A LABORATORY METHOD FOR THE STUDY OF MARINE BENTHIC DIATOMS[1]

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ABSTRACT

Effects of light intensity and of exposure to desiccation on the vertical distribution and growth of populations of marine benthic diatoms were investigated in a laboratory model ecosystem and a respirometer chamber. The diatom flora that developed in the ecosystem was similar to that from field stations in lower Yaquina Bay, Oregon. The vertical distribution of many species was closely related to light intensity and period of exposure to desiccation. Biomass accumulated most rapidly on substrates subjected to high light intensities, without exposure to desiccation. Communities acclimated to different light intensities and periods of desiccation responded differently to changes in light intensity in the respirometer chamber. Results of these experiments show that the laboratory apparatus described can be useful in the study of simplified intertidal communities.

INTRODUCTION

Field investigations of marine benthic algae have been concerned chiefly with description of the distribution and zonation of macrophytes in various coastal areas and estuaries and with the determination and measurement of the important ecological factors in different habitats. In general, sublittoral macrophytes are less tolerant of desiccation and relatively wide ranges of light intensity, temperature, and salinity than species that inhabit the higher littoral zones (Biebl 1962). To what extent this generalization also applies to marine benthic diatoms is not yet established, although a few papers have contributed some information (Aleem 1949, 1950; Castenholz 1963, 1964, 1967; Hendey 1964).

This paper describes a laboratory method for the study of marine benthic diatoms and reports the results of two experiments designed to determine effects of light intensity and of exposure to desiccation on their vertical distribution and growth. A laboratory model ecosystem and a new respirometer chamber are described in detail. This work represents a part of a general program to investigate the physiological ecology of littoral diatom communities in the Yaquina River estuary between Elk City and Newport, Oregon, that eventually should serve as a basis for predicting and understanding the distribution and production of benthic diatoms in the estuary.

APPARATUS AND METHODS

Intertidal model ecosystem

A fiberglassed wooden box was assembled. The bottom of the box was graduated with a water depth of about 64 cm at one end and a small uncovered area at the opposite end when full (Fig. 1). A 12-rpm electric motor pivoted a board back and forth at the deep end to circulate the water. When the box was more than half full of water, the movement of the board generated waves that had a period greater than 1 sec and a height of 1 or 2 cm.

Seawater for the box came from polyvinyl chloride (PVC) pipelines at the Marine Science Center, Newport, Oregon. Water for the laboratory was from lower Yaquina Bay and had salinities that normally ranged from 28 to 34‰, except during periods of high river flow in winter. A plastic garbage can served as a settling tank. Freshwater and seawater entered separate compartments of a wooden head

[1] This work is a contribution from the Oregon State University Marine Science Center, Technical Paper No. 2621 of the Oregon Agricultural Experiment Station, and was supported in part by National Science Foundation research grant GB-7203. R. E. Dimick, G. E. Davis, and H. K. Phinney kindly supplied ideas that were eventually incorporated into the design of the laboratory equipment. The technical assistance of Miss J. Yokoyama is gratefully acknowledged.

