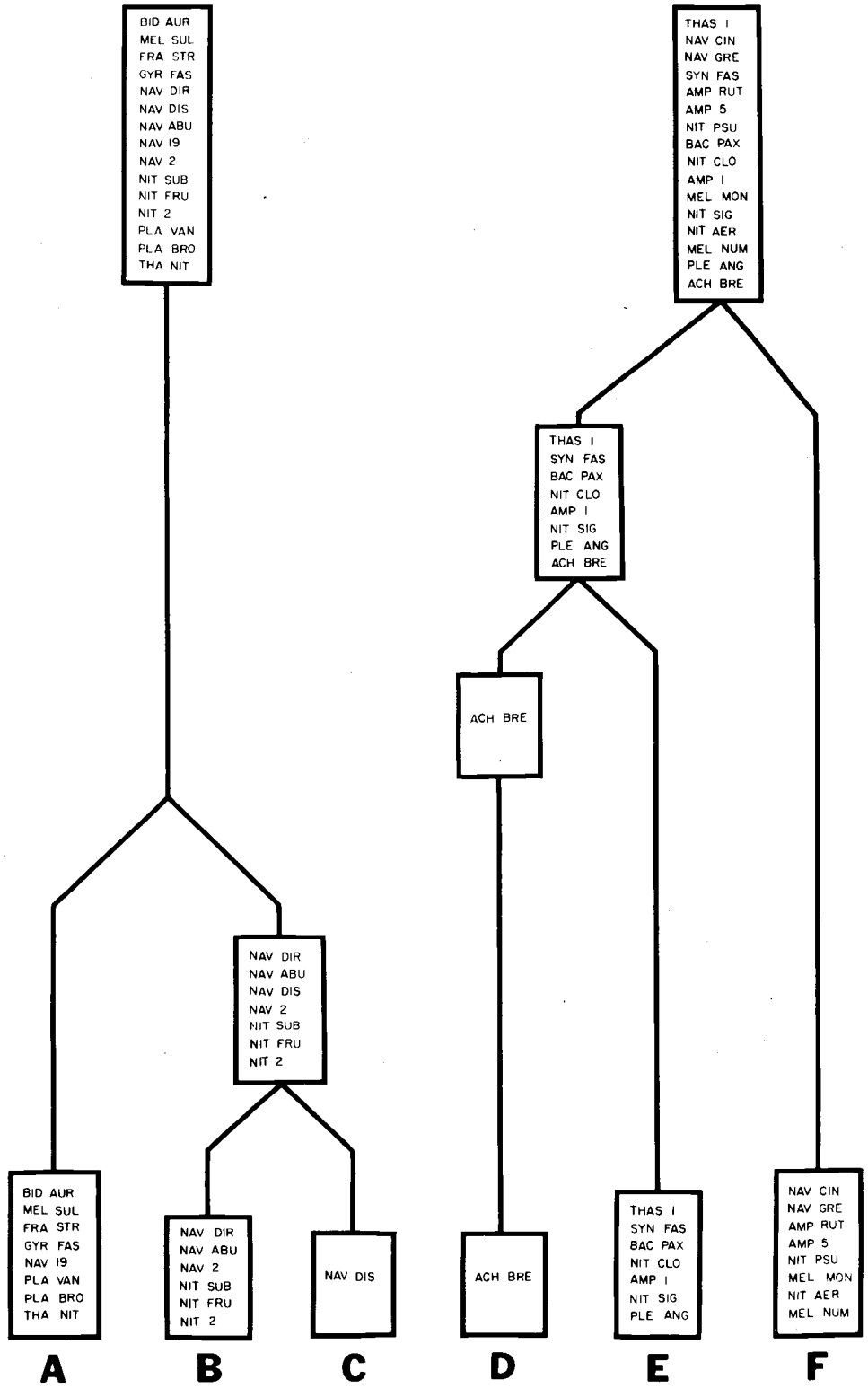

Figure 12. Cluster analysis of the 31 most abundant diatoms found in both ecosystems. The species symbols are identified in Table 3.

the data into three clusters partitioned out Cluster F, a group of species that did particularly well on Board 1 in the heated ecosystem. Further partitioning into four clusters defined Clusters D and E. Cluster D consisted of Achnanthes brevipes v. intermedia, a taxon that was particularly abundant on Board 2 of the heated ecosystem; Cluster E included species that were prominant on Board 3 of the heated ecosystem, apparently relatively tolerant of desiccation. Partitioning into five and six clusters defined clusters A, B, and C, clusters associated with the control ecosystem. Cluster A could be related to Board 3, Cluster B to Board 1, and Cluster C consisting of a single species, Navicula diserta, to Board 2.

Community Properties

The number of diatom taxa (Table 4 and Figure 13) found in the control ecosystem (mean sample size of 513.3 individuals) varied from a maximum of 39 species in 519 individuals for Board 1 (sample 7) to a minimum of 19 species in 510 individuals on Board 2 (sample 3). Estimates of Simpson's species composition parameter (SDI) ranged from a minimum of 0.698 (Board 1, sample 4) to a maximum of 0.858 (Board 1, sample 2) with a mean value of 0.777. The highest mean SDI value for assemblages on each board (mean for the seven samples) was 0.789 (Board 2). Relatively low SDI values corresponded to the occurrence of such dominant diatom taxa as Navicula directa, Navicula

Table 4. The number of individuals (N), the number of species (S), and expressions of diversity and dominance for samples obtained from the control and heated ecosystems during the experiment. The Information measure of diversity is expressed as bits per individual.

					Simpson	Information	
Tank	Board	Substrate	N	S	SDI	H"	R'
Control	1	1	509	26	0.847	3.33	0.326
		2	510	23	0.859	3.29	0.301
		3	518	28	0.769	2.85	0.458
		4	513	20	0.698	2.36	0.499
		5	519	22	0.705	2.45	0.497
		6	509	34	0.747	3.00	0.472
		7	533	34	0.855	3.79	0.293
	2	1	514	25	0.718	2.48	0.520
		2	510	29	0.817	3.16	0.397
		3	510	19	0.829	3.01	0.318
		4	510	26	0.779	2.89	0.432
		5	510	23	0.699	2.35	0.534
		6	510	38	0.843	3.52	0.383
		7	510	34	0.844	3.45	0.372
	3	1	510	30	0.700	2.52	0.553
		2	510	31	0.727	2.76	0.505
		3	510	30	0.799	2.95	0.454
		4	510	30	0.808	3.06	0.427
		5	511	29	0.727	2.78	0.484
		6	513	30	0.761	2.89	0.466
		7	519	39	0.812	3.30	0.437
Mean			515	29	0.778	2.96	0.435
Heated	1	1	513	35	0.868	3.57	0.351
		2	510	31	0.888	3.74	0.280
		3	559	41	0.910	4.04	0.285
		4	508	36	0.923	4.13	0.233
		5	517	34	0.917	4.07	0.230
		6	516	34	0.906	3.84	0.282
		7	502	31	0.879	3.59	0.315
	2	1	507	22	0.528	1.97	0.617
		2	506	37	0.587	2.43	0.623
		3	510	32	0.639	2.57	0.557
		4	513	45	0.870	3.90	0.346
		5	511	35	0.873	3.70	0.322
		6	515	34	0.865	3.60	0.336
		7	505	35	0.889	3.78	0.305
	3	1	510	25	0.540	2.02	0.631
		2	509	36	0.571	2.27	0.650
		3	507	33	0.702	2.85	0.500
		4	510	33	0.807	3.37	0.381
		5	512	43	0.865	3.73	0.364
		6	538	28	0.869	3.59	0.285
		7	515	38	0.914	4.08	0.259
Mean			514	34	0.800	3.37	0.388

