Qualitative Characterization of Aquatic Environments using Diatom Life-form Strategies[1]

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Abstract. Diatom associations collected from polyurethane foam (PF) substrates were surveyed through time along a nutrient enrichment gradient in Smith Mountain Lake, Virginia. A qualitative model is proposed which emphasizes the adaptive characteristics, or life-form strategies, of the most abundant diatoms in an association and relates them to generalized environmental conditions. The model provides a framework for readily describing complex habitat variations within the lake and supplies a means of interpreting successional changes occurring on the substrates.

Ecological research generally is approached from one of two perspectives: (1) as autecology, which involves the study of individuals and individual species; or (2) synecology, which considers relatively complex species groups as units of study. The former often concentrates upon physiological, behavioral, and life history characteristics of a species. The latter focuses upon characteristics manifested at higher levels of organization, such as community structure and succession. Despite the fact that this arbitrary division occasionally segregates ecologists as well as perspectives, both approaches share the same concern—to relate organisms to their environments. This paper attempts to utilize both autecological and synecological information to relate diatom associations collected on artificial substrates to prevailing environmental conditions. Associations were surveyed through time at each of six stations along a eutrophic gradient in Smith Mountain Lake, Virginia. A model is proposed which relates the generalized adaptive characteristics (life-form strategies) of the most abundant diatoms in an association to environmental conditions. The model provides a framework for describing complex aquatic habitats and interpreting successional changes occurring on the substrates.

STUDY SITE

Smith Mountain Lake (Fig. 1) is the upper storage impoundment of a two-reservoir, pumped-storage system located southeast of Roanoke, Virginia. A

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dam completed in 1964 impounds waters of the Roanoke and Blackwater Rivers forming a 8,900-ha lake. Major municipal and industrial discharges originating from the Roanoke metropolitan area enter the lake at the headwaters of the Roanoke River arm. Carbon assimilation rates reported by Simmons & Neff (1969) indicated that these upper reaches showed definite signs of eutrophy as early as 1966, and Jennings et al. (1970) presented further evidence to substantiate this trend. Because the Roanoke River acts as a point-source discharge into the lake, Benfield & Hendricks (1975) were able to clearly demonstrate a gradient of decreasing eutrophy along the northern reaches of the reservoir to the confluence using standard measures of primary production, chlorophyll-a concentration, light penetration, and percent saturation of dissolved oxygen. A similar gradient in total Kjeldahl nitrogen and orthophosphate concentrations was reported by the Virginia State Water Control Board (VSWCB, 1975). Nutrient levels in the Blackwater arm, although lower than in the Roanoke arm, also decrease downstream. These nutrients probably originate from various agricultural sources and reflect the high non-point pollution potential of the area (VSWCB, 1975).

Water quality parameters measured by the VSWCB (Fig. 1) illustrate the gradient from eutrophy to mesotrophy in the lake. This gradient is not a simple one; locations differ with respect to morphometry and disturbance, as well as with type and degree of enrichment. Confounding climatic and meteorological variations between locations are, however, minimized because the gradient is contained within a single system.

Materials and Methods

Since Smith Mountain Lake appeared to provide an ideal experimental situation for investigating the effects of varying eutrophic states on diatom associations, six sampling stations (see Fig. 1) were chosen to coincide with those regularly monitored by the VSWCB: two stations along the Roanoke arm (1 and 2), two along the Blackwater arm (5 and 6), one at the confluence (4), and one near Smith Mountain Dam (3). In late summer 1975, polyurethane foam (PF) substrates identical to those described by Cairns et al. (1969, 1979) were placed in each station. PF substrates were attached to a nylon rope with monofilament line and suspended near the surface above approximately 3 m of water. On days 1, 3, 6, 15, and 21 after placement, a substrate was removed at random from the line in each station, placed in a sample jar, and fixed with 10% formalin. Station water chemistry was monitored each day using a Hach Water Kit (Hach Chemical Co. Inc., Ames, Iowa).

PF substrates were later placed in a 1,000-ml beaker with 200 ml of 27% hydrogen peroxide and kept immersed for at least 2 h. Substrates were then squeezed with a rubber-gloved hand to ensure removal of attached forms. Diatoms were cleaned following the procedure of Werff (1955). Cleaned diatoms from each collection were mounted in Hyrax medium for analysis with the light microscope. A random point was selected on each slide. The slide was scanned horizontally from left to right using an oil immersion objective

STATION 1

	Sept. 1975	mean 1975	Sept. 1976
BOD_5	5	4.33	3
DO	14.2	10.3	–
TKN	0.6	0.6	0.7
$NH_3 \cdot N$	–	0.28	–
$NO_3 \cdot N$	0.21	0.37	1.1
$NO_2 \cdot N$	0.05	0.08	0.14
TOT·P	0.20	0.20	< 0.10
mean PO_4 (1970 - '73) = 0.08			
Σ (DO, TKN, PO_4) = 14.88 *			