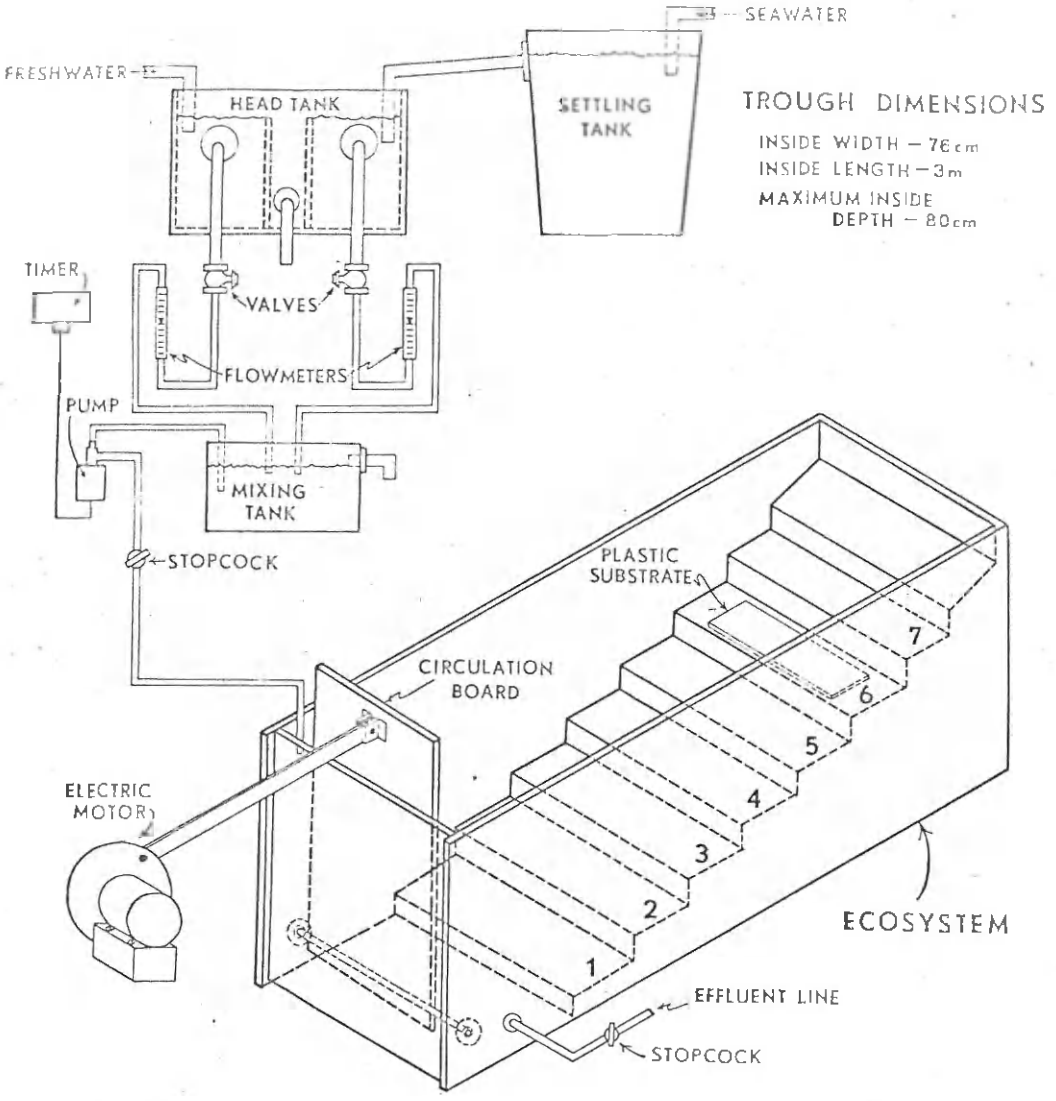

FIG. 1. Diagram of the box and water supply system.

tank and subsequently flowed downward through flowmeters into a mixing tank. Thus, by the manipulation of PVC ball valves and observation of the flowmeters, the salinity of the water supply in the mixing tank was regulated. All water lines for the box were 1.9-cm (ID) black plastic pipe. The settling, head, and mixing tanks had overflow outlets to provide a constant head. Water was pumped from the mixing tank into the box by a centrifugal pump. The effluent line was located near the bottom of the box at the deep end, and both influent and effluent flow were controlled by glass stopcocks.

The box was lighted by six 244-cm (8 ft) "cool white" fluorescent lamps supplemented with sixteen 60-w incandescent lamps mounted on a fixture that could be raised or lowered to control light intensity. Intensities were as high as about 18,000 lux on the upper steps when the light fix-

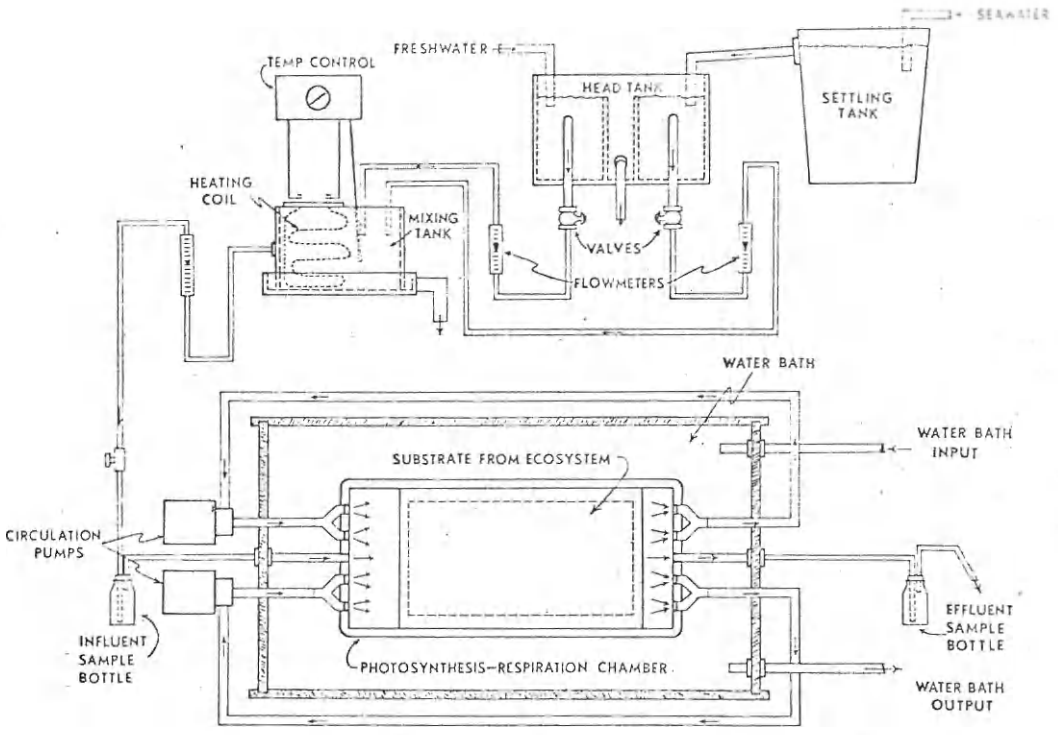

FIG. 2. Diagram of the respirometer chamber and associated water supply system.

ture was at its lowest level. Light intensity was measured with an illumination meter (Weston Model 756) in the air and with a hermetically sealed selenium barrier photocell (International Rectifier DP-3) under water; this unit had been calibrated with the Weston meter. Photoperiod could be controlled by timers.

Smooth acrylic plastic plates, 51.3 × 26.5 × 0.5 cm, on each step provided substrate for the colonization and growth of organisms and could be transferred from the box to a respirometer chamber for studies of community metabolism. The substrates were seeded naturally by organisms entering the box through the water supply. During the two experiments reported in this paper, the communities consisted almost entirely of diatoms and associated heterotrophic microorganisms. The species composition of the diatom flora that developed in the box was similar to that from field stations in lower Yaquina Bay—particularly with respect to the more abundant taxa.