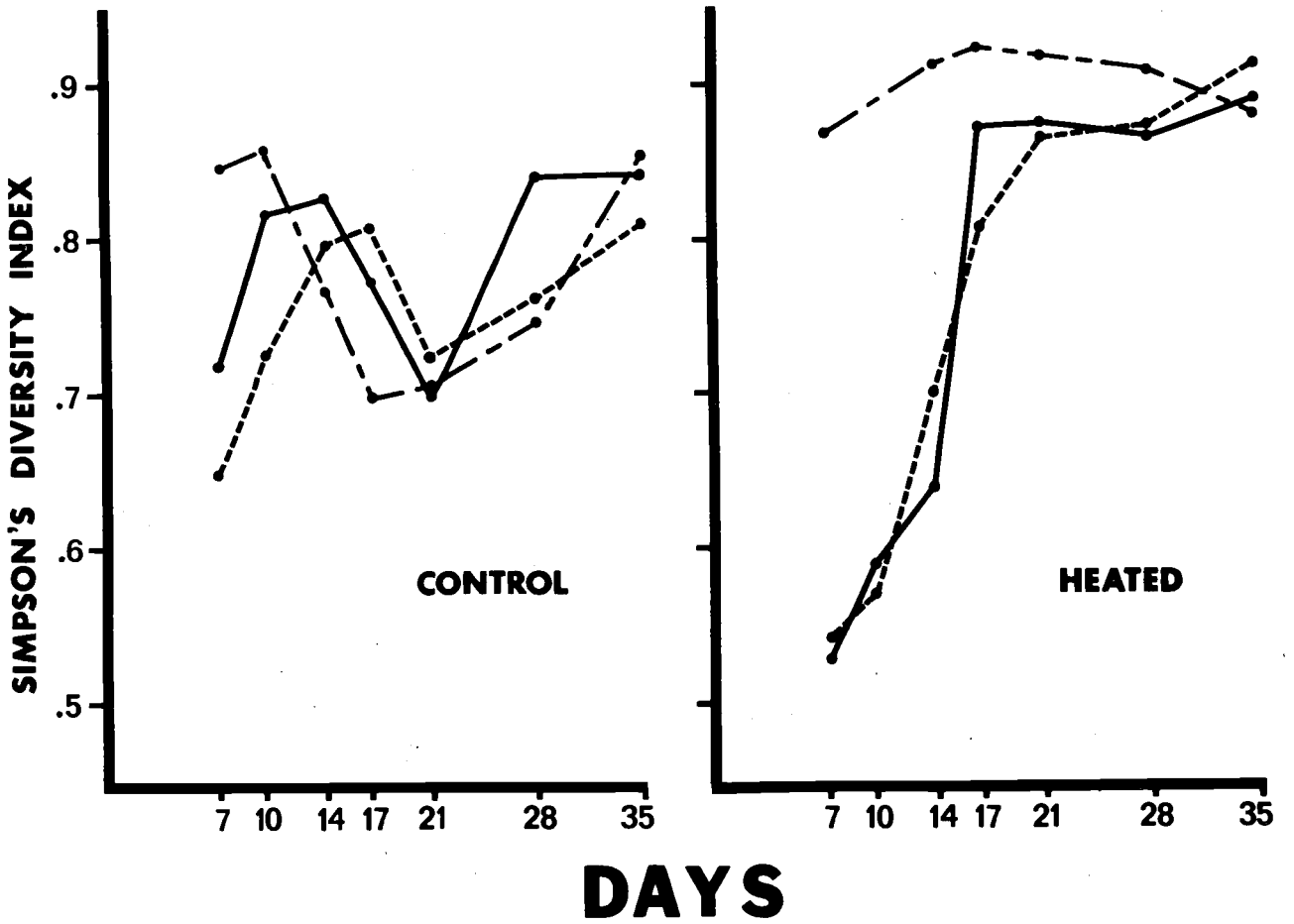

Figure 13. SDI values for the control ecosystem and the heated ecosystem. The long-short dashed line, the solid line, and the dashed line represent Boards 1, 2, and 3, respectively.

diserta, and Nitzschia no. 2. Values of SDI also were affected on Board 1 by a marine fungus and the grazing activities of the protozoan Euplotes charon Müller. As these organisms became abundant by day 17 (sample 4), the diatom biomass decreased, and SDI increased in subsequent samples.

The mean size of samples from the heated ecosystem was 513.9. The number of diatom taxa varied from a maximum of 45 in 513 individuals for Board 2 (sample 4) to a minimum of 22 in 507 individuals for sample 1 of the same board. The mean SDI for the heated ecosystem (0.796) was slightly higher than that for the control ecosystem, and SDI ranged from 0.527 (Board 2, sample 1) to 0.923 (Board 1, sample 4). Board 1 of the heated ecosystem had the highest mean SDI value of both ecosystems. Values of SDI for Board 1 were relatively high for all seven samples, varying between 0.868 and 0.923, while for Board 2 and Board 3 SDI increased from 0.528 (sample 1) to 0.889 (sample 7) and from 0.540 (sample 1) to 0.914 (sample 7), respectively (Table 4).

Matrices of similarity values SIMI and of proportions of co-occurring taxa P_{hk} for comparisons of diatom assemblages from the different boards in the heated and control ecosystems are presented in Tables 5, 6, 7, and 8. For this analysis, the data have been pooled in two ways: 1) data for the seven samples from each board were pooled and treated as one assemblage; 2) data for the three samples

taken at a particular time from each ecosystem were pooled and treated as one assemblage. A matrix of SIMI values comparing all the individual samples to one another for each ecosystem is presented in Appendix 2.

In general, the diatom assemblages were more similar in the control ecosystem than in the heated ecosystem. The mean SIMI value for comparisons of pooled samples taken at different times was 0.798 for the control ecosystem and 0.708 for the heated ecosystem (Tables 5 and 6). The mean SIMI value for comparisons of pooled

Table 5. A matrix of similarity values SIMI (lower left half) and of proportions of co-occurring taxa P_{hk} (upper right half) for comparisons of diatom assemblages at different times in the control ecosystem. The values in the table are expressed as SIMI X 10^3 and P_{hk} X 10^3.