STATION 2

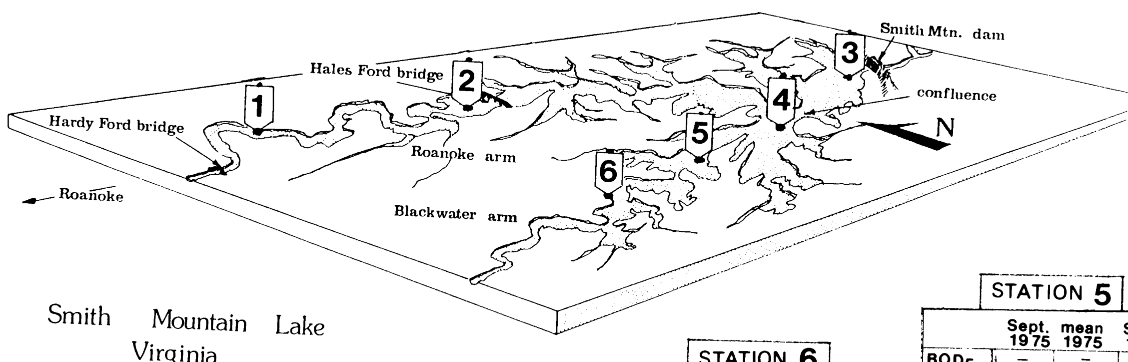
	Sept. 1975	mean 1975	Sept. 1976
BOD_5	3	3	3
DO	11.7	9.8	–
TKN	0.3	0.322	0.1
$NH_3 \cdot N$	–	0.099	–
$NO_3 \cdot N$	<0.05	0.12-0.20	<0.05
$NO_2 \cdot N$	<0.01	0.011	<0.01
TOT·P	<0.10	0.10	<0.10
mean PO_4 (1970 - '73) ≃ 0.05			
Σ (DO, TKN, PO_4) = 12.05*			

STATION 4

	Sept. 1975	mean 1975	Sept. 1976
BOD_5	–	–	1
DO	10.3	8.9	–
TKN	0.2	0.17-0.22	0.2
$NH_3 \cdot N$	–	0.099	–
$NO_3 \cdot N$	<0.05	0.08-0.12	<0.05
$NO_2 \cdot N$	<0.01	< 0.01	<0.01
TOT·P	<0.10	< 0.10	<0.10
mean PO_4 (1970 - '73) ≃ 0.05			
Σ (DO, TKN, PO_4) = 10.55 *			

STATION 3

	Sept. 1975	mean 1975	Sept. 1976
BOD_5	–	–	< 1
DO	10.4	8.4	–
TKN	0.1	0.19	0.2
$NH_3 \cdot N$	–	0.099	–
$NO_3 \cdot N$	<0.05	0.08	< 0.05
$NO_2 \cdot N$	<0.01	0.099	< 0.01
TOT·P	<0.10	< 0.10	< 0.10
mean PO_4 (1970 - '73) < 0.05			
Σ (DO, TKN, PO_4) = 10.55*			



STATION 6

	Sept. 1975	mean 1975	Sept. 1976
BOD_5	–	–	2
DO	11.0	–	–
TKN	0.2	–	0.1
$NH_3 \cdot N$	–	–	–
$NO_3 \cdot N$	< 0.05	–	<0.05
$NO_2 \cdot N$	< 0.01	–	<0.01
TOT·P	< 0.10	–	<0.10
mean PO_4 (1970 - '73) ≃ 0.05			
Σ (DO, TKN, PO_4) = 11.45*			

STATION 5

	Sept. 1975	mean 1975	Sept. 1976
BOD_5	–	–	1
DO	10.9	–	–
TKN	0.2	–	0.1
$NH_3 \cdot N$	–	–	–
$NO_3 \cdot N$	<0.05	–	<0.05
$NO_2 \cdot N$	<0.01	–	<0.01
TOT·P	<0.10	–	<0.10
mean PO_4 (1970 - '73) ≃ 0.05			
Σ (DO, TKN, PO_4) = 11.15 *			

FIG. 1. Smith Mountain Lake sampling stations and water chemistry data as reported by the Virginia State Water Control Board. TKN, DO, and PO_4 values were summed to represent the enrichment gradient (see Results). Modified from Cairns et al. (1979).

TABLE I

Mean (n = 6) chemical-physical measurements for each station during the indicated sampling period

Station	Water temp. (°C)	pH	Alk. ppm	Hardness ppm	DO ppm	Monitoring period
1	26.9	9.45	90.1	116.8	11.5	8/26/75 9/16/75
2	25.1	9.30	84.8	99.2	9.0	9/03/75 9/24/75
3	25.8	9.10	70.7	79.8	8.4	8/26/75 9/16/75
4	24.8	9.16	65.7	71.8	8.7	9/03/75 9/24/75
5	25.8	9.08	61.5	61.1	8.4	8/26/75 9/21/75
6	25.2	9.10	43.9	49.6	8.3	9/03/75 9/24/75

in conjunction with 10× oculars. The first 500 diatom valves encountered in the scan were identified and recorded.

The summed difference succession rate index (SD) (Lewis, 1978) was calculated on the resulting data. This index reflects the amount of composition change occurring between two samples. The SD index is estimated as

$$SD = \frac{\sum i \left| \frac{b_i(t_1)}{B(t_1)} - \frac{b_i(t_2)}{B(t_2)} \right|}{t_2 - t_1}$$

where $b_i(t)$ = the number of individuals of species i at time t_i and $B(t)$ = the total number of individuals in the sample at time t.

Results

Figure 1 illustrates the nature of the water chemistry gradient in Smith Mountain Lake. Table I lists the mean values for all water chemistry determinations (6 sampling days) made at each station during the actual sampling period. September 1975 values for total Kjeldahl nitrogen (TKN), dissolved oxygen (DO), and 1970–1973 mean values for orthophosphate, reported by the VSWCB, were summed and the sums ordered to represent the gradient of increasing enrichment. This produced an ordering $3 \leq 4 < 5 < 6 < 2 < 1$ among the stations.