Respirometer chamber

The respirometer chamber was a modification of the P-R chamber described by McIntire et al. (1964). It was constructed entirely of acrylic plastic and measured 31.6 × 55.7 × 10.8 cm (Fig. 2). The main compartment was separated from a smaller chamber on each end by a perforated baffle. This arrangement provided a more laminar flow over the samples than the original P-R chamber. The top portion of the chamber was lined with a rubber 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 between the influent sample bottle and the mixing tank. The general water supply system for the respirometer was similar to that described for the box, except that a 1,500-w immersion heater and temperature control unit was inserted into the mixing tank. Rates of photosynthesis and community respira-

tion expressed as g O_2 m^{-2} hr^{-1} were estimated by measurements of the dissolved oxygen concentration of influent and effluent water at regular time intervals. The rate of gross photosynthesis was estimated by summing the measurements of net oxygen evolved during a period of illumination and oxygen consumed during an equivalent dark period. Details of this procedure were described by McIntire et al. (1964) and McIntire and Phinney (1965).

The respirometer chamber was lighted by six 122-cm (4 ft) "cool white" fluorescent lamps and ten 60-w incandescent lamps mounted on a fixture that could be raised or lowered; the light quality was similar to that received by the communities in the box. In its lowest position the fixtures provided intensities up to 20,000 lux. Lower intensities were obtained by raising the fixture, by placing one or more layers of nylon screen over the chamber, or both.

Methods

After an experiment in the respirometer chamber, the established community material was loosened from the substrate with a rubber spatula, transferred into a bucket of distilled water, and its volume adjusted to 2 liters. The sample then was placed in a blender (4-liter capacity) and mixed for 20 sec. Subsamples were taken from this suspension for determination of biomass, pigment concentrations, and species composition. Biomass, expressed either as g/m^2 dry weight or ash-free dry weight, was determined by the procedure outlined by McIntire (1968). Chlorophylls *a*, *b*, and *c* and total carotenoids were measured by the methods of the Scientific Committee on Oceanic Research (SCOR-UNESCO 1966). We used the grinding procedure instead of sonification.

Daily fluctuations in the water temperature of the model ecosystem were recorded by a thermograph. The oxygen concentration of the influent and effluent water of the respirometer chamber was measured using the azide modification of the Winkler method (American Public Health Association 1965).

To determine the composition of the diatom flora, material from a subsample of the algal suspension was transferred to a beaker and boiled in concentrated nitric acid. After oxidation of the organic matter, the empty frustules were mounted in Hyrax (Patrick and Reimer 1966). Each slide was examined in detail and a list of taxa compiled for each sample. When a particular diatom was relatively abundant and could not be identified, it was given a temporary number to be used during the counting procedure. A mechanical stage was used to traverse each slide under 1,250× magnification, and approximately 1,000 diatoms were identified and counted as they appeared in the field.

The following statistics were used to characterize the structure of the diatom communities: 1) number of diatom cells (N) counted on each slide; 2) number of individuals (n_i) belonging to the ith species; 3) number of species (S) observed in N individuals; 4) diversity index (H) expressed as bits per individual; and 5) number of equivalent equally common species (E). The index of diversity used in this work was

$$H = -\sum_{i=1}^{s} \frac{n_i}{N} \log_2 \frac{n_i}{N}.$$

Lloyd, Zar, and Karr (1968) discussed the derivation, limitations, and ecological implications of this index and presented a useful table for its calculation. MacArthur (1965) has shown that if all S species were equally common,

$$H = -S\left[\frac{1}{S} \log_2 \frac{1}{S}\right]$$
$$= \log_2 S.$$

Therefore, the equivalent number of equally common species which would result in the same H value for any given sample was equal to 2^H, that is, $E = 2^H$.

DESCRIPTION OF EXPERIMENTS AND RESULTS

The apparatus described above was used in two experiments. Experiment TC-68

TABLE 1. *Biomass and pigment concentrations for samples obtained from the laboratory ecosystem during experiment TC-68*

Substrate from step	Exposure to air (hr/day)	Light intensity (lux)		Biomass (g/m²)		Chlorophylls (g/m²)			Carotenoids SPU/m²
		"High tide"	"Low tide"	Dry wt	Ash-free dry wt	*a*	*b*	*c*	
1	0	2,700	4,600	453.2	128.2	0.837	0	0.250	0.734
2	0	3,300	5,400	342.6	98.7	0.558	0	0.206	0.440
3	1.0	3,700	6,200	165.8	41.1	0.191	0.005	0.081	0.147
4	4.5	4,600	6,900	120.6	32.8	0.117	0.007	0.051	0.103
5	8.0	4,600	7,400	71.4	17.2	0.037	0.008	0.012	0.041

lasted from 26 June through 3 August 1968 and was designed to examine the effects of tidal cycle (i.e., period of exposure to desiccation and direct illumination) on the structure and productivity of diatom communities developed in the model ecosystem. Another experiment, LI-68, from 21 August to 18 September 1968, investigated the effect of light intensity on the communities.

Before experiment TC-68 was started, one acrylic plastic plate was secured on each of the seven steps of the box. The steps will be referred to by number, beginning with step 1 at the deep end and progressing upward to step 7 at the shallow end (Fig. 1). The effluent stopcock was adjusted so that the water would drain from a level of about 10 cm above step 7 to the level of step 2 in 6 hr. After the 6-hr draining period, a timing device energized the centrifugal pump, and water was pumped into the box. The influent stopcock was adjusted so that the influent water exceeded the effluent loss and refilled the system to its original level by the end of the next 6 hr. At this time, the timer stopped the pump and the cycle started again. The illumination intensity and period of exposure to desiccation at the steps sampled during the experiment are listed in Table 1. The variation in water temperature was from 12 to 17C, and in salinity from 28.1 to 34.6‰.