	1	2	3	4	5	6	7
1		435	371	428	459	406	423
2	968		435	525	574	541	493
3	721	860		419	426	406	394
4	503	683	955		400	380	428
5	468	639	899	957		550	471
6	527	674	896	943	957		612
7	618	736	876	883	943	958	

samples taken from different boards was 0.781 for the control ecosystem and 0.578 for the heated ecosystem (Tables 7 and 8). In the heated ecosystem, the structure of the pooled assemblages taken on a

Table 6. A matrix of similarity values SIMI (lower left half) and of proportions of co-occurring taxa P_{hk} (upper right half) for comparisons of diatom assemblages at different times in the heated ecosystem. The values in the table are expressed as SIMI X 10^3 and P_{hk} X 10^3.

	1	2	3	4	5	6	7
1		542	543	527	544	472	425
2	988		690	550	619	468	487
3	982	985		600	606	661	533
4	895	907	950		644	538	471
5	625	641	710	847		623	618
6	397	409	494	647	840		618
7	374	378	465	605	778	958	

particular date gradually changed as the experiment progressed, and the lowest SIMI value (0.374) was found for a comparison between pooled sample 1 and pooled sample 7. In the control ecosystem, the structure of such pooled assemblages changed appreciably between sample 1 and sample 5, but similarity between pooled samples 4, 5, 6, and 7 was relatively high. SIMI values for comparisons of pooled assemblages from Board 1 with those of Board 2 and Board 3 in the heated ecosystem were relatively low (0.404 and 0.349), while pooled assemblages from Board 2 and Board 3 were quite similar (Table 8). In other words, the assemblages on the two boards exposed to desiccation were similar to each other but somewhat different from the assemblages found on the board that was submerged throughout the experiment. In the control ecosystem, differences between pairs of

pooled assemblages from the different boards were not as great as in the heated ecosystem, and the lowest SIMI value (0.660) was found for the comparison between the pooled assemblages from Board 1 and Board 3 (Table 7).

Table 7. A matrix of similarity values SIMI (lower left half) and of proportions of co-occurring taxa P_{hk} (upper right half) for comparisons of diatom assemblages on different boards in the control ecosystem. The values in the table are expressed as SIMI X 10^3 and P_{hk} X 10^3.

	1	2	3
1		537	543
2	805		505
3	660	878	

Table 8. A matrix of similarity values SIMI (lower left half) and of proportions of co-occurring taxa P_{hk} (upper right half) for comparisons of diatom assemblages on different boards in the heated ecosystem. The values in the table are expressed as SIMI X 10^3 and P_{hk} X 10^3.

1		559	642
2	404		463
3	349	982	

Pairs of pooled assemblages in the heated ecosystem on the average had more taxa in common than in the control ecosystem (Tables 5, 6, 7, and 8). The mean P_{hk} value for pairs of pooled samples taken at different times was 0.561 for the heated ecosystem and 0.456 for the control ecosystem; corresponding mean P_{hk} values for pooled samples

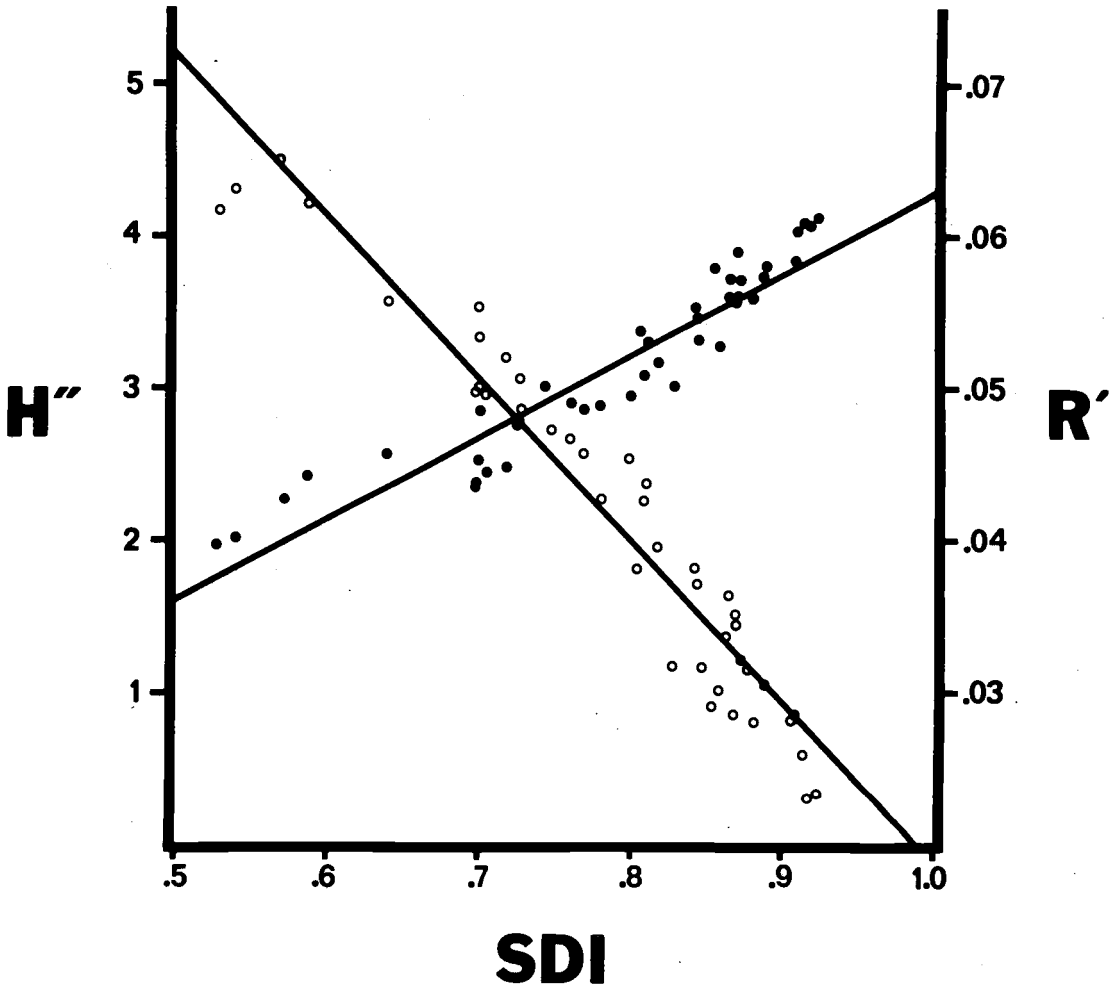

Figure 14. Regression of H'' and R' on SDI.

taken from different boards were 0.555 and 0.528, respectively.

The relationship between the Information measure (H''), the redundancy measure (R') and the complement of Simpson's measure of concentration (SDI) are illustrated in Figure 14. A straight line relating H'' to SDI had an intercept of -1.07 and a slope of 5.37 and explained 88% of the variability ($R^2 = 0.88$). A straight line relating R' to SDI accounted for 93% of the variability ($R^2 = 0.93$) and had a slope of -1.06 and an intercept of 1.25.

DISCUSSION

Succession is characterized by progressive changes in species composition, organic structure, and energy flow. More efficient species will replace other species until the whole community is replaced by a more complex one, and rates of change and limitations are controlled by the physical environment. As the ecosystem matures, however, it develops mechanisms to buffer strong abiotic fluctuations. The culmination of succession is a mature ecosystem with high diversity, a high biomass:unit energy flow ratio, complex food chains, slow nutrient exchange rate between the organism and the environment, and high stability (Odum, 1969).