A total of 234 species were observed during the study. Table II lists numbers of species found in each station on each sampling day. Actual changes in diatom composition on PF substrates are summarized in Fig. 2. These data reflect relative changes in the more abundant species (those that attained at least 10% relative abundance during monitoring) on substrates from each

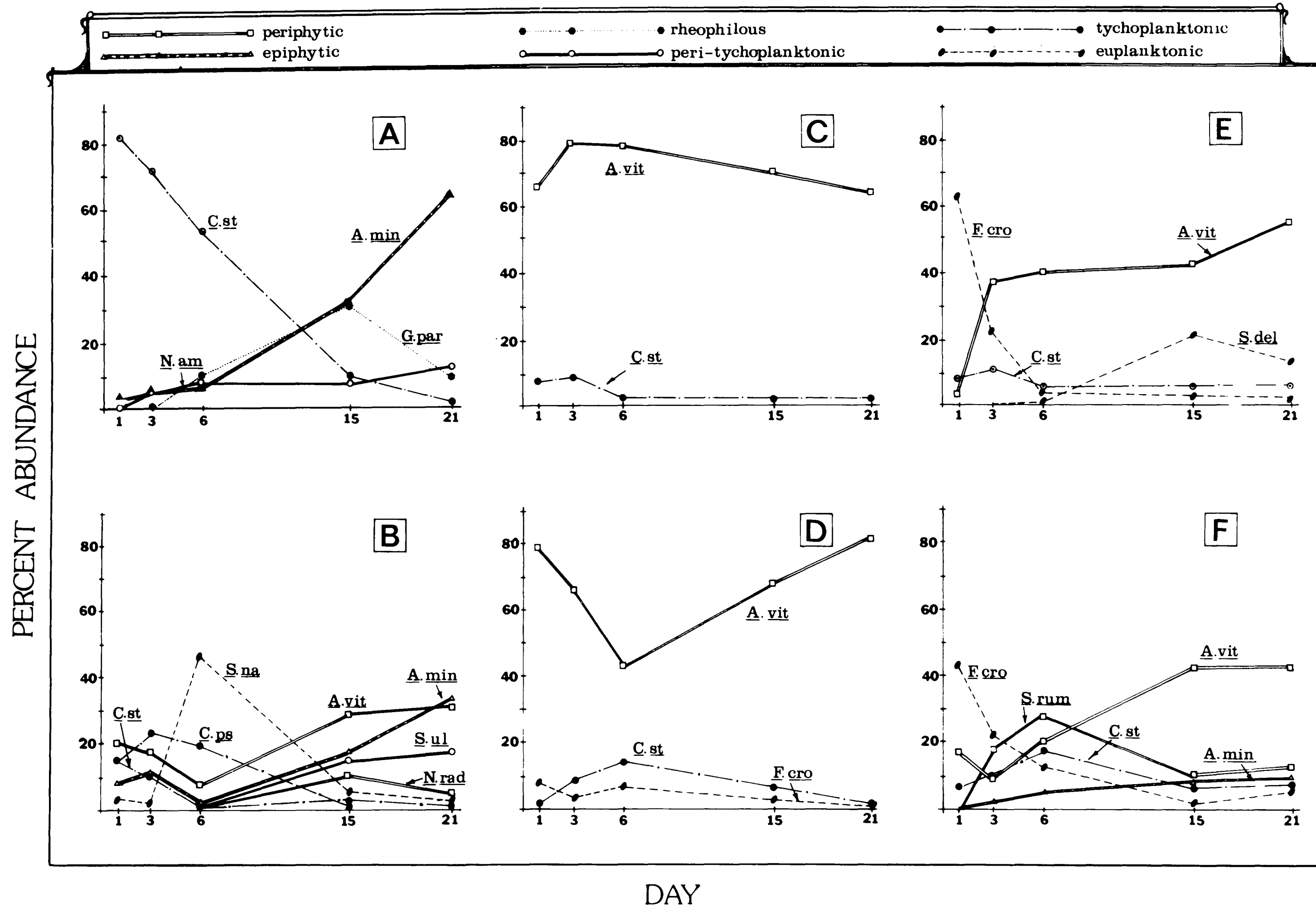


FIG. 2. Actual changes in relative abundance of diatom species that attained at least 10% relative abundance during the sampling period. Species are characterized as to life-form strategy (see Table III), A, station 1; B, station 2; C, station 3; D, station 4; E, station 5; F, station 6.

TABLE II

Number of diatom species observed in samples from PF substrates, counting 500 valves

Days of immersion	Station					
	1	2	3	4	5	6
1	26	31	24	20	34	28
3	29	40	23	31	36	43
6	34	34	24	33	41	30
15	28	40	22	30	32	37
21	22	19	24	28	30	33

station. Some important adaptive characteristics of these species are summarized in Table III.

Associations from stations 3 and 4 underwent little compositional change and remained strongly dominated by *Anomoeoneis vitrea* (Grun.) Ross throughout the sampling period. Station 5 substrates showed a direct and abrupt transition from *Fragilaria crotonensis* Kitt. to *A. vitrea,* while those from station 6 manifested the same shift with an intermediate dominance by *Synedra rumpens* Kütz. Samples from station 2 do not show strong dominance by any single species. Station 1 underwent a dramatic shift from dominance by *Cyclotella stelligera* Cl. u. Grun. to *Achnanthes minutissima* Kütz., with day 15 showing an increase in the importance of *Gomphonema parvulum* Kütz.

Even though the particular species involved differ, similar qualitative shifts in composition occurred at the four most enriched stations (stations 1, 2, 5, and 6). Initially dominant non-benthic forms were inevitably replaced by periphyton species on all PF substrates. By the end of the sampling period, PF associations at all stations (except 1) were dominated, to varying degrees, by *A. vitrea,* the periphytic form which dominated less enriched stations 3 and 4 throughout the sampling period.