In experiment LI-68, the pump operated continuously to maintain water at a constant level of 10 cm above step 7; the influent and effluent flows were the same for the entire experiment. Nylon screens were placed over the top of the box to regulate the light intensities at steps 1, 3, 5, and 7 (Table 2). Salinity varied between 27.8 and 30.5‰ during the experiment, and the mean rate of water exchange in the box was about 6 liters/min. Water temperature ranged from 13.5 to 15C.

At the end of experiment TC-68, plastic substrates with their established communities from steps 1 through 5 were transferred to the respirometer. Colonization of steps 6 and 7 was negligible, and the corresponding substrates were not examined. After a substrate was placed in the respirometer, the chamber was covered with a black sheet of plastic, and community respiration was measured for a period of 2 hr. The next morning the chamber was uncovered, and rates of photosynthesis were

TABLE 2. *Biomass and pigment concentrations for samples obtained from the laboratory ecosystem during experiment LI-68*

Substrate from step	Light intensity (lux)	Biomass (g/m²)		Chlorophylls (g/m²)			Carotenoids SPU/m²
		Dry wt	Ash-free dry wt	*a*	*b*	*c*	
1	1,300	103.0	30.0	0.044	0.032	0.078	0.053
3	2,400	109.9	88.7	0.096	0.024	0.084	0.106
5	5,500	442.0	101.0	0.175	0.022	0.095	0.182
7	11,300	537.5	170.6	0.538	0	0.269	0.520

TABLE 3. *Relative abundance of diatom taxa identified for samples obtained from the laboratory ecosystem during experiments TC-68 and LI-68*

Taxon	TC-68 substrate			LI-68 substrate			
	1	3	5	1	3	5	7
Achnanthes brevipes Ag.	— —	+	++				
Achnanthes brevipes var. *intermedia* (Kütz.) Cl.		— —	—		— —		
Achnanthes brevipes var. *parvula* (Kütz.) Cl.		—	—				
Achnanthes deflexa Reim.					— —		
Achnanthes haukiana Grun.				— —	— —		— —
Achnanthes lanceolata (Bréb.) Grun.					— —		
Achnanthes longipes Ag.			— —				
Achnanthes minutissima Kütz.					— —	— —	
Actinoptychus senarius Ehr.		— —	— —	— —			— —
Amphipleura rutilans (Trent.) Cl.	—	—	—	— —	— —	—	+
Amphora ovalis Kütz.				—		— —	
Auliscodiscus probabilis A. S.			— —			— —	
Bacillaria paxillifera (Mull.) Hendey	—	—	—	—	+	++	—
Biddulphia aurita (Lyngb.) Bréb. & Godey	— —		— —	— —			
Chaetoceros cinctum Grun.				— —	— —	— —	— —
Cocconeis costata Greg.				—	— —	— —	
Cocconeis scutellum Ehr.				— —		— —	
Cocconeis scutellum var. *parva* Grun.	— —	— —	— —	++++	—	— —	— —
Coscinodiscus excentricus Ehr.				— —			
Coscinodiscus lineatus Ehr.	— —			— —	— —		— —
Coscinodiscus radiatus Ehr.	— —				— —		
Dimerogramma minor var. *nana* (Greg.) V.H.						— —	
Diploneis bombus Ehr.			— —				
Eunotogramma marinum (W. Smith) Per.					— —		
Fragilaria striatula var. *californica* Grun.	—	—	—	—	—	+	++++
Gomphonema subclavatum var. *montana* Schum.				— —			
Gyrosigma fasciola (Ehr.) Griff. & Henfr.	— —			— —			
Gyrosigma spencerii var. *curvula* (Grun.) Reim.				— —			
Melosira nummuloides (Dillw.) Ag.	++	—	—		— —	— —	+
Melosira sulcata (Ehr.) Kütz.	—	— —	—	— —	— —	— —	— —
Meridion circulare (Grev.) Ag.						— —	
Navicula abunda Hust.	—	— —	— —	—	—	— —	— —
Navicula cancellata var. *apiculata* Greg.	— —	— —	— —	— —	— —	— —	
Navicula comoides (Ag.) Per.			— —				
Navicula complanatula Hust.	— —	— —	— —	— —	— —	— —	— —
Navicula crucigera (W. Smith) Cl.	— —	— —		— —	— —	— —	
Navicula cryptocephala Kütz.	— —			— —	— —	— —	— —
Navicula directa W. Smith	+++	+	+	— —		— —	— —
Navicula diserta Hust.	—	— —	—	—	—	—	—
Navicula diversistriata Hust.		— —	— —		— —		
Navicula grevillei (Ag.) Heiberg	— —		— —	— —	— —		— —
Navicula mutica Kütz.		—	—				
Navicula ramosissima Ag.						— —	
Nitzschia apiculata (Greg.) Grun.		— —					
Nitzschia dissipata (Kütz.) Grun.				—	—	— —	— —
Nitzschia frustulum var. *perpusilla* (Rabh.) Grun.		— —	— —	— —	—	— —	
Nitzschia lanceolata var. *minor* V. H.	— —	++	+				
Nitzschia longissima (Bréb.) Ralfs	— —	—		—	+	+	—
Nitzschia sigma (Kütz.) W. Smith	—	+	+	— —		— —	
Nitzschia socialis Greg.	+++	++	++	—	—	— —	
Nitzschia sublybrida Hust.	+	—	—	— —	—	— —	— —
Plagiogramma vanheurckii Grun.		— —	— —	—	—	—	— —
Pleurosigma angulatum var. *aestuarii* (Bréb.) V. H.				— —		— —	
Pseudo-Nitzschia sicula var. *migrans* Cl.				— —	— —	— —	— —
Rhaphoneis amphiceros Ehr.	— —		— —		— —	— —	
Rhoicosphenia curvata (Kütz.) Grun. ex Rabh.		— —	— —	— —			