Goulden (1969) divided colonization into three phases. The first is characterized by the rapid invasion of the substrates and a rapid increase in species diversity. In the second phase, diversity continues to increase as individual organisms become more evenly distributed among the species. In the last phase, rare species continue to invade the substrates, replacing local extinctions. Diatoms colonizing the substrates of the laboratory ecosystem originate from a common species pool in the influent seawater. The success of a particular taxon depends on its density in the species pool, its ability to attach to the substrate, its tolerance of the environment, and its ability to compete and reproduce (McIntire and Overton, 1971).

ZoBell and Allen (1934) and Hendey (1951) agree that the initial colonizers of substrates are bacteria rather than diatoms. After the establishment of a bacterial slime, the efficiency of attachment by diatoms apparently increases, and additional slime is produced by the diatoms themselves. Besides acting as a substrate, the slime slows the evaporation of water during periods of desiccation and perhaps acts as a nutrient trap for free amino acids and sugars secreted by the diatoms (Hostetter and Hoshaw, 1970).

Colonization was rapid on the continually submerged substrates of Board 1 in the heated ecosystem. The diatom assemblages consisted of a dense mat of filamentous and tube dwelling, colonial species 25.5 cm in height. However, filamentous forms did relatively poorly in the control ecosystem leaving the tube dwellers as the most conspicuous colonial form on Board 1. After 16 days, the highest colony in the control ecosystem was only 10 cm in height--less than half the size of the colonies in the heated ecosystem. At the same time, large discolored circular patches began to appear on Board 1 in the control ecosystem. These patches were caused by a large population of Euplotes charon Müller that was grazing heavily on the diatom assemblage, particularly on the species Navicula directa. At the end of the experiment, a marine fungus was also found in this area. Neither the fungus nor the protozoans were found in abundance in the heated

ecosystem. A large quantity of material sloughed off the substrates in the heated ecosystem, but no sloughing occurred in the control.

The length of time required to colonize the substrates on Boards 2 and 3 of both ecosystems was directly proportional to the time the substrates were exposed to desiccation. As the water level dropped, the overhanging lights produced enough heat to raise the temperature on the boards to approximately 40 C. Because water tended to accumulate in the spaces between the substrates and because the rate of evaporation was slower there, colonization by bacteria and diatoms began at the edges of the substrates and moved inward as the experiment progressed. At the end of the experiment, diatoms formed only a thin layer on Boards 2 and 3 as compared to a dense mat on Board 1.

There seems to be two basic successional patterns for artificial substrates. The pattern followed depended on whether or not the substrates were exposed to desiccation. Substrates that were continuously submerged were rapidly invaded by both motile, solitary diatoms and by taxa capable of attaching to either the substrates or the bacterial slime. These taxa included such species as Navicula directa, Navicula diserta, Navicula no. 2, Navicula cincta, and Nitzschia no. 2. Taxa were continually being replaced by other taxa as the experiment progressed. By the end of the experiment, both filamentous and tube dwelling colonial diatoms, such as Fragilaria striatula var. californica, Amphipleura rutilans, Melosira nummuloides, and Melosira

moniliformis, had become well established with many motile, solitary and epiphytic diatoms interspersed between the colonies.

Diatoms capable of attaching to the substrates had difficulty in establishing themselves on Boards 2 and 3 in both ecosystems. Planktonic taxa, such as Thalassiosira no. 1 and Thalassionema nitzschioides, were the first to invade the substrates by settling down on them and becoming embedded in the available bacterial mucilage . These taxa were prominent in the early samples, but were gradually replaced both by taxa that had previously colonized the lowermost board (Navicula directa, Navicula diserta, Navicula no. 2 and Nitzschia no. 2) and by several species that could not compete on Board 1 very well, but were tolerant of exposure and high air temperatures (Nitzschia sigma, Pleurosigma angulatum, and Synedra fasciculata). Again, colonial forms were beginning to become established by the end of the experiment.

Using the same equipment as that used in this experiment, Wulff (1971) did a preliminary experiment concerning the effects of heated water on diatom assemblages along with other experiments on the effects of reduced salinity, tidal cycle, and light intensity. In the heated water experiment, Wulff allowed communities to develop for 17 days at a temperature of 25 $\pm$ 2.5 C with the trough continuously filled with water. In contrast, temperature was allowed to vary and a tidal cycle was introduced in the colonization experiment reported here. In both

experiments, Melosira mats formed on substrates that received a relatively high light intensity and were continuously submerged. Even though the species Melosira nummuloides and Melosira moniliformis made up the bulk of the biomass on Board 1 in the colonization experiment, diversity was high because of the presence of many other species living inside the mats. It would be interesting to find out whether or not there was any stratification of diatoms within the mats because of decreasing light intensity. Melosira moniliformis tended to invade the boards exposed to desiccation at a faster rate than Melosira nummuloides, but the latter increased in relative abundance at a faster rate. Castenholz (1964) suggested that the growth of Melosira moniliformis was inhibited by high light intensities during 15-hour light periods.

Melosira moniliformis and Melosira nummuloides have been found on both artificial substrates and on macroalgae in Yaquina Bay (McIntire and Overton, 1971; Main, 1973). Hopkins (1964b) found both species growing on chalk, macroalgae, and wood with limiting factors appearing to be high air temperatures and the concentration of dissolved nutrients. A Fragilaria-Melosira community was found by Aleem (1950) growing on sloping concrete beneath an Achnanthes-blue-green algae community. Melosira nummuloides was also found in association with Fragilaria on the upper part of a vertical cement block (Castenholz, 1963). Unlike Aleem and Castenholz, I found no relationship between Melosira and Fragilaria. Fragilaria striatula

var. californica was present, but was abundant on Board 3 of the heated ecosystem. The species of Melosira, however, had their largest populations on Board 1.

Nitzschia aerophila is rarely found in Yaquina Bay (McIntire and Overton, 1971; Main, 1973), but can become abundant under laboratory conditions (Wulff, 1971). Wulff found that this species had no preference for a particular light intensity, no definite pattern of zonation, and was not tolerant of reduced salinities. However, he did find that it competed well at elevated temperatures. In the colonization experiment, Nitzschia aerophila was found in large populations distributed over all three boards in the heated ecosystem, with the largest population occurring on Board 2. Invasion of the substrates occurred rather early in the experiment. Apparently, this species finds it difficult to compete under normal circumstances, but is able to take advantage of unnatural conditions produced in the laboratory.

Nitzschia sigma, Amphora no. 1, Navicula cincta, and Nitzschia closterium were also tolerant of elevated temperatures. Nitzschia sigma was found to be more abundant in Yaquina Bay than Nitzschia aerophila and was more abundant in the control ecosystem than in the heated ecosystem. However, Nitzschia sigma seemed to compete more efficiently on boards exposed to desiccation. Navicula cincta did well only on Board 1 in the heated ecosystem where it has been considered to be an early colonizer. Nitzschia closterium has been

described by Hopkins (1964b) as a mud diatom that prefers shade and is frequently found in association with Pleurosigma. No such association was evident in this experiment. Like Navicula cincta, Nitzschia closterium had its largest population on continuously submerged substrates. Amphora no. 1 was a late colonizer in the heated ecosystem with relatively equal sized populations on each of the levels. None of these species were found in abundance in the control ecosystem.