Values for the SD succession rate index are summarized in Table IV. Station 1 had moderate but constant change at each time interval, reflecting continual composition turnover throughout the sampling period. Station 2 manifested increased change through days 3–6, and subsequently a declining rate. Stations 3, 4, 5, and 6 showed a decrease in rate from initial values. SD values were higher in stations 5 and 6 during the initial sampling interval, reflecting larger compositional changes (Fig. 2). By the end of the sampling period, rates at all stations dropped below that of station 1 and showed signs of approaching zero.

Discussion

Although sample composition varied little with time at stations 3 and 4, PF substrate associations at more eutrophic stations changed substantially during the sampling period. These compositional shifts could have resulted from major changes in natural communities surrounding the substrates, but it is

TABLE III

Adaptive characteristics (life-form strategies) of the most abundant diatoms sampled from PF substrates

Dominant species

Achnanthes minutissima Kütz.
Periphytic (8, 14) but with tychoplanktonic capacity when (a) turbulence is high (1), or (b) can attach to large phytoplankters (13, 14). Adapted moderately to highly enriched environments (8), able to survive anywhere within the littoral (13) under low nutrient conditions (12).

Anomoeoneis vitrea (Grun.) Ross
Strictly periphytic form (14) restricted to the shallow littoral (13). Primarily found under low nutrient conditions but can appear in certain polluted zones (8).

Cyclotella pseudostelligera Hust.
Probably a tychoplankter (9). Abundant in eutrophied inshore waters (6, 14). Occurrence correlates with that of other species associated with enriched or polluted conditions (6).

Cyclotella stelligera Cl. & Grun.
Tychoplanktonic (8). Capable of blooming in either littoral (12, 13) or pelagic habitats (8, 12) depending upon season and nutrient conditions (5).

Fragilaria crotonensis Kitton
Euplanktonic (8, 14): Favored by moderate-to-high enrichment (1, 8, 11). Eliminated from extremely polluted habitats by blue-green or tychoplankters (14). Prefers runoff and mineralized nutrients to particulate organics (1, 2).

Gomphonema parvulum Kütz.
Although strictly periphytic (8, 14), morphologically and physiologically adapted to withstand physical disturbance (8) and benefit from organic enrichment (3, 8, 9, 10).

Important subdominant species

Navicula radiosa var. *tenella* (Breb. ex Kütz.) Grun.
Periphytic (8).

Nitzchia amphibia Grun.
Periphytic (8); Tychoplanktonic, eutrophic (3, 8).

Synedra delicatissima var. *angutissima* Grun.
Euplanktonic (7, 8, 14), eutrophic (8).

Synedra nana Meist.
Euplanktonic (7); Cosmopolitan, current indifferent (8, 14).

Synedra rumpens Kütz.
Periphytic (7, 8, 14); Littoral form in lakes (8).

Synedra ulna var. *contracta* Østr.
Periphytic to tychoplanktonic (7, 14). Abundant in shallow, enriched zones (4). Associated with dense growth of *Cyclotella* in many rivers and Great Lakes stations when biological oxygen demand is near 5 ppm (15).

Numbers in parentheses indicate the following references: (1) Bradbury, 1975 (2) Bradbury & Megard, 1972 (3) Cholonky, 1968 (4) Evans & Stockner, 1972 (5) Holland & Beeton, 1972 (6) Holland & Claflin, 1975 (7) Huber-Pestalozzi, 1942 (8) Lowe, 1974 (9) Lowe & McCullough, 1974 (10) McIntire, 1968 (11) Rawson, 1956 (12) Stockner, 1971 (13) Stockner & Armstrong, 1971 (14) Stoermer & Yang, 1969 (15) Williams & Scott, 1962.

more probable that these shifts represent succession occurring on the PF substrates themselves—a greater proliferation of better adapted periphytic species relative to planktonic species whose populations are maintained primarily by invasion pressure (the "rescue effect," Brown & Kodric-Brown, 1977). Ultimate dominance by the same species at 5 of the 6 stations further implies that the process is directional and tends toward an endpoint which is similar to that found in, and characteristic of, less enriched environments.

TABLE IV

Summed difference succession rate values (SD index; Lewis, 1978) for six Smith Mountain Lake stations

	Station	Day 1–3	3–6	6–15	15–21
Eutrophic gradient ↓	3	0.172*	0.096	0.040	0.048
	4	0.294	0.271*	0.088	0.074
	5	0.534	0.233*	0.072	0.079
	6	0.432	0.241	0.108*	0.060
	2	0.259	0.400	0.177*	0.078
	1	0.194	0.178	0.138	0.132

* Approximate times at which succession rates become small, indicating acquisition of compositional stability. Ordering stations according to the amount of time required for substrate compositions to stabilize ($3 < 4 \simeq 5 < 6 \simeq 2 < 1$) yields a sequence comparable to that produced by water chemistry data ($3 \simeq 5 < 4 < 6 < 2 < 1$).

Succession can be defined broadly as a temporal shift in the composition of an association caused by environmental change. Conceptually, two aspects of the process are important: (1) the quantitative *rate* of compositional change; and (2) the qualitative *direction* of the change as represented by particular species following one another in time.