TABLE 3. Continued

Taxon	TC-68 substrate			LI-68 substrate			
	1	3	5	1	3	5	7
Skeletonema costatum (Grev.) Cl.					— —	—	— —
Surirella gemma Ehr.	— —			— —	— —	— —	
Synedra fasciculata (Ag.) Kütz.	+	+	—	+	—	—	—
Thalassionema nitzschioides Grun.	—	+	++	+	+	—	—
Trachyspenia australis Petit		— —					
Triceratium alternans Bailey			— —				

* Relative abundance is expressed as: ++++, 30% or over of the total number counted; +++, 20 to 30% of the total number counted; ++, 10 to 20% of the total number counted; +, 5 to 10% of the total number counted; —, 1 to 5% of the total number counted; — —, less than 1% of the total number counted.

† The following species were observed during the preliminary examination but did not appear during the counting procedure: *Amphora angusta* Greg.; *Asteromphalus heptactis* (Bréb.) Ralfs; *Caloneis westii* (W. Smith) Hendey; *Cocconeis californica* Grun.; *Cocconeis decipiens* Cl.; *Cocconeis notata* Petit; *Cocconeis scutellum* var. *stauroniformis* W. Smith; *Dimerogramma marinum* (Greg.) Ralfs; *Frustulia vulgaris* (Thwaites) DeT.; *Grammatophora angulosa* Ehr.; *Grammatophora marina* (Lyng.) Kütz.; *Gyrosigma nodiferum* (Grun.) Reim.; *Licmophora californica* Grun.; *Navicula agnita* Hust.; *Navicula clavata* Greg.; *Navicula lyra* f. *denudata* Grun.; *Navicula palpebralis* Bréb.; *Nitzschia angularis* W. Smith; *Nitzschia punctata* var. *coarctata* Grun.; *Opephora marina* (Greg.) Petit; *Plagiogramma staurophorum* (Greg.) Heiberg; *Pleurosigma decorum* W. Smith; *Pleurosigma peragalli* Brun; *Trachyneis aspera* Ehr.; *Tropidoneis lepidoptera* var. *minor* Cl.; *Tropidoneis maxima* var. *gracilis* Grun.

measured for 1-hr periods at each of eight different illumination intensities ranging from 590 to 18,450 lux. After experiment LI-68, the same procedure was repeated, in this case with the substrates from steps 1, 3, 5, and 7. The average time required for the respirometer experiments was one day per substrate. The species compositions of communities from steps 1, 3, and 5 were determined in experiment TC-68 and from steps 1, 3, 5, and 7 in experiment LI-68.

The diatom flora

Table 3 presents the relative abundance of diatoms from samples at the conclusion of the two experiments. Some species could not be identified with certainty and are not included in the table. This table also represents a new distributional record for a large number of the listed diatoms, as many of them have never been reported from either the estuaries or coastal regions of Oregon.

The species included in the five most abundant taxa on any one of the three substrates sampled in experiment TC-68 were *Achnanthes brevipes*, *Melosira nummuloides*, *Navicula directa*, *Nitzschia lanceolata* var. *minor*, *Nitzschia sigma*, *Nitzschia sociales*, *Nitzschia subhybrida*, *Synedra fasciculata*, and *Thalassionema nitzschioides*. A similar list for the four substrates examined in experiment LI-68 included *Amphipleura rutilans*, *Bacillaria paxillifera*, *Cocconeis costata*, *Cocconeis scutellum* var. *parva*, *Fragilaria striatula* var. *californica*, *M. nummuloides*, *Nitzschia longissima*, *Nitzschia* sp. No. 1, *Nitzschia* sp. No. 2, *S. fasciculata*, and *T. nitzschioides*. *Nitzschia* sp. No. 1 very closely resembled *Nitzschia aerophila* Hust. and was the most abundant unidentified diatom; by the same criteria as in Table 3, it was dominant (++++) on steps 3 and 5 and frequent (++) on steps 1 and 7 during experiment LI-68. *Nitzschia* sp. No. 2 was much less abundant and was related morphologically to *Nitzschia hungarica* Grun. Some of the smaller specimens of the genus *Cocconeis* were extremely difficult to sort out on the basis of cell wall morphology. These variable forms tended to cooccur and apparently had similar physiological and ecological properties; they are lumped temporarily under *C. scutellum* var. *parva*. A few very rare diatoms, for example, *Achnanthes lanceolata*, *Achnanthes minutissima*, and *Gomphonema subclavatum* var. *montana*, were obviously freshwater species that presumably had washed down the estuary from the lower Yaquina River.

Effect of tidal cycle

There was an inverse relationship between biomass and period of exposure to desiccation (Table 1). The ratio ash-free

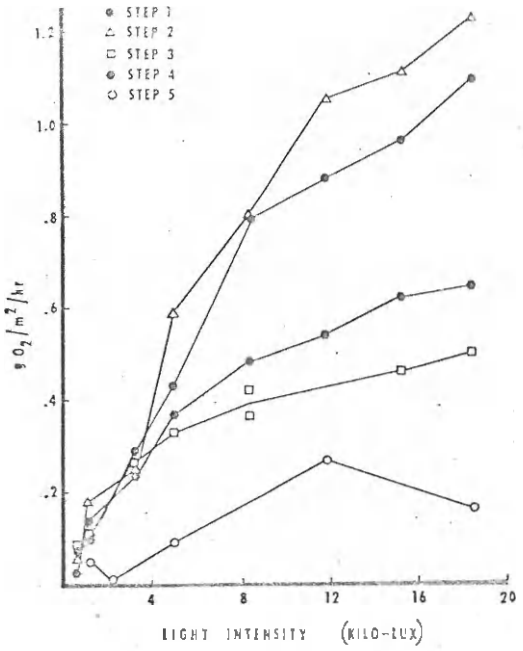

FIG. 3. Relationship between light intensity and rate of gross photosynthesis of diatom communities from steps 1, 2, 3, 4, and 5 determined in the respirometer chamber at the conclusion of experiment TC-68.