In the colonization experiment reported here, Achnanthes brevipes var. intermedia invaded the substrates quite late in the experiment--on the 21st day on Board 2 and on the 28th day on Board 3. However, by the last sample taken on Board 2, this species had obtained a relative abundance of 22.2%. If the experiment had run longer, it is probable that such a population size also could have been reached on Board 3. Interestingly enough, no specimens of this taxon were found on Board 1. This taxon has been found in the upper litoral or supralittoral zone by Aleem (1950), Castenholz (1963), Edsbagge (1965), Hendey (1964), and McIntire and Overton (1971); both Hopkins (1964b) and Main (1973) found it growing epiphytically on macroalgae. Hopkins also found it growing on wood and concrete, but not on chalk.

Navicula directa was dominant on all three boards in the control ecosystem, but maintained only small, relatively constant populations in the heated ecosystem. McIntire and Overton (1971) found only a few individuals on artificial substrates in Yaquina Bay; however, Main

(1973) found it as an epiphyte in May at lower depths near River Bend (Yaquina Bay). Navicula directa followed no distinct seasonal patterns while growing on the lower part of a vertical concrete block below Fragilaria and Melosira at Gregory Point, Oregon (Castenholz, 1963). After finding no consistent correlation between the rate of growth and light intensity, Wulff (1971) suggested that the growth of Navicula directa could be inhibited by species such as Melosira nummuloides and Nitzschia aerophila when exposed to reduced salinity. Perhaps it is more appropriate to say that Navicula directa has a much smaller tolerance of both reduced salinity and heated water than Melosira nummuloides and Nitzschia aerophila.

Navicula diserta has been shown to be one of the most abundant diatoms in Yaquina Bay (McIntire and Overton, 1971; Main, 1973). Wulff (1971) found it tolerant of a broad range of environmental conditions including desiccation and temperature. He also found that it favored moderate light intensities. In the colonization experiment, Navicula diserta was one of the early colonizers on Board 1 in both ecosystems, but obtained its largest population on Board 2 in the control ecosystem. Cholnoky (1963) found this species sensitive to salinity changes. This is interesting because this taxon is found in both salt water and brackish water at many locations in the estuary. This might indicate the development of many sub-populations, each with their own range of salinity tolerances (Wulff, 1971).

Odum (1969) and other ecologists feel that diversity increases as an ecosystem matures. Diversity (SDI) was found to be relatively high on Board 1 in the heated ecosystem and on all three boards in the control ecosystem (Figure 13). Apparently, sampling was not initiated soon enough on these boards to record the increase in species diversity that corresponds to the early invasion of new species. However, sampling was sufficient to trace the increase in diversity on Boards 2 and 3. This was due to a lag in colonization of the substrates because of the combined stress of elevated water temperatures and high air temperatures. SDI values for all three boards in the control ecosystem decreased rather sharply in the middle of the experiment and then increased again. This fluctuation did not occur in the heated ecosystem. The decrease in diversity could be explained by the establishment of dominant species such as Navicula directa, Navicula diserta, and Nitzschia no. 2. The subsequent increase in diversity, on the other hand, closely corresponded with the introduction of grazers into the ecosystem. The population of Navicula directa was decreased by consumer organisms making the invasion of rarer species possible.

If sampling had been initiated earlier in the experiment on Board 1, it is quite probable that planktonic taxa would be found to be the initial colonizers on these substrates as well as on those exposed to desiccation. Of course, they might be prominant for only a few

hours because of the ability of the attached diatoms to colonize submerged substrates. Sampling was not begun earlier than a week because of the small amount of growth on Boards 2 and 3.

The question of how the time of exposure to colonization and exposure to desiccation was related to the similarity between diatom assemblages was considered by estimating the parameters of the regression model

$$\widehat{SIMI} = b_0 + b_1 \Delta E + b_2 \Delta T + b_3 \Delta E \cdot \Delta T$$

where $\widehat{SIMI}$ was the predicted similarity value, ΔE was the difference in the period of exposure to desiccation, ΔT was the difference in the period of exposure to colonization in the h-th and k-th assemblages, and b_0, b_1, b_2, and b_3 are the partial regression coefficients. The only t-value not significant at the 95% level was that for the interaction between the difference in the period of exposure to desiccation and the difference in the period of exposure to colonization in the control ecosystem (Tables 9 and 10). The relationship between the within cluster sum of squares (Figure 11), the results of the regression analysis (Table 9), and the matrix of similarity values (Appendix 2) all indicate that the heated ecosystem contained more discrete assemblages than the control ecosystem. More or less discrete assemblages were obtained by Wulff and McIntire (1972) when there was an interaction between a relatively high light intensity and either sudden reduction in

Table 9. Summary of partial regression coefficients, t-values, and the order of variable entry for the model $\widehat{SIMI} \times 10^3 = b_0 + b_1 \Delta E + b_2 \Delta T + b_3 \Delta T$ where $\widehat{SIMI}$ is the predicted similarity value between the h-th and k-th assemblage, ΔE is the difference in the period of exposure to desiccation and ΔT is the difference in the period of exposure to colonization in the control ecosystem.

Independent Variable	$\hat{b}$	t(207 d.f.)	Step
ΔE	-26.9	-3.53	2
ΔT	-11.2	-3.25	3
$\Delta E \Delta T$	0.74	1.31	1

Intercept = 858

$R^2 = 0.13$

Table 10. Summary of partial regression coefficients, t-values, and the order of variable entry for the model $\widehat{SIMI} \times 10^3 = b_0 + b_1 \Delta E + b_2 \Delta T + b_3 \Delta E \Delta T$ where $\widehat{SIMI}$ is the predicted similarity value between the n-th and k-th assemblage, ΔE is the difference in the period of exposure to desiccation and ΔT is the difference in the period of exposure to colonization in the heated ecosystem.

Independent Variable	$\hat{b}$	t(207 d.f.)	Step
ΔE	-47.5	-6.56	3
ΔT	-23.3	-6.83	2
$\Delta E \Delta T$	1.33	2.48	1

Intercept = 906

$R^2 = 0.30$

salinity or an elevation in water temperature (no tidal cycle was introduced in this set of experiments). In Yaquina Bay, as in the control ecosystem, the distribution of attached diatoms was a continuum along environmental gradients without well defined groups of species with similar distributions (McIntire and Overton, 1971).