Succession Rate

The SD index is a parameter which reflects the rate of composition change (Lewis, 1978). The succession rates at the Smith Mountain Lake stations (Table IV) indicated that most PF diatom associations appeared to attain compositional stability within the 21-day monitoring period. Ordering these stations according to the amount of time required to reach this condition yields a sequence comparable to that indicated by conventional water-quality measures; i.e., station 3 requiring less time and being less enriched ($<$) than station 4 which is similar to ($\simeq$) station 5 $<$ station 6 $\simeq$ station 2 $<$ station 1. Consideration of the SD index thus corroborates the basic conclusions drawn from the chemical data ($3 \leq 4 < 5 < 6 < 2 < 1$; see Results) and independently generates a comparable ordering of the stations.

Succession rate simply is indicative of the overall amount of environmental change per unit time (Lewis, 1978), however, and gives little information about the nature of that change. For example, a high correlation between succession rate and absolute variation in a given environmental parameter should implicate that factor as a controlling agent in the successional process (Jassby & Goldman, 1974). But, for any given system, there might be no single variable in overriding control. Indistinguishable values for succession rate could be produced either by a large change in one environmental factor or by relatively small changes in several parameters. The qualitative aspect of succession, directionally, also must be considered if specific relationships among environmental variables and the successional processes they affect are to be clarified.

Succession Direction

Lewis (1978) referred to any overall trends in the quality of an association as "succession direction." "Direction" is more specifically defined here as the sequence of life-form strategies manifested by the numerically dominant species during a succession.

Diatom life-form strategies. Grime (1977) convincingly documented a relationship between the survival strategies adopted by a habitat's dominant land plants and prevailing environmental conditions. Similarly, identifying the strategies of numerically important diatom species at Smith Mountain Lake stations should elucidate the ecological factors which select for the dominant forms in a successional sequence.

Three basic diatom life-form strategies, which probably represent arbitrary divisions of an adaptive continuum (Hutchinson, 1967), can be roughly described.

(1) Euplankters are adapted to maximize capture of light resources. They require abundant dissolved nutrients to maintain large populations suspended in the open waters. Euplankters typically have rapid reproductive rates and high surface to volume ratios which retard sinking and increase their capacity to gather nutrients (Fogg, 1965). They are most successful in high nutrient conditions and can quickly dominate nutrient-rich waters.

(2) Periphytic diatoms are adapted morphologically for attachment to and movement along substrate surfaces. They are able to capitalize upon nutrients and other resources adsorbed to surfaces, or derived from higher aquatic plants (Bradbury, 1975). Because benthic areas function as nutrient sinks, periphytic species can maintain viable populations even during periods when nutrients are scarce in open water.

(3) Tychoplankton[3] can invade both benthic and pelagic habitats to obtain resources. Although they are not always as successful as euplankters in open water, tychoplankters are able to capitalize quickly upon resource opportunities in alternative habitats. Tychoplankters, like other opportunists, often dominate areas where resources are unpredictable or disturbance is great.

Generally, adequate morphologic, taxonomic, reproductive, and distributional information exists to assign most diatoms to a basic life-form strategy (Table III).

Environmental Descriptors

Three synthetic factors, which might be likened to principal components and thus encompass several more specific parameters, are sufficient to describe most aquatic environments. Although treated individually here, these factors are interrelated and may not be independent.

(1) *Viable benthic habitat* represents the amount of benthic habitat space

[3] The term "tychoplankton" is defined broadly here to include both pseudoplankton and meroplankton (Hutchinson, 1967). Tychoplanktonic species occupy specific benthic niches but, under appropriate conditions, also can proliferate large open-water populations.

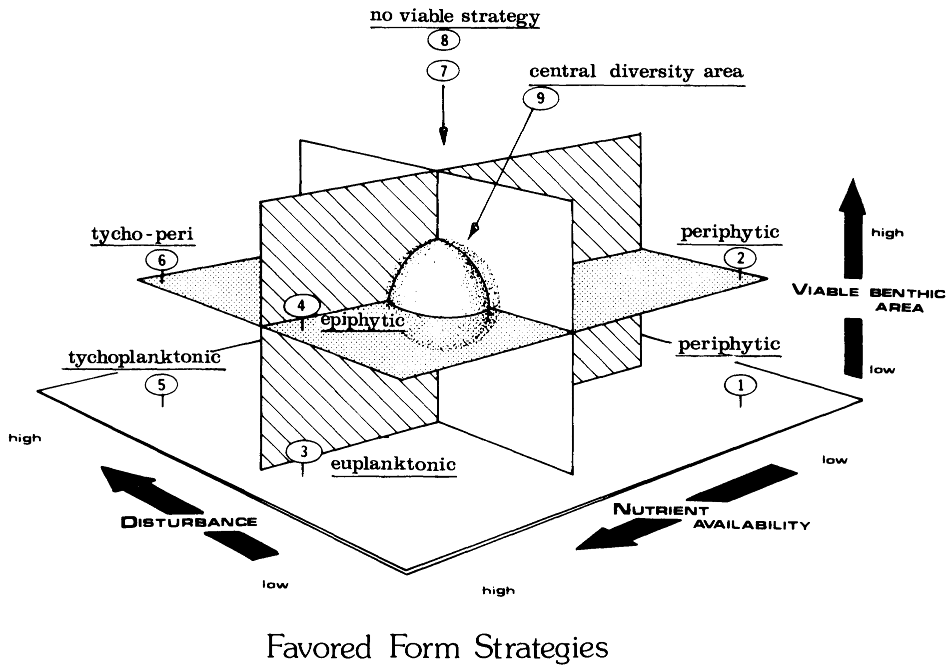


FIG. 3. A model space qualitatively defined by three environmental descriptors: viable benthic area, nutrient availability, and disturbance.

available to periphyton. A viable algal habitat space, whether pelagic or benthic, must be in the photic zone. As the benthic area increases, the amount of periphyton habitat increases, and the periphytic component of the algal flora increases as a result (Stockner, 1971).