dry weight : dry weight in samples from the five substrates varied between 0.24 and 0.29 and was typical of communities dominated by diatoms (McIntire and Phinney 1965; McIntire 1968). Concentrations of chlorophylls *a* and *c* and total carotenoids followed a pattern similar to biomass, with values decreasing progressively from step 1 to step 5; the concentration of chlorophyll *b* was very low or negligible on all five substrates.

Rates of gross photosynthesis were approximately the same for samples from steps 1, 2, 3, and 4 at illumination intensities below 4,000 lux (Fig. 3). 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. The maximum rate of photosynthesis for these samples was at the highest illumination intensity (18,450 lux) and ranged from 0.50 (step 3) to 1.23 g O_2 m^{-2} hr^{-1} (step 2).

TABLE 4. *Statistics expressing the structure of diatom communities sampled from seven substrates during experiments TC-68 and LI-68, 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 E is 2^H, the number of equivalent equally common species*

Expt	Substrate	*N*	*S*	*H*	*E*
TC-68	1	1,063	46	3.68	12.8
	3	1,007	45	3.97	15.6
	5	1,024	53	4.24	18.9
LI-68	1	1,020	53	3.69	12.9
	3	1,003	65	4.43	21.5
	5	1,042	65	3.59	12.1
	7	1,030	41	2.70	6.5

The curve for the community from step 5 was irregular and the photosynthetic rate never exceeded 0.27 g O_2 m^{-2} hr^{-1}.

The diversity index for communities examined during experiment TC-68 (Table 4) ranged from 3.68 (step 1) to 4.24 (step 5) bits/individual, and the number of taxa ranged from 45 in 1,007 individuals counted (step 3) to 53 in 1,024 individuals (step 5). Surprisingly, the index was slightly higher for the community from step 5 than for those with less exposure. The number of equivalent equally common species for communities from steps 1, 3, and 5 were 12.8, 15.6, and 18.9.

A distinct zonation of the more abundant diatoms clearly was related to period of exposure to desiccation (Fig. 4). *Navicula directa*, *N. socialis*, *M. nummuloides*, *S. fasciculata*, and *N. subhybrida* were more abundant on the substrate with no exposure to desiccation than on the substrates with 1 or 8 hr/day exposure. *Nitzschia lanceolata* var. *minor* and possibly *N. sigma* were able to compete best on the substrate with an exposure period of 1 hr/day. *Achnanthes brevipes* and varieties and *T. nitzschioides* were extremely tolerant of desiccation and represented 21.2 and 12.8%, respectively, of the number of individuals counted from step 5.

Effect of light intensity

The greatest accumulation of biomass during experiment LI-68 was on the step

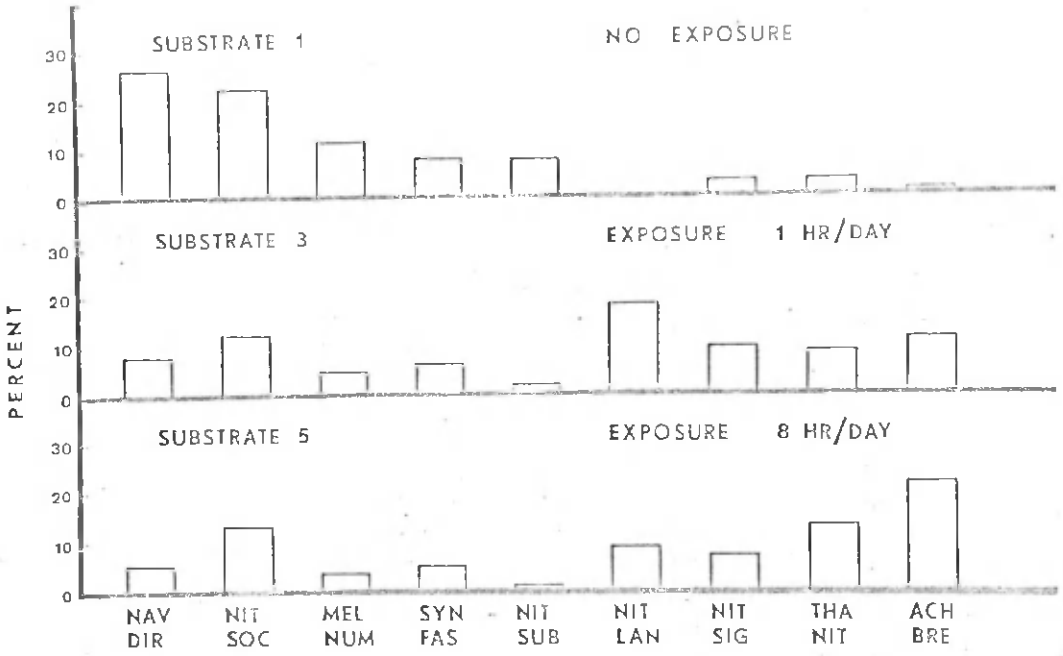

FIG. 4. Relative abundance of the five most abundant diatom taxa on steps 1, 3, and 5 at the conclusion of experiment TC-68. The abbreviations below the horizontal axis correspond to *Navicula directa*, *Nitzschia socialis*, *Melosira nummuloides*, *Synedra fasciculata*, *Nitzschia subhybrida*, *Nitzschia lanceolata* var. *minor*, *Nitzschia sigma*, *Thalassionema nitzschioides*, and *Achnanthes brevipes* and varieties.

that received the highest light intensity (Table 2). The ratio ash-free dry weight : dry weight in the samples varied between 0.20 and 0.32. Concentrations of chlorophylls *a* and *c* and total carotenoids also were greatest on step 7 and least on step 1, while the concentration of chlorophyll *b* was again low or negligible.