Nevertheless, partitioning of the 31 most abundant species in the cluster analyses for the heated ecosystem and the control ecosystem resulted in the formation of ten clusters for each ecosystem with two clusters held in common by both ecosystems. The first group included such species as Navicula diserta, Navicula no. 2 Nitzschia no. 2, and Navicula gregaria which are attached forms that compete well on continuously submerged substrates. The second cluster includes Thalassiosira no. 1, Thalassionema nitzschioides, Melosira sulcata, Gyrosigma fasciola, Navicula no. 19, Plagiogramma vanheurckii, and Plagiogramma brockmanni--all planktonic or solitary diatom taxa that were tolerant of exposure to desiccation. Presumably, the species within each cluster have similar ecological properties as long as their presence is not by chance. These clusters are considered to have biological significance. However, there is no similarity between these clusters and any of the associations described by Aleem (1950), Edsbagge (1964), Hendey (1964) and Hopkins (1964b).

Laboratory model ecosystems have a great potential for simplifying complex natural ecosystems. Open laboratory models allow the development of normal algal communities together with control over several environmental factors--in this case, salinity, exposure to desiccation, temperature, and light intensity. But, because of the complexity of natural ecosystems and because of the technical restrictions imposed on laboratory models, care must be used when interpreting results. An amount of reality is given up in exchange for simplicity (Warren and Davis, 1971). However, if used in close correspondence with field studies, laboratory model ecosystems can provide valuable information concerning individual species and their interactions. Most of the taxa found in the ecosystems by McIntire and Wulff (1969), Wulff (1971), Wulff and McIntire (1972), and myself have been found in field studies of Yaquina Bay, Oregon (Main, 1973; Martin, 1970; McIntire and Overton, 1971; and Riznyk, 1969). Distributions of attached diatoms in the ecosystems also closely correspond to distributions at selected field stations in Oregon (Castenholz, 1963; McIntire and Overton, 1971) and in Europe (Aleem, 1950; Edsbagge, 1965; Hendey, 1964; and Hopkins, 1964b).

BIBLIOGRAPHY

Aleem, A. A. 1950. Distribution and ecology of British marine littoral diatoms. Journal of Ecology 38:75-106.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42:783-794.

_____. 1963. An experimental study of the vertical distribution of littoral marine diatoms. Limnology and Oceanography 8:450-463.

_____. 1964. The effect of daylight and light intensity on the growth of littoral marine diatoms in culture. Physiologia Plantarum 17:951-963.

Cholnoky, B. J. 1963. Beitrage zur Kenntnis des marinen Litorals von Südafrika. Botanica Marina 5:38-83.

Cooke, W. B. 1956. Colonization of artificial bare areas by microorganisms. Botanical Review 22:613-638.

Davis, J. S. 1972. Survival records in the algae, and the survival role of certain algal pigments, fat, and mucilaginous substances. The Biologist 54:52-94.

Drum, R. W. 1969. Light and electron microscope observations on the tube-dwelling diatom Amphipleura rutilans (Trentepohl) Cleve. Journal of Phycology 5:21-26.

Drum, R. W. and J. T. Hopkins. 1966. Diatom locomotion; an explanation. Protoplasma 62:1-33.

Drum, R. W. and E. Webber. 1966. Diatoms from a Massachusetts salt marsh. Botanica Marina 9:70-77.

Edsbagge, H. 1965. Vertical distribution of diatoms. Svensk Botanisk Tidskrift. 59:463-468.

Goulden, C. E. 1969. Developmental phases of the biocoenosis. Proceedings of the National Academy of Sciences 62:1066-1073.

Harper, M. A. 1969. Movement and migration of diatoms on sand grains. British Phycological Journal 4:97-103.

Hendey, N. I. 1951. Littoral diatoms of Chichester Harbor with reference to fouling. Journal of the Royal Microscopical Society 71:1-86.

_____. 1964. An introductory account of the smaller algae of British coastal waters. Part V. Bacillariophyceae (Diatoms). London. 317 pp. (Great Britain. Ministry of Agriculture and Fisheries. Fishery Investigations, ser. 4).

Hopkins, J. T. 1963. A study of the diatoms of the Ouse Estuary, Sussex. I. The movement of the mud-flat diatoms in response to some chemical and physical changes. Journal of the Marine Biological Association of the United Kingdom 43:653-663.

_____. 1964a. A study of the diatoms of the Ouse Estuary, Sussex. II. The ecology of the mud-flat diatom flora. Journal of the Marine Biological Association of the United Kingdom 44: 333-341.

_____. 1964b. A study of the diatoms of the Ouse Estuary, Sussex. III. The seasonal variation in the littoral epiphyte flora and the shore plankton. Journal of the Marine Biological Association of the United Kingdom 44:613-644.

_____. 1966. Some light induced changes in behavior and cytology of an estuarine mud flat diatom. British Ecological Society Symposium 6:335-358.

Hostetter, H. P. and R. W. Hoshaw. 1970. Environmental factors affecting resistance to desiccation in the diatom Stauroneis anceps. American Journal of Botany 57:512-518.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577-587.

Main, S. P. 1973. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon. Ph.D. thesis. Corvallis, Oregon State University. 112 numb. leaves.

Mann, K. H. 1969. The dynamics of aquatic ecosystems. Advances in Ecological Research 6:1-81.

Martin, J. V. 1970. Salinity as a factor controlling the distribution of benthic estuarine diatoms. Ph.D. thesis. Corvallis, Oregon State University. 114 numb. leaves.

McIntire, C. D. 1966. Some effects of current velocity on periphyton communities in laboratory streams. Hydrobiologia 27:559-570.

McIntire, C. D. and W. S. Overton. 1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. Ecology 52:758-777.

McIntire, C. D. and B. L. Wulff. 1969. A laboratory method for the study of marine benthic diatoms. Limnology and Oceanography 14:667-678.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164:262-270.

Patrick, R. 1961. A study in the numbers and kinds of species found in rivers in Eastern United States. Proceedings of the Academy of Natural Sciences of Philadelphia 113:115-158.

_____. 1967. The effect of invasion rate, species pool, and size of area on the structure of the diatom community. Proceedings of the National Academy of Sciences 58:1335-1342.

Patrick, R., M. H. Hohn and J. H. Wallace. 1954. A new method for determining the pattern of the diatom flora. Natulae Naturae of the Academy of Natural Sciences of Philadelphia, No. 259. 12 pp.

Patrick, R. and C. Reimer. 1966. The diatoms of the United States. Vol. I. Philadelphia. 688 pp. (Academy of Natural Sciences of Philadelphia. Monograph no. 13).

Rees, C. B. 1940. Preliminary study of the ecology of a mud flat. Journal of the Marine Biological Association of the United Kingdom 24:185-200.

Reisen, W. K. and D. J. Spencer. 1970. Succession and current demand relationships of diatoms on artificial substrates in Prater's Creek, South Carolina. Journal of Phycology 6:117-122.

Riznyk, R. Z. 1969. Ecology of benthic microalgae of intertidal sediments. Ph. D. thesis. Corvallis, Oregon State University. 196 numb. leaves.

Round, F. E. 1960. The diatom flora of a salt marsh on the River Dee. New Phytologist 49:332-348.

Shannon, C.E. and W. Weaver. 1949. The mathematical theory of communication. University of Illinois Press: Urbana. 117 pp.

Simpson, E.H. 1949. Measurement of diversity. Nature 163:688.