(2) Open water *nutrient availability* is another useful descriptor. Periphyton, intimately associated with benthic nutrient sources, dominate systems with low pelagic nutrients, while euplankton are favored under high nutrient conditions. Nutrient availability also can affect viable benthic area; nutrient stimulated euplankton development can decrease light penetration and thus reduce benthic habitat.

(3) *Disturbance* (in the sense of Woodin, 1978), which is physically injurious or disruptive to the diatoms, creates opportunity for certain species. In order to dominate a disturbed environment, a form must be able to survive a disruption intact (be resistant), or quickly recolonize afterwards. Tychoplankters usually are best able to capitalize on the unpredictable resource opportunities in disturbed areas.

A Model Space

Interaction of the above three environmental factors selects for a dominant life-form strategy and largely determines the composition of an aquatic habitat's diatom flora. Figure 3 represents a three-dimensional space qualitatively defined by these three descriptors. Even though they are illustrated with distinct boundaries, strategies grade continuously into one another.

(1) *Low viable benthic habitat—low pelagic nutrients—low disturbance.* There is little periphyton habitat; very low available nutrients make the open water a generally hostile environment. Because they can tolerate these conditions by obtaining nutrients from the existing benthos, periphytic forms are favored. Representative lakes in which periphytic forms qualitatively dominate the diatom flora are: Lake Baikal, Siberia (Skvortzow, 1937a), Ikeda Lake, Japan (Skvortzow, 1937b), Ochrida Lake, Yugoslavia (Jurilj, 1954), and Crater Lake, Oregon (Sovereign, 1958). Most lakes conventionally considered oligotrophic have periodic (seasonal) pelagic nutrient pulses; e.g., overturn. Forms which are principally periphytic and/or maintain viable seed populations in benthic areas invade the open water and capitalize on these opportunities. Tychoplankton would be expected to dominate the plankton during such periods. Although these species may contribute heavily to the lake's total yearly primary production, their strategies and forms are not indicative of the generally low nutrient conditions, but rather the brief periods of increased nutrient supply.

(2) *High viable benthic habitat—low pelagic nutrients—low disturbance.* This situation should favor the same dominant strategy as discussed in (1), but with an even greater selection for periphyton because of the larger benthic area. In many of the shallow Canadian Shield Lakes (e.g., Lake 114 in the Experimental Lakes Area; Stockner, 1971), periphytic diatoms dominate.

(3) *Low viable benthic habitat—high pelagic nutrients—low disturbance.* Most of the available habitat is open water continuously rich in nutrients. Because they can maintain large populations in the photic zone when supplied with sufficient nutrients, euplankters dominate these environments (e.g., Clear Lake, Iowa; Begres, 1971).

(4) *High viable benthic habitat—high pelagic nutrients—low disturbance.* This combination of environmental variables should favor periphytic species adapted to high nutrient conditions. Such situations commonly are dominated by green and blue-green algae or aquatic macrophytes. Thus, for a diatom species to be successful, it is likely to have a pronounced epiphytic tendency and have few restrictive distributional requirements with respect to light and substrate quality (e.g., Kirchner Marsh, Minnesota; Florin, 1970).

(5) *Low viable benthic habitat—high pelagic nutrients—high disturbance.* To be successful in a highly disturbed situation, a form must be able to survive the disruption intact or recolonize quickly after the disturbance subsides. Forms which can maintain propagules in littoral areas and/or in the open water have a greater likelihood of maintaining viable populations than do restricted forms. Since most habitat is open water (and there are ample nutrients here to allow recovery), a planktonic expression of a tychoplanktonic form is likely to dominate these conditions (e.g., Devil's Lake, North Dakota; Stoermer & Armstrong, 1971).

(6) *High viable benthic habitat—high pelagic nutrients—high disturbance.* Again, disturbance probably selects for a tychoplanktonic form, but

greater littoral habitat enhances the periphytic expression of the form. Rheophilous forms which can survive physical disturbance due to their large size and firm attachment also can do well in such habitats. The western basin on Lake Erie (Hohn, 1969) and the Sandusky River (Lowe & Kline, 1976) exemplify such conditions.

(7) *Low or (8) high viable benthic habitat—low pelagic nutrients—high disturbance.* Although low nutrient availability would select primarily for periphytic forms, capacity to survive disturbance is the fundamental determinant of the dominant form. There are no resources available to accommodate recovery if forms are eliminated by disturbance (e.g., Grand River, Ontario; Sreenivasa & Duthie, 1973).

(9) *Central diversity area.* A central area within the model space where the various combinations of environmental factors overlap and grade into one another should allow many successful life-form strategies and foster high compositional diversity. Strongly dominated associations are to be expected in environments where physical conditions are extremely rigorous and mere survival in tenuous (Whittaker, 1975), or in habitats where competition is intensely focused upon the aquisition of a few limiting resources (Petersen, 1975). To the extent that successional trends in fact reflect complex environmental gradients in time, relatively diverse associations also might be expected at intermediate, rather than extreme, periods of a succession. This prediction is essentially drawn from Connell's (1978) argument that maximum diversity during succession should be attained when a critical environmental variable (e.g., disturbance) reaches intermediate rather than extreme levels.