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 (Fig. 5). Apparently, communities from the lower steps approached light saturation at a lower intensity than the community developed at the top step. Rates of photosynthesis at 18,450 lux ranged from 0.206 (step 1) to 0.921 g O_2 m^{-2} hr^{-1} (step 7).

The diversity index for the four communities examined during experiment LI-68 ranged from 2.70 (step 7) to 4.43 (step 3),

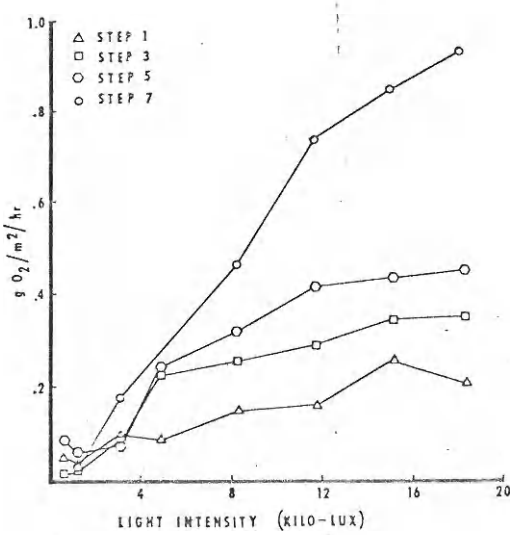

FIG. 5. Relationship between light intensity and the rate of gross photosynthesis of diatom communities from steps 1, 3, 5, and 7 determined in the respirometer chamber at the conclusion of experiment LI-68.

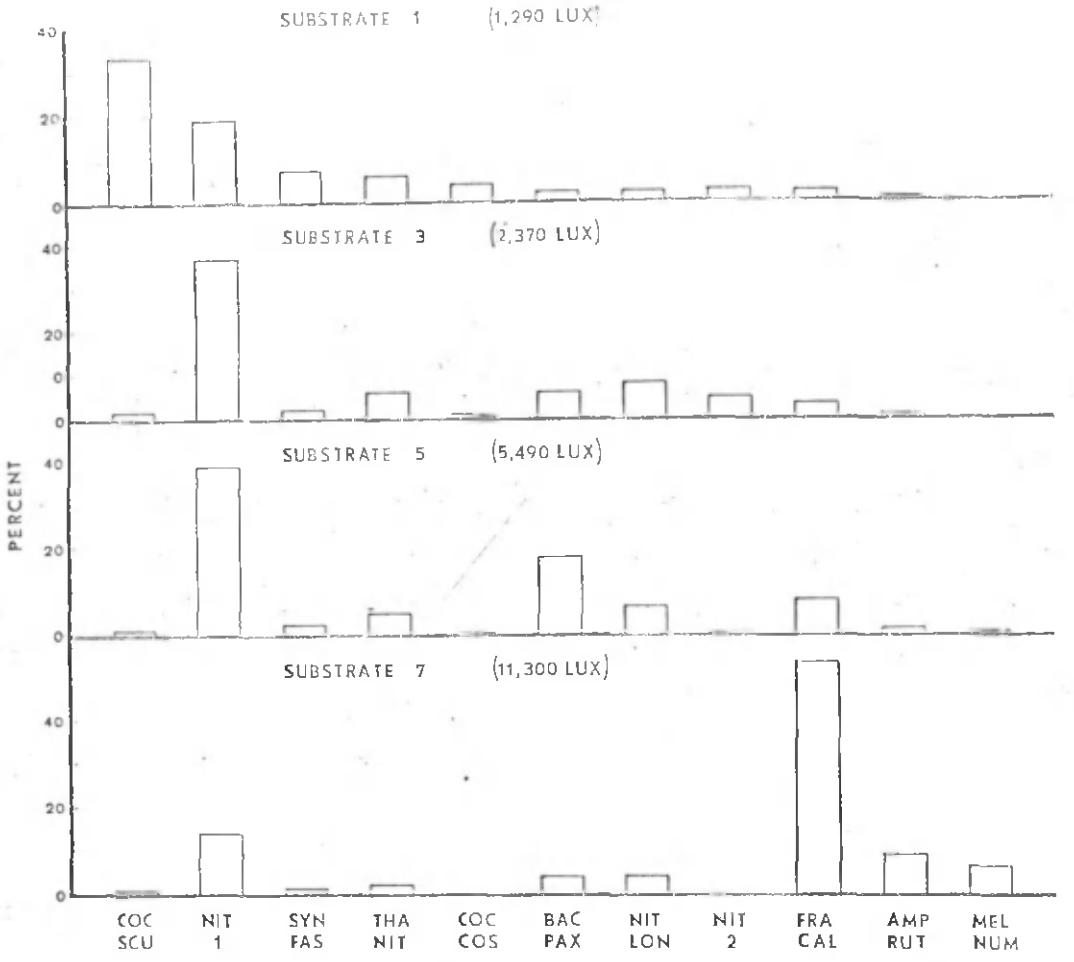

FIG. 6. Relative abundance of the five most abundant diatom taxa on steps 1, 3, 5, and 7 at the conclusion of experiment LI-68. The abbreviations below the horizontal axis correspond to *Cocconeis scutellum* var. *parva*, *Nitzschia* sp. No. 1, *Synedra fasciculata*, *Thalassionema nitzschioides*, *Cocconeis costata*, *Bacillaria paxillifera*, *Nitzschia longissima*, *Nitzschia* sp. No. 2, *Fragilaria striatula* var. *californica*, *Amphipleura rutilans*, and *Melosira nummuloides*.