Stander, J.M. 1970. Diversity and similarity of benthic fauna off Oregon. Masters thesis. Corvallis, Oregon State University. 72 numb. leaves.

Stockner, J.G. 1968. The ecology of a diatom community in a thermal stream. British Phycological Bulletin 3:501-514.

Thayer, O.E. and R.G. Redmond. 1969. Budget salinity recorder. Limnology and Oceanography 14:641-643.

Warren, C.E. and G.E. Davis. 1971. Laboratory stream research: objectives, possibilities, and constraints, p. 111-144. In R.F. Johnston, P.W. Frank, and C.D. Michener, Annual Review of Ecology and Systematics. Palo Alto, California.

Williams, R.B. 1962. The ecology of diatom populations in a Georgia salt marsh. Ph.D. thesis. Cambridge, Harvard University. 146 numb. leaves.

_____. 1964. Division rates of salt marsh diatoms in relation to salinity and cell size. Ecology 45:877-880.

_____. 1965. Unusual motility of tube dwelling pennate diatoms. Journal of Phychology 1:145-146.

Wilson, O.T. 1925. Some experiemental observations of marine algal succession. Ecology 6:303-311.

Wulff, B.L. 1971. Structure and productivity of marine benthic diatom communities in a laboratory model ecosystem. Ph.D. thesis. Corvallis, Oregon State University. 115 numb. leaves.

Wulff, B.L. and C.D. McIntire. 1972. Laboratory studies of assemblages of attached estuarine diatoms. Limnology and Oceanography (in press).

Zobell, C.E. 1943. The effects of solid surfaces upon bacterial activity. Journal of Bacteriology 46:39-56.

Zobell, C.E. and E.C. Allen. 1934. The significance of marine bacteria in the fouling of submerged surfaces. Journal of Bacteriology 29:239-251.

APPENDICES

Appendix Table 1. Diatom taxa in samples from the laboratory ecosystem and their abundance on Boards 1, 2, and 3 in the control ecosystem and on Boards 1, 2, and 3 in the heated ecosystem.

Taxon	Control Ecosystem Board			Heated Ecosystem Board		
	1	2	3	1	2	3
Achnanthes brevipes var. intermedia (Kütz.) Cl.	0	5	1	0	168	41
Achnanthes deflexa Reim.	0	0	2	0	0	1
Achnanthes hauckiana Grun.	11	5	3	10	11	9
Achnanthes lanceolata (Bréb.) Grun.	1	1	4	0	6	1
Achnanthes parvula Kutz.	0	1	1	0	0	0
Achnanthes turgida Ehr.	0	0	0	0	0	1
Achnanthes no. 1	0	0	2	0	0	3
Achnanthes no. 2	0	0	1	2	0	1
Actinoptychus undulatus (Bail.) Ralfs	1	7	6	1	8	7
Amphipleura rutilans (Trent.) Cl.	28	32	12	196	1	6
Amphiprora alata Kütz.	0	0	1	0	0	0
Amphora angusta Greg.	0	0	0	0	0	1
Amphora exigua Greg.	0	0	0	0	0	1
Amphora graeffii var. minor Per.	0	0	0	0	0	1
Amphora proteus Greg.	0	0	0	0	1	0
Amphora no. 1	2	16	3	154	165	212
Amphora no. 2	0	0	0	11	3	0
Amphora no. 3	19	0	4	5	0	0
Amphora no. 4	1	1	2	23	1	0
Amphora no. 5	7	17	5	94	66	26
Amphora no. 14	4	0	2	20	1	1
Amphora no. 15	0	1	0	0	0	2
Aulocodiscus probablis A. S.	0	0	0	0	1	1
Bacillaria paradoxa Gmelin	3	0	0	29	17	37
Biddulphia aurita (Lyngb.) Bréb et Godey	10	11	29	6	3	0
Cocconeis costata Greg.	0	1	0	0	3	0
Cocconeis diminuta Pant.	0	0	2	0	1	0
Cocconeis dirupta Greg.	0	0	0	0	1	0
Cocconeis disculus (Schum.) Cl.	0	0	2	0	0	0
Cocconeis fluviatilis Wallace	0	0	1	0	0	0
Cocconeis placentula var. euglypta (Ehr.) Cl.	3	15	5	5	5	5
Cocconeis placentula var. lineata (Ehr.) Cl.	0	0	4	0	0	0
Cocconeis scutellum Ehr.	0	2	3	4	14	13
Cocconeis scutellum var. parva Grun.	2	0	2	2	7	2
Cocconeis scutellum var. stauroneiformis Sm.	0	2	0	0	0	0
Coscinodiscus excentricus Ehr.	0	2	0	0	5	2
Coscinodiscus lineatus Ehr.	0	1	5	0	5	8
Coscinodiscus marginatus Ehr.	0	2	0	0	0	0
Coscinodiscus obscurus A. S.	0	0	1	0	0	0
Denticula subtilis Grun.	0	0	0	0	0	3
Dimerogramma minor Greg.	0	0	1	0	0	0
Dimerogramma no. 2	0	0	0	0	2	1

Appendix Table 1. Continued.

Taxon	Control Ecosystem Board			Heated Ecosystem Board		
	1	2	3	1	2	3
Diploneis bombus Ehr.	0	0	1	0	0	1
Diploneis pseudovalis Hust.	0	0	1	0	1	0
Eunotia vanheurckii var. intermedia (Krasske ex Hust.) Patr.	0	0	1	0	0	0
Eunotogramma marinum (W. Smith) Per.	0	0	0	0	1	0
Fragilaria construens var. venter (Ehr.) Grun.	7	12	12	1	2	3
Fragilaria striatula var. californica Grun.	31	35	29	2	4	29
Gomphoneis parvulum Kütz.	0	0	0	1	0	0
Gomphonema valentinica Nik.	0	1	0	0	0	0
Gyrosigma arcticum Cl.	0	0	0	2	0	0
Gyrosigma fasciola (Ehr.) Griff. et Henfr.	57	53	62	7	24	22
Gyrosigma peisoneis (Grun.) Cl.	0	0	0	0	0	2
Licmophora gracilis (Ehr.) Grun.	0	0	9	1	9	11
Melosira moniliformis Ag.	8	3	5	202	36	28
Melosira nummuloides (Dillw.) Ag.	2	2	2	102	54	25
Melosira sulcata (Ehr.) Kütz.	34	143	170	20	92	113
Navicula abunda Hust.	20	16	12	0	4	0
Navicula admissa Hust.	7	0	0	0	0	0
Navicula auriculata Hust.	0	0	0	0	0	1
Navicula cincta Ehr.	2	5	1	421	38	40
Navicula comoides (Ag.) Per.	0	0	3	0	0	0
Navicula cryptocephala Kütz.	0	0	4	0	0	0
Navicula decussis Østr.	0	0	0	0	0	1
Navicula directa (W. Smith) Ralfs	1164	842	999	10	54	180
Navicula diserta Hust.	373	577	35	234	25	64
Navicula diversistriata Hust.	0	4	2	2	3	4
Navicula finmarchica (Cl. et Grun.) Cl.	0	2	0	0	0	1
Navicula gregaria Donk.	27	13	6	81	11	5
Navicula grevillei (C. Ag.) Heib.	5	1	5	0	0	0
Navicula mutica Kütz.	0	1	1	0	17	1
Navicula tripunctata (Müll.) Bory	0	1	2	0	0	3
Navicula tripunctata var. schizonemoides (V.H.) Patr. (V. H.) Patr.	0	2	0	0	1	0
Navicula viridula var. avenacea Cl. et Grun.	0	3	1	0	0	0
Navicula no. 1	0	0	1	0	1	0
Navicula no. 2	322	127	90	392	91	91
Navicula no. 3	8	0	1	11	0	0
Navicula no. 4	3	0	0	0	0	0
Navicula no. 5	5	3	4	3	6	2
Navicula no. 19	11	18	24	0	15	10
Navicula no. 35	0	0	1	0	2	1
Nitzschia apiculata (Greg.) Grun.	1	1	5	7	2	1
Nitzschia aerophila Hust.	2	1	0	371	302	113
Nitzschia closterium Sm.	5	1	0	77	47	51
Nitzschia fonticola Grun.	0	0	0	21	0	0