Changes in the Substrate Environment During Succession

Initial and final PF associations from the various Smith Mountain Lake stations were placed in the model space (Fig. 4) using the information presented in Table III on the autecological and distributional characteristics of the most abundant diatom species. Table V summarizes the rationale for each placement. Straight lines connecting these placements represent the essential course of each association through the model space and implicate the strategies of intermediate successional dominants at each station. For example, the successional course of substrate association at station 1 passes from box 5 through box 6, implicating the transient importance of a disturbance-resistant periphytic form adapted to nutrient-rich conditions. *Gomphonema parvulum* Kütz., a rheophilous form which ascends to 32% relative abundance on day 15 and then declines (Fig. 2), is just such a form (see Table IV). Similarly, complex compositions are predicted accurately by courses which pass through (station 2) or near (station 6) the central diversity area of the model space.

Tracing the course of compositional change also permits generalizations about the way in which important environmental attributes are modified during succession. Certain environmental factors which influence the direction of PF association succession appear to be altered merely as a consequence of introducing virgin attachment space into the upper photic zone.

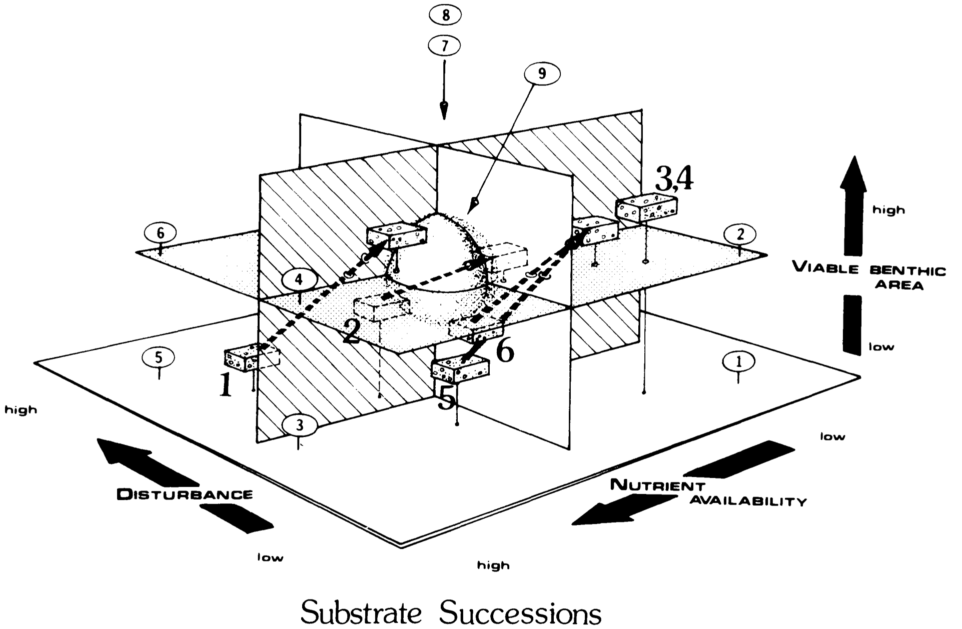


FIG. 4. The course of PF substrate diatom successions through the model space indicates succession direction. Positioning of initial and final diatom associations are based on the life-form strategies of the most abundant species (see Table V).

(1) Although placed in the open water, PF substrates closely mimic newly exposed benthic habitat while supplying colonizing diatoms with ready access to light. The principal advantages of open-water forms over periphyton species (i.e., adaptations which retain plankters in the photic zone and shade benthic algae) are largely negated. The overall effect is to increase the influence of viable benthic habitat on most substrate association compositions. Where the introduced substrates closely resemble the predominant natural habitat of a site, as at comparatively oligotrophic stations 3 and 4, PF associations exhibit minimal successional change.

(2) The three-dimensional PF substrate material (Paul et al., 1977) supplies many minute refuges from predators (Spoon, 1975), currents, and waves (Cairns et al., 1979), thereby reducing the amount of disturbance to which associations are subjected.

Another trend reflected in the successional courses is the apparent reduction of nutrient availability to the changing substrate associations through time. This phenomenon is considered a basic attribute of developing homeostasis accomplished through the entrapment of nutrients as biomass (Odum, 1969). Stations which initially show substantial displacement from oligotrophic conditions (stations 1, 2, 5, and 6) display this trend, with the noteworthy exception of station 1. Continuously heavy nutrient input apparently retains station 1 in a bloom state and overrides the PF association's capacity to reduce nutrient availability appreciably during the monitoring period.

TABLE V

Rationale for positioning initial and final PF substrate associations in the model space (see Fig. 4)

Station	Initial	Final
3 & 4	Dominance (80%) by periphytic *Anomoeoneis vitrea* places these samples in periphytic box 2. Subdominance by *Cyclotella stelligera* (10%) moves them slightly in the direction of the tychoplanktonic box 6.	Relative position in the same, but decline in *Cyclotella stelligera* suggests disturbances may have decreased slightly.
5	Dominance by *Fragilaria crotonesis* (60%) places this in euplanktonic box 3. Subdominance by *Cyclotella stelligera* is similar to initial 3 & 4 samples indicating comparable levels of disturbance.	The substrates are dominated by *Anomoeneis vitrea* (50%) and are in periphytic box 2. The subdominance of euplanktonic *Synedra delicatissima* and *Cyclotella stelligera* suggests that the final position is displaced slightly in the direction of euplanktonic box 3.
6	*Fragilaria crotonesis* dominance places this in euplanktonic box 3. Subdominance by periphytic *Anomoeoneis vitrea* suggests a higher position in this box than 5.	Although less dominated by *Anomeoneis vitrea* (45%) than the final sample from station 5, its position in periphytic box 2 is about the same.
2	No single species dominates this sample. The abundance of tychoplankters *Cyclotella stelligera* and *pseudostelligera* (33.4%) suggests that the initial position is in tychoplanktonic box 5. Shared dominance places samples near or within the high diversity area.	The final sample has shared dominance between periphytic *Anomoeoneis vitrea* and epiphytic-periphytic *Anchnanthes minutissima*. This sample is still close to the high diversity area, but in periphytic box 2 (close to the epiphyte boundary).
1	Dominance by *Cyclotella stelligera* (82%) places this sample in the tychoplanktonic box 5.	Dominance by *Achnanthes minutissima* places this sample in the epiphytic box 4 near periphyton box 6. It is in a similar disturbance place as the final sample from station 2 (10% tychoplanktonic subdominance-*Nitzchia amphibia*).