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 4). The number of equivalent equally common species was highest (21.5) for the sample from step 3 and lowest (6.5) for that from step 7.

Zonation of the more abundant diatoms was closely related to differences in light intensity at which the four communities were developed. *Cocconeis scutellum* var. *parva* represented 32.6% of the community on step 1 but was considerably less abundant on the higher steps (Fig. 6). The highest proportions of *S. fasciculata* and *C. costata* also were found on step 1, the substrate that received the lowest light intensity. The relative abundance of *Nitzschia* sp. No. 1, *B. paxillifera*, and *N. longissima* was higher on steps 3 and 5 (the intermediate levels) than on either steps 1 or 7. Three species, *F. striatula* var. *californica*, *A. rutilans*, and *M. nummuloides*, obviously competed best at the highest illumination intensity (11,300 lux). In fact, *F. striatula* var. *californica* was 51.8% of

the community on step 7, the highest percentage recorded for a single species during either experiment.

DISCUSSION

Communities acclimated to different periods of desiccation in the laboratory model ecosystem responded differently to changes in light intensity in the respirometer chamber. Biomass accumulated much more rapidly on substrates from steps 1 and 2 than on those from steps 3, 4, and 5. A series of increases in illumination intensity also allowed the lower, shaded layers of cells on the substrates with high biomasses to approach light saturation. Consequently, the photosynthetic rate 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 the mat was thinner, and the entire communities approached their maximum rate at a relatively low light intensity.

Communities adapted to different light intensities also responded differently in the respirometer. The community from step 7 approached light saturation at a higher intensity than the other three communities. The biomass effect described above probably accounted for some of this difference, as the community from step 7 had the greatest biomass. Moreover, a physiological adjustment of individual cells to low light intensities may have been involved. Physiologists have long recognized that plants acclimated to low light intensities reach their maximum photosynthetic rates at lower light intensities than plants grown at relatively high intensities (Rabinowitch 1951).

Only *M. nummuloides*, *S. fasciculata*, and *T. nitzschioides* were among the five most abundant diatom taxa on at least one substrate from both experiments. Differences in the general nature of the diatom flora between the two experiments were probably the result of both changes in laboratory conditions and seasonal changes in the properties of the water in the lower estuary.

Many of the diatoms found in the laboratory model ecosystem also have been reported from estuaries and coastal regions in other parts of the world (Castenholz 1967; Aleem 1949, 1950; Hustedt 1939, 1955; Hustedt and Aleem 1951; Cholnoky 1968). Furthermore, the zonation of some of the more abundant species 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 *A. brevipes* was present in the greatest numbers near the uppermost limit of the diatom cover. In experiment TC-68, *A. brevipes* was the most abundant diatom species (21.2% of the community) on step 5, the level exposed to desiccation for 8 hr/day. On the substrate with no exposure period and on the four substrates examined in experiment LI-68, this diatom represented less than 1% of the communities. Castenholz also concluded that *F. striatula* var. *californica* grew poorly at low light intensities, an observation supported by experiment LI-68.

In general, the diatom communities were characterized by a relatively large number of species represented by one individual. For example, on step 3 during experiment LI-68, 26 of the 65 species counted (40%) were represented by only one specimen. This large proportion of very rare diatoms accounted for the large differences between the observed number of species (S) in the samples and the calculated number of equivalent equally common species (E) and was the most obvious property that distinguished the diatom communities from many sympatric associations of higher plants and animals. There also was a strong possibility that many of the rare species were nonliving, empty frustules that washed down from the lower Yaquina River and became lodged in the growing community. The presence of a few rare freshwater species supported this contention. Therefore, it appeared that a diversity index that deemphasized the importance of very rare species, such as the H value used here, was the most appropriate for our work.

The high diversity on step 5 at the end

of experiment TC-68 was difficult to explain. Preliminary observations of samples from substrates at different depths in the estuary at seven different field stations definitely indicated that diversity was severely reduced at the upper littoral zones—areas exposed to long periods of desiccation and direct insolation. Some of the diversity at step 5 may have resulted from empty frustules settling on the substrate, but as mentioned above, these were rare species in the community and probably would not appreciably influence the magnitude of *H*. If experiment TC-68 had been continued for a longer period, steps 6 and 7 might have been colonized sufficiently to show a reduction in diversity that corresponded to long exposure periods. In any case, the question of how diversity is related to tidal cycle needs clarification.

Results of these experiments demonstrate the potential of the laboratory model ecosystem as a tool for the investigation of simplified intertidal communities. The system provides some laboratory control over salinity, light intensity, and tidal cycle, and eventually a temperature control system can be installed. Flexibility could be increased by stacking the steps to provide a vertical surface to study the movements and grazing activities of small marine invertebrates on such a surface. However, it must be emphasized that the use of all such laboratory ecosystems is subject to certain limitations that result from simplifications of nature. Some reality is usually sacrificed in the process of gaining control over the environment, and the interpretation of data must be made with this in mind. In our opinion, laboratory ecosystems are best used to gain information that can supplement and help understand concurrent observations in the field.

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