Appendix Table 1. Continued.

Taxon	Control Ecosystem Board			Heated Ecosystem Board		
	1	2	3	1	2	3
Nitzschia frustulum var. perpusilla (Rabh.) Grun.	32	17	13	7	16	14
Nitzschia hungarica Grun.	0	1	0	2	0	3
Nitzschia hybrida Grun.	6	0	1	0	1	0
Nitzschia hybridaeformis Hust.	0	0	0	1	1	0
Nitzschia incerta Grun.	0	0	0	0	4	0
Nitzschia incrustans Grun.	6	0	1	4	2	0
Nitzschia lanceolata var. minor V. H.	0	0	0	1	18	29
Nitzschia pseudohybrida Hust.	43	2	0	159	2	1
Nitzschia punctata var. coarctata Grun.	0	0	0	1	2	0
Nitzschia sigma (Kütz.) W. Smith	18	41	34	93	337	357
Nitzschia socialis Greg.	1	0	3	0	0	0
Nitzschia subhybrida Hust.	63	16	25	34	28	8
Nitzschia no. 1	4	0	8	1	3	1
Nitzschia no. 2	752	249	58	440	32	17
Nitzschia no. 5	0	0	2	0	0	0
Nitzschia no. 9	0	0	1	12	1	0
Nitzschia no. 15	0	0	0	1	0	0
Nitzschia no. 16	1	0	0	0	0	0
Nitzschia no. 17	2	0	0	0	0	0
Nitzschia no. 18	0	1	0	0	0	0
Nitzschia no. 19	0	0	0	1	0	0
Nitzschia no. 28	0	0	0	0	0	1
Nitzschia no. 30	0	0	0	0	0	1
Nitzschia no. 31	0	0	0	6	0	0
Nitzschia no. 32	0	0	0	19	0	0
Opephora marina (Greg.) Petit	0	2	0	0	0	1
Opephora no. 1	4	0	1	0	20	3
Plagiogramma brockmanni Hust.	61	53	98	12	60	60
Plagiogramma staurophorum (Greg.) Heib.	0	0	1	0	0	0
Plagiogramma vanheurckii Grun.	64	36	49	16	39	49
Pleurosigma angulatum var. aestuarii (Bréb.) V.H.	0	0	11	8	24	24
Pseudo-Nitzschia no. 2	0	0	1	2	3	0
Rhaphoneis amphiceros Ehr.	4	6	5	0	8	4
Rhaphoneis surirella (Ehr.) Grun.	1	0	0	1	0	0
Rhaphoneis no. 1	0	0	4	2	0	6
Rhaphoneis no. 3	8	0	2	0	6	0
Rhaphoneis no. 4	1	0	0	1	0	1
Surirella ovata Kütz.	0	0	0	0	2	1
Synedra fasciculata (Ag.) Kütz.	23	25	36	17	35	65
Synedra fasciculata var. truncata (Grev.) Patr.	1	2	1	0	3	3
Tabellaria flocculosa K.	0	1	0	0	0	0
Thalassionema nitzschioides Grun.	126	507	588	56	326	416
Thalassiosira no. 1	178	566	1187	212	1255	1426

Appendix Table 2. A matrix of similarity values SIMI for comparisons of diatom assemblages in different samples in the control ecosystem (upper right half) and the heated ecosystem (lower left half). The values in the table are expressed as SIMI x 10^3. The first number in the heading refers to the board number and the second refers to the number of the sample.

	Control SIMI																				
	1-1	1-2	1-3	1-4	1-5	1-6	1-7	2-1	2-2	2-3	2-4	2-5	2-6	2-7	3-1	3-2	3-3	3-4	3-5	3-6	3-7
1-1		915	518	470	500	629	702	194	332	695	663	780	706	818	181	259	446	563	562	547	522
1-2	805		789	754	767	789	804	243	418	832	827	841	854	866	220	322	546	708	682	658	631
1-3	772	815		984	961	756	670	169	358	729	775	519	742	527	151	256	479	683	625	568	550
1-4	600	648	868		978	788	683	99	289	716	790	530	758	515	85	195	439	679	644	588	562
1-5	554	571	857	927		882	788	117	313	785	869	545	827	520	94	215	499	769	759	720	673
1-6	392	374	618	735	841		961	209	385	898	973	681	955	646	177	308	628	892	938	906	872
1-7	459	397	647	672	753	807		313	473	917	956	687	954	690	278	402	696	911	947	932	920
2-1	339	169	253	216	225	138	95		975	579	382	174	375	273	939	938	862	584	430	503	569
2-2	353	185	270	227	233	141	95	999		720	546	294	537	389	918	943	929	723	573	632	686
2-3	376	200	287	250	257	164	128	999	999		969	710	949	726	507	618	850	958	917	922	919
2-4	406	308	497	445	477	385	403	883	888	902		717	972	699	317	445	734	941	943	928	907
2-5	262	237	421	423	473	414	447	472	481	506	758		785	968	139	231	404	534	550	558	531
2-6	138	174	423	409	494	601	752	204	208	227	556	701		783	353	476	737	913	924	916	901
2-7	117	94	212	248	314	437	412	279	282	298	435	562	719		231	316	464	549	535	553	545
3-1	346	175	261	222	230	141	96	999	998	996	885	473	202	276		979	862	551	419	477	544
3-2	349	179	264	226	233	143	101	998	998	997	887	481	208	283	998		924	656	539	587	646
3-3	359	191	288	254	272	190	161	989	990	993	903	518	255	332	989	992		886	803	833	869
3-4	404	244	354	328	337	233	199	954	957	969	923	610	286	350	956	960	974		969	974	969
3-5	316	209	331	325	366	312	292	747	751	771	868	891	523	559	748	752	783	827		987	970
3-6	227	152	298	314	398	446	443	570	572	589	726	849	674	743	567	573	622	654	912		986
3-7	249	194	393	413	500	559	598	506	511	537	754	873	818	771	506	514	571	614	860	937	

Heated SIMI