The environmental modifications produced by the introduction of the artificial substrate initiate successions which manifest various qualitative strategy changes. Together these changes constitute an overall direction that reflects the environmental influences affecting the diatoms. The time until the successions are complete (SD rate index approaches zero—asterisks in Table III) reflects the time required for the composition to equilibrate with the substrate modified environment. It is, in other words, the length of the direction vector in the model space. If the model's descriptor axes could be scaled, rate possibly could be coupled with direction allowing the relative importance of the environmental influences to be distinguished.

In this context, there is nothing predestined about direction—it is solely a consequence of the kinds of change stimulating the succession. When environmental changes have a defined periodicity (or controlled sequence), successions may seem to have an inherent, reproducible quality. Successions produced by action of the biota (autogenic forces) might appear to manifest intrinsic direction because they are often more controlled than those stimulated by abiotic (allogenic) forces. Organisms can consistently, and sometimes profoundly, alter their environments in certain general ways. For example, available nutrients can be decreased through binding them as biomass, disturbance can be modified by competition (Glesener & Tilman, 1978) and predation (Caswell, 1978), and viable benthic areas can be reduced by shading. When these biotically induced changes predominate over confounding abiotic interferences, the resulting successions generally are more reproducible. However, whether biotic or abiotic factors predominate, which is usually a question of degree, the direction of any succession still reflects the quality of environmental change.

Characterization of Stations; Model Predictions and Actual Site Descriptions

Because they orient to the specific environment of the PF unit, substrate associations eventually develop compositions which do not directly reflect the conditions of the surrounding water. Although some distinctions between stations are still evident late in the monitoring, the samples from the initial periods should reflect station conditions most accurately. The positions of these initial associations within the model space (Fig. 4) qualitatively describe environmental conditions of the six Smith Mountain Lake stations. Moreover, the model provides an interpretive characterization of environmental conditions based only on the biology of the most abundant species; it is entirely independent of the chemical data.

Station 1. The position of the initial sample of station 1 in the model space (Fig. 4) indicated a highly enriched, highly disturbed environment with little viable benthic area.

Although the channel near station 1 is shallower and narrower than any other Smith Mountain Lake site, the shoreline abuts high ridges on both sides of the channel which rise to 60 m above the normal pool height of the lake (Benfield & Hendricks, 1975). Steeply sloping banks in combination with heavy shading from dense algal growth (Simmons & Neff, 1969) afford little viable benthic habitat. Industrial and domestic effluents from the Roanoke area inflict a large nutrient load and produce occasional heavy metal violations in the vicinity of station 1 (VSWCB, 1975). This station also is subject to drastic fluctuations in flow from urban storm runoff.

Station 2. Substrate associations at station 2 imply a moderately enriched, moderately disturbed environment with a moderate amount of viable benthic habitat.

The effects of municipal discharge still are apparent at station 2, although somewhat ameliorated. Greater midchannel depth (30 m) and width (450 m) compared to station 1 (6 m; 96 m, respectively) allow greater dilution of the discharge from upstream. The resulting reduction in nutrients also is reflected in lower rates of primary production (Benfield & Hendricks, 1975). More gently sloping banks, greater channel width, and less phytoplankton growth also increase visible benthic habitat over that of station 1. Variations in flow due to storm runoff still are considerable (Simmons & Neff, 1969) and probably constitute the major component of disturbance at the site.

Stations 3 and 4. Diatom associations at these stations indicate relatively oligotrophic conditions; low available nutrients make the open water comparatively unproductive and emphasize the importance of littoral habitat as the primary site of algal reproduction. Disturbance seems minimal at these stations.

Lake depths in the vicinity of the confluence (station 4) and the Smith Mountain Dam (station 3) permit considerable dilution of any upstream nutrient input. Smith Mountain Game Reserve borders the southeast end of the reservoir and probably buffers these stations from effects of runoff and agricultural perturbation. These stations also have the lowest rates of primary production in the lake (Benfield & Hendricks, 1975).

Stations 5 and 6. Both initial associations were strongly dominated by the euplankter *Fragilaria croteonensis*, indicating inorganic enrichment of the open water and minimal disturbance. A somewhat greater influence of littoral substrate at station 6 vs. station 5 also is implied.

Unlike Roanoke River stations 1 and 2, Blackwater River stations are not affected by any appreciable municipal discharges. However, the VSWCB (1975) considers this area to have a very high non-point source pollution potential, due to the nature of the soils and ground cover surrounding the channel and its high average slope. Recently expanded housing development along the shore line contributes to the partial fulfillment of this potential. Nutrient inputs are primarily inorganic and probably originate from natural soils. Turbidity may increase somewhat downstream and limit the contribution of littoral habitat at station 5.